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VOLUME I

# The Behaviour of Ungulates and its relation to management

The Papers of an International Symposium
held at

THE UNIVERSITY OF CALGARY, ALBERTA, CANADA
2-5 November 1971

Union Internationale
pour la Conservation de la Nature
et de ses Ressources

International Union
for Conservation of Nature
and Natural Resources

Morges, Switzerland, 1974

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VOLUME 1

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*Edited by*
**V. Geist & F. Walther**
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# Symposium on the Behaviour of Ungulates and its Relation to Management

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*V. Geist*

*F. Walther*

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# General Introduction

VALERIUS GEIST and FRITZ. R. WALTHER

The symposium on the behaviour of ungulates and its relation to management was held from November 2-5, 1971, at the University of Calgary, Canada. It was called to satisfy several academic as well as practical needs that are best understood in the light of the history of studies of ungulate behaviour.

Despite notable attempts by pioneers in behavioural studies, such as that of Fraser Darling prior to World War II, the literature of ruminant behaviour is exceedingly young. Only in the last decade have diverse studies on wild and also captive ungulates begun to blossom. It became apparent that these studies had theoretical and utilitarian contributions to make, but the field suffered from a lack of communication and agreement on terminology, methodology and theoretical concepts. There existed what could be termed a 'gray' area of uncertain knowledge that is the inevitable consequence of occasional observations and the speculations of an alert mind. This gray area also included valuable thoughts about management which tended to remain unrecorded due to the inadequate data at the disposal of one individual. Yet the discussions of occasional observations and fragile ideas can produce, in proper company, confirmation of such observations and thoughts. In short, it was felt to be high time that a symposium was called in order to bring together for the first time as many as possible of the widely dispersed fieldworkers.

It was also recognized that such a meeting would be less than complete in the absence of those who must look after the welfare of ungulates in national parks or game reserves, or manage game for sport, recreation or meat. It is essential for the sake of conservation that scientists be acquainted with the concerns of managers and vice versa. Furthermore, short cuts to the successful conservation of endangered species must be found, and studies which reveal the principles of ungulate biology may be of help here. Hence, the symposium was organized with an eye towards not only academic needs, but also towards those of conservation and management.

It appeared to us that our diverse objectives could best be realized by asking senior workers to concentrate on syntheses, and by requesting those who had recently finished major field studies to report directly on their work. Hence, we asked for review papers from senior workers, but afforded most time to the presentations of those fresh from the field. We particularly sought papers on the relationship of ecology to social behaviour, in recognition of the close relationship of these disciplines so evident when working with free-living animals, as well as papers dealing with the management of ungulates—be they wild or domesticated. A series of films, well-illustrated presentations of field work, a field trip to Waterton National Park, and discussions, rounded out the symposium.

A major aim of the gathering was to produce a reference book useful to those engaged in research or in management. The contributions of the authors who participated in the proceedings of the symposium form its core, but, in addition, papers are included from workers unable to attend but willing to help in making this review of current studies more complete. Following the symposium authors were free to reassess their papers and submit revised versions. Papers were also sent out for refereeing and the resulting comments turned over to the authors for their attention. As editors, we do not necessarily agree with all the views expressed in the papers, but the author's view remains supreme. We did strive to bring diversity on record so that it may serve as a basis for discussion.

Volume I deals primarily with our first attempts at syntheses of social behaviour and ecology, with theoretical and classification problems, as well as with overviews of taxonomic groups and new work on the social behaviour of previously unstudied species. It addresses itself to the knowledge base and will serve as a record of concepts and data for those needing such information. Volume II concerns itself primarily with ecological and management matters. Both volumes cover material on endangered species. The papers thus brought together are not to be regarded as definitive, but as a reflection of our present knowledge and/or ignorance.

The two volumes, despite their size, have some serious weaknesses. They are heavily slanted towards bovids and have relatively little material on cervids, except, perhaps, the caribou (*Rangifer*). Nevertheless, a synthesis of cervid behaviour would not have been possible at this time. There are no papers dealing in detail with one very important aspect of ruminant behaviour— antipredator strategy and behaviour. Fortunately, a number of recent books contain good treatment of, or information on, this topic. We draw attention here to Kruuk's (1972) book on the spotted hyena; Schaller's (1967, 1972) books on lions and tigers; Mech's (1970) work on wolves; Hornocker's (1970) monograph on the mountain lion; and Hoogerwerf's (1970) extensive treatise on various Indonesian ungulates and their predators.

A further weakness of these volumes is the absence of contributions by some important workers on ungulate behaviour and ecology, whether due to the fact that they could not attend the conference, could not be contacted, or were simply unknown to us at the time the event was being planned. Some, but not all, of their publications can be found in the references quoted in this book: we have often been most pleasantly surprised by the number and value of these contributions of ecologists or physiologists to our knowledge and understanding of ungulate behaviour. We may perhaps pick out for mention McCullough's (1969) and Knight's (1970) work on elk; du Plessis's (1972) work with the blesbok; the work of Bannikov and his colleagues (1961) on the saiga: Sikes's (1971) work on the African elephant; Egorov's (1967) studies of ungulates in Siberia; Zhigunov's (1961) volume on reindeer husbandry; and Taylor's extensive work on the bioenergetics of African antelopes.* We must also draw attention to a major Russian study on the behaviour and ecology of reindeer by one of the contributors to the present book, L. M. Baskin (1970). At the time of writing, this work is not yet available in English translation, but hopefully will be soon. Fortunately, A. A. Nasimovich's (1955) work on the role of snowcover is now available in English translation and interested readers should enquire at the Canadian Wildlife Service, Ottawa. Formozov's (1946) classic study on this subject is available in translation from the Boreal Institute, The University of Alberta, Edmonton.

In contemplating the papers presented in this and the second volume, one begins to identify some of the research required which would best serve both academic and practical interests. Quite evidently we need to know much more about the basic biology of species not adequately covered by field studies, in particular about the small-bodied antelope and deer from the tropical and sub-tropical regions, about the Asiatic and American cervids, and about the rare forest and mountain forms. We need studies carried out in pristine ecosystems so that the work may reflect the action of natural forces rather than that of human management, and lead to an understanding of the evolutionary forces shaping the animals. We may enter a special plea for studies of remnant populations of aboriginal races, not only because these could be exterminated, but also because reintroductions of related forms could forever obliterate their uniqueness. For example, one wonders if any red deer races in Europe have escaped the introduction of 'fresh blood' from Siberia, from America, or from the 'better' red deer populations of the Balkans or Caucasus, or wherever. Above all, we need continuous studies on populations of known individuals. Ungulates are long-lived animals and in two to three years—the common duration of most studies—one cannot gain a great understanding of the role of individuals in their society. Yet it is such knowledge that we can expect to be most useful in clarifying pertinent questions, not only in ethology, but also in population dynamics and ecology, as well as in conservation and management. We may have answered the question as to which are genetically the fittest males, but we have no such answers for females. We have much to learn about learning in ungulates and its relation to feeding habits, habitat preferences, and home range formation of individuals. These concerns are raised primarily by papers in the second volume, where we become somewhat uncomfortably aware of the link between psychology and ecology. We also need detailed research on questions of concern to managers so that ungulates may make a greater contribution to our recrea-

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* Taylor's publications are too numerous to list in this short introduction. His address is: C. R. Taylor, The Biological Laboratories, Harvard University, 16 Divinity Avenue, Cambridge, Mass. 02138 U.S.A.

tional and economic as well as to our cultural requirements. Meanwhile, we hope that these volumes make a small but useful step in that direction.

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Paper No. 1

# Mother—Infant Relationships in Ungulates

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## ABSTRACT

The precocial nature of the ungulate infant and the active care provided by the mother in most representatives of this order results in a period of intense reciprocal stimulation between mother and infant following birth. While no single sensory input is a requisite for the elicitation of maternal behavior, the movements, odor and vocalizations of neonates all act to stimulate normal maternal responses. Mothers, in turn, use visual, tactual and vocal stimuli to elicit and direct neonatal activities. This phase of intense interaction is called the post-partum period. It varies in length from less than 1 hour to more than 10, depending upon the species.

Most ungulate species clearly fall into one of two categories with regard to the type of mother-infant relationship occurring after the post-partum period. These two types are referred to as the 'hiders' and the 'followers'. We are indebted to Fritz Walther for the early development of this concept.

The hiders are primarily species using forested habitats or small species able to take advantage of low cover in relatively open habitats. Most cervid species fall into the hider category, as do the gazelles and many antelope species. At the end of the post-partum phase the mother and infant in hider species enter into a phase during which the two are separated and out of contact for long periods of time. During this hiding period nursing and care sessions may be as infrequent as two or three per day in some species. Infants of hider species tend to act independently in the selection of hiding sites, but are dependent, at least initially, upon their mothers for initiation of activity periods. The hiding behavior complex functions as a strategy for avoiding predation and as a means of gradually introducing the infant into a closed social group.

Follower type species include the equids, most large bovines, sheep and related genera, the muskox and the caribou. These species tend to be associated with grassland or tundra habitats. Many of the follower types are characterized by great seasonal mobility. In these species there is no ontogenetic phase corresponding to the hiding period. Mother and infant maintain close spatial relationships and frequent communication following the post-partum period. This strategy provides for protection against predation by maternal defense and permits extensive movements of mother and young in large aggregations during early stages of infancy.

In the genus *Capra* and perhaps also in the mouflon and some other alpine species the hiding period is either short or absent and associated behavior is weakly expressed.. Some evidence suggests intraspecific variation in this regard.

The prone response is an infantile behavior pattern associated primarily with hider species. This withdrawal response may be elicited by certain maternal behavior patterns or it may occur as a result of alarming stimuli. This response is expressed weakly or for a shorter period after birth in some follower species.

Following responses are part of the behavioral repertoire of all ungulate infants. This behavior first occurs as a general tendency to follow any moving object of an appropriate size range. The activity is associated with an imprinting process which may eventually result in only the mother or mother-object eliciting its occurrence. A generalized following response continues to function in stress situations in later ontogeny, especially among follower species.

Mothers rapidly form closed bonds with their offspring during the post-partum phase. In goats, olfaction has been shown to be essential for this process. Visual and auditory recognition have been demonstrated in several species. The time necessary for bond formation is referred to as the 'critical period'. It may be as short as 5 minutes (in goats) or as long as several hours (in pronghorn). Infants are much slower in forming a fixed bond and fixating their behavior on their mother. This may not occur until the hiding phase wanes. Infant social behavior remains more opportunistic and appears to make less use of olfactory cues.

Our understanding of the processes of weaning and bond breakdown is especially poor. Maternal-infant bonds normally continue beyond weaning and probably aid infant survival in several ways. Mothers of several species permit yearlings (primarily females) to suckle if they lose their offspring of the year. Long term associations may exist in certain species (cervids) involving 3 generations of females.

In ungulates, a major function of maternal behavior is the facilitation of learning processes in the infant by the provision of optimum levels of stimulation and of a relatively stable social environment.

The application of knowledge of maternal-infant behavior has progressed rapidly in agriculture and zoo management. There is a great need, however, for further basic research and application of existing knowledge in this field to problems of wildlife and wild lands management. This need increases as humans and wild ungulates interact with greater frequency and in increasingly complex ways.

## INTRODUCTION

My aim in this review is to deal primarily with the behavioral interactions of ungulate mothers and their offspring. Thus aspects of infant behavior such as play behavior and other interactions between young conspecifics are dealt with only briefly. Obviously the secondary socialization process in which the young ungulate interacts with older conspecifics besides its mother and learns social roles in relation to other classes of individuals is of the greatest interest, but to date there is relatively little information on the subject. This latter aspect of mammalian social behavior has recently been reviewed by Spencer-Booth (1970). I have emphasized the bovids and cervids in this review both because of my own interests and because of the relative sparsity of information regarding other groups. In particular I have found surprisingly little information available on the equids.

In order to make the reading of this review somewhat less tedious I have omitted scientific names in the text and relegated these to an appendix.

Ungulates in general are to be considered the most precocial of mammals. Because of their rapid motor and sensory development it is difficult to view their ontogeny in terms of the periods of social development described by Scott and Marston (1950) and Scott (1958) which seem most applicable to altricial mammals. There is no period in ungulates coinciding with Scott's neonatal period during which, for example, the infant is not receiving information by certain sensory modes and is apparently extremely limited in its learning capacity. Conditioning of lambs may be easily accomplished before they are 4 hours old (Moore, 1958). Scott and Marston (1950: 53) remarked, 'For lambs life may be said to begin with the transition period'. However, Scott (1960) considered that the infant ungulate at birth entered into a phase identical with his previously defined period of socialization. I find the former viewpoint more acceptable in that there is a brief period of rapid motor and sensory improvement following the birth of the infant ungulate during which little socialization on the part of the infant takes place. I have used the term 'neonate' in this review to refer to the infant ungulate during this brief post-partum period in its ontogeny which normally is only a few hours in duration. I describe this period in detail in Section II.

## I. PARTURITION AND ASSOCIATED BEHAVIOR

The degree to which mothers of gregarious species isolate themselves from conspecifics before parturition appears to vary both inter- and intra-specifically. Experienced mothers may be more likely to do so than primiparous females as Couturier (1938) suggests regarding chamois. Isolation appears to be a general rule in the Camelidae (Pilters, 1956). Couturier (1962) and Pitzman (1970) give detailed descriptions of the process in ibex and Dall sheep, respectively. McCullough (1969) reports that elk cows do so, but M. Altmann (1963) states that they remain on the margin of groups. Pronghorn mothers apparently always isolate themselves (Prenzlow, 1964). Bison behavior is on the other hand reportedly variable in this respect (Marjoribanks-Egerton, 1962; Engelhard, 1970). Pruitt (1960) believed that caribou cows do so but my own observations (Lent, 1966) and those of Bergerud (this volume) did not substantiate this.

In species which normally seek isolation and have a distinct birth period, abnormal confinement of large numbers of females together may result in attempts by females to adopt other neonates before they give birth themselves. This can occasionally be a problem in sheep ranching (Alexander, 1960; Rowley, 1970).

The timing of parturition in relation to the diurnal cycle of a given ungulate species has been the subject of considerable discussion in the literature but there is very little concrete information available. Slijper (1960) believed that, in general, parturition in ungulates tended to occur during the time of least activity, that is during normal resting periods of the species in question. However, studies of specific species have not clearly born this out (Bubenik, 1965; Lent, 1966). In fact in the most detailed study of this subject, involving data collected from 1270 parturitions among various breeds of ewes, Lindahl (1964) found evidence indicating quite the opposite. His study also revealed more distinct peaks in the diurnal parturition pattern of ewes three years of age or older compared with younger ewes.

Certain representatives of the Suidae are apparently the only species of Ungulata in which a nest is prepared before parturition (see Frädrich, 1965 & 1967). Reports of preparation of special birth beds are discussed by Bannikov *et al.* (1961) with regard to saiga but these authors do not believe that the pawing and scraping associated with birth places differs in any way from that performed at normal bedding sites. Shortridge (1934) states that steenbuck use burrows of other animals.

Many authors have described physical and behavioral changes by which an imminent birth may be predicted (Van Doom and Slijper, 1959; Naaktgeboren, 1963; Fraser, 1968). Nevertheless, such indicators do not always occur and the literature of zoological garden management is replete with examples of totally unexpected births. This seems to be especially true of Camelidae (Kraft, 1957) and zebras (Walther, 1961b). The Equidae seem to have ability to delay parturition when disturbed but there has been no definitive study of this subject.

The position of the mother during labor and at the time of birth has been described for numerous species and I will not attempt a full compilation of these observations here. The subject has been thoroughly reviewed by Slijper (1960) who concludes that the lying position is normal or most common in ungulates. The exceptions seem almost as numerous as the rule, however Among the Suidae and Hippopatamidae, including *Choeropsis*, contractions and birth while reclined on the side is certainly a typical pattern and this is also apparently a general rule among Camelidae (Pilters, 1956). Nevertheless, Naaktgeboren and Vandendriessche (1962) described a dromedary giving birth while standing. In other species such as domestic cattle (Naaktgeboren, 1963) muskoxen (Fig. 1) (Lent, unpublished), Pere' David's deer (Van Doom and Slijper, 1959), and some gazelles (Walther, 1968), alternate bouts of contractions while on the side and while standing plus a general restlessness are the rule. Among other deer species it is also common for the mother to undergo alternate bouts of standing and lying down, but the reclining may also include resting on the brisket and generally the legs are not as forcibly extended during labor contractions. The wisent, on the other hand, maintains a defecation posture during labor and apparently always gives birth standing (Naaktgeboren and Vandendriessche, 1962).

The infant may be born while the mother is standing, crouching, or lying down. Examples of births in all three of these positions have been described for *Rangifer*. For mule deer one observer reports the females standing (Voss, 1965), as is apparently always the case in the giraffe (Hediger, 1955; Robinson *et al.*, 1965). Klingel and Klingel (1966) describe a zebra foal born while the mother is lying down. Among gazelles the lying position is common but occasionally the mother is crouched in a 'defecation posture' (Walther, 1968).

Fig. 1 Muskox cow in labor

Among the Suidae the time span between multiple births may be as short as a minute or two (Frädrich, 1965). Howard (1966) reports only 2 minutes between the births of pronghorn twins, Voss (1965) reports 5 minutes between mule deer twins, and Haugen and Speake (1957) observed an 8 minute gap between white-tailed deer fawns The longest time span between births, about 20 minutues, is reported by Hediger (1955) for nilgai twins.

When parturition occurs without isolation, either in the wild or under conditions of captivity, the event frequently attracts the attention of other conspecifics, even males. Females are described interacting with mothers and their offspring during or immediately after birth in wildebeest (Talbot and Talbot, 1963), klipspringer (Cuneo, 1965), bushbuck (Dittrich, 1970), roe deer (Prior, 1968), bison (Marjoribanks-Egerton, 1962), and muskoxen (Lent, unpublished)

## II. POST-PARTUM BEHAVIOR

Hediger (1955) distinguished clearly between the passive and active types of ungulate mothers in reference to their behavior in the immediate post-partum period. The Suidae and the Camelidae provide most of the examples of the former. The Camelidae do not usually lick the neonate or aid in removal of the membranes. Nevertheless, camelid mothers will use their lips and tongues to aid urination and elimination in much the same manner as is common in 'active' species particularly those of the hiding type. Even among the so-called passive swine, the sow may make contact with her piglets soon after birth and aid in their proper disposition relative to her own body and the nest by rooting movements of her head (Hafez and Signoret, 1969). Among the active type mothers, which includes the vast majority of ungulate species, the process of licking and grooming of the neonate typically begins a few minutes after birth. This activity has been described in detail by many authors including Hediger (1955), Blauvelt (1955), Collias (1956), Herscher *et al.*, (1963a), Alexander (1960), Kurt (1968) and Espmark (1969). Licking may initially include the entire body of the neonate starting especially at the cephalic end although relatively neglecting the limbs. Later, it is typically concentrated at the anogenital region. Gunther (1967) and Walther (1964, 1968) have both mentioned the possibilities for observers to sex young by observing where the mother licks it. This would seem to be possible only with the hider type species (see later). Licking (especially in these species) is not confined to the neonate itself but may include objects in the environment which have received fluid, either from the breaking of the amniotic sac or the fetal membranes and afterbirth. The latter are sometimes chewed and swallowed. Bubenik (1965) reports such licking to be more thorough in pluriparous roe deer than in primiparous individuals.

Numerous functions have been suggested for post-partum licking. Perhaps the best discussion of this subject appeared in Blauvelt (1955). The various discussants viewed licking as one mode of reciprocal stimulation between mother and neonate. Numerous observations suggest that this stimulation aids in increasing neuro-excitability and thus promotes rapid motor development in the infant, increasing its chances for survival. At the same time the mother receives olfactory and gustatory stimuli which appear to be important in strengthening maternal behavior in general and in particular the social bond with her infant. Experimental evidence for this will be described later. Lip curling (Flehmen) by mothers during such activity has been observed commonly in muskoxen (Fig. 2), and has been observed in domestic mares (Fraser, 1968) and ewes (E Banks, pers. comm.). The role of licking in drying the neonate's coat and thus aiding thermoregulation is believed to be important in caribou (Hart *et al.*, 1961; Kelsall, 1968). Pruitt (1961) suggests that the lower neonatal mortality seen in caribou populations during severe cold weather in comparison to that

Fig. 2. Muskox cow retracts lips after licking neonate

Fig. 3. Muskox cow licking and pushing neonate, which is 30 minutes old

recorded for domestic reindeer in the Soviet Union may be due to a physiological difference in the fawns of these two subspecies. Nevertheless it seems equally possible that the difference is due to more intensive maternal care by wild caribou mothers. Thermoregulation in neonatal lambs has been studied by Alexander (1964) and co-workers. These sheep studies are reviewed by Rowley (1970) who mentions that maternal grooming by the domestic ewe is relatively inefficient as a drying mechanism and that evaporation must account for much of the drying process which may take up to three hours post-partum for completion. Interspecific differences certainly exist with regard to maternal licking. There also seems to be interspecific variation in the amount of moisture present on the surface of the neonate but specifics on this point are lacking.

Although Naaktgeboren and Vandendriessche (1962) suggests that the lack of licking by camel mothers during the post-partum period is associated with the presence of a well-developed epitrichium, licking is very intensive among muskoxen in which the neonate also possesses such a strong covering (Fig. 3). Vigorous licking may sometimes appear to actually hinder the first standing attempts of neonates. I have seen this among perhaps over-solicitous muskox mothers.

Obviously the birth itself provides a shock effect for the neonate particularly if, as is frequently the case, the mother is standing or stands up at the moment of delivery. Mothers of many species will tactually stimulate their offspring by means other than licking. Cattle will do so by prodding the neonate with the head (Naaktgeboren and Vandendriessche, 1962) as will bison (Fraser, 1968). I have observed the same following several muskox births. Von Raesfeld (1957) and Bubenik (1965) have described similar activity by roe deer. Bubenik also relates unpublished observations on the use of the forelegs by red deer to induce activity in their neonatal calves and he associates this maternal behavior pattern with an unusually cold calving environment. Gilbert (this volume) described vigorous kicking by a fallow deer mother directed towards her stillborn fawn. The use of the forelegs to prod and stimulate the neonate is perhaps most developed in Dall sheep (Pitzman, 1970), particularly in the first few

TABLE 1. TIME AFTER BIRTH (in minutes) FOR FIRST OCCURRENCE OF THREE INFANT ACTIVITIES

| Species | First standing* | First walking | First nursing | No of obs. | Reference |
|---|---|---|---|---|---|
| CERVIDAE | | | | | |
| Muntjak | 25 | | 30 | 1 | Lau, 1968 |
| Pudu | | | 270 | 1 | Hick, 1969 |
| Pere David's deer | 80<br>(30-240) | | 103<br>(60-200) | 3 | Lau, 1968 |
| Fallow deer | 15 | | 25 | 2 | Lau, 1968 |
| Red deer | 15 | | 44 | 4 | Lau, 1968 |
| | 24 | 40 | 49 | 3 | Bubenik, 1965 |
| | 30 | | 55 | - | Naaktgeboren, 1966 |
| White-tailed *Met* | 20<br>(8.5-32) | | | 2 (twins) | Haugen & Speake, 1957 |
| | | 21 | 50 | 2 (twins) | Haensel, 1966 |
| Mule deer | | | 26.5 | 2 (twins) | Voss, 1965 |
| Roe deer | 34 | 40 | 40 | 1 | Espmark, 1969 |
| | 73 | 82 | 103 | 2 | Bubenik, 1965 |
| Caribou | 30 | 48 | 90+ † | 5 | Lent, 1966; Kelsall, 1960 |
| Reindeer | | | 15 | 1 | Lau, 1968 |
| EQUIDAE | | | | | |
| Zebra | 11 | 19 | 67 | 1 | Klingel & Klingel, 1966 |
| BOVIDAE | | | | | |
| *Cephalophus* hybrid | 10 | | | 1 | Frädrich, 1964 |
| Impala | 20 | | | - | Talbot & Talbot, 1963 |
| Grant's gazelle | 19 | | 21 | 1 | Walther, 1968 |

| | | | | | |
|---|---|---|---|---|---|
| Dorcas gazelle | 29 | | 43 | 1 | Walther, 1968 |
| Gerenuk | 60 | 60 | 120 | 1 | Kirchshofer, 1963 |
| Nilgai | 20 | | 47 | 1 | Hediger, 1955 |
| Bontebok | 23 | 22(1) | 96 | 2 | Altmann, 1971 |
| Addax | 28 | | 58 | 1 | Dittrich, 1970 |
| Eland | 70 | | 148 | 3 | Kirchshofer, 1963 |
| Defassa Waterbuck | | | 30 | - | Spinage, 1969 |
| Kongoni | 45 | | | - | Talbot & Talbot, 1963 |
| Coke's hartebeest | 31 | 34.5 | 42 | 3 | Gosling, 1969 |
| Wildebeest | 3-5 | 5-10 | | - | Talbot & Talbot, 1963 |
| | 7 | 12 | 33 | 1 | Hediger, 1955 |
| | 3-10 | | | - | Lawick-Goodall, 1970 |
| Bison | | | 26‡ | 1 | Seton, 1929 |
| | 23 | | | 2 | McHugh, 1958 |
| | 15 | | | 2 | Marjoribanks-Egerton, 1962 |
| Dall sheep | 24 | | all > 60 | 3 | Pitzman, 1970 |
| Mouflon | 15 | 80* | 120 (?) | - | Pfeffer, 1967 |
| Muskox | 35<br>(16-60) | | 40 | 3 | Lent, unpubl. |
| ANTILOCAPRIDAE | | | | | |
| Pronghorn | 26 | 31 | | 1 | Prenzlow, 1964 |

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* Mean values are given for multiple observations with range of extremes in brackets

† Two had not nursed after 3 hours

‡ 26 minutes from time labor began!

minutes post-partum. The activity itself seems to be stimulated by the struggles of the lamb to coordinate itself. The infant itself provides visual stimulation which in turn heightens the state of awareness and the activity of the mother. Chamois are reported to attempt lifting weak young with their horns (Hediger, 1955) and bison will move the young upward and towards them with the under surface of their muzzles (Engelhard, 1970). In the case of the primiparous mothers however, the total effect of the neonate may sometimes be frightening to the mother and lead to postponement of maternal-young contact, including nursing. This is well described in reindeer and caribou (see Lent, 1966) and sheep (Alexander, 1960), and in many observations of ungulate births in zoological gardens.

The mother may be further stimulated by vocalizations of the neonate. Such vocalizations immediately after birth have been reported for several species including mouflon and bontebok (D. Altmann, 1970, 1971), roe deer and red deer (Bubenik, 1965), muntjak (Dubost, 1971) and some neonate muskoxen (Lent, unpublished).

The lack of such reciprocal stimulation can obviously affect the post-partum behavior of ungulate mothers. Evidence for this is available from observations of maternal behavior associated with stillbirths such as I have described for caribou (Lent, 1966). Alexander (1960) noted that merino ewes with stillborn lambs will frequently desert them soon after birth and attempt to adopt the young of other mothers. Van der Hammen and Schenk (1963) described the lack of normal behavior in connection with stillborn goats.

While all ungulates are considered relatively precocial in comparison with other mammalian orders, there nevertheless exists within the order significant differences between various species with regard to their rate of development during the post-partum period. These differences may relate to their exposure to predation and other selection pressures. The wildebeest, for example, has frequently been referred to as the most precocial species (Talbot and Talbot, 1963). It seemed of interest to tabulate the times of first occurrence of various events during the post-partum period for as many species as possible. Three events were selected because they were most frequently referred to in the literature (1) first standing, (2) first walking, (3) first successful nursing. The compiled figures, as given in Table 1, must be considered as crude indicators at best. Obviously the timing of such events can be greatly influenced by environmental conditions and first nursing, in particular, may be influenced markedly by whether or not the mother is primiparous.

Table 1 does not include domesticated species. It is not clear whether domestication has led to slower motor development in the post-partum period. The data presented by Herscher *et al.* (1963a) adapted from Wallace (1949) does not suggest a significant difference in domestic sheep compared to related wild species. At least 70 per cent of the lambs observed were standing in less than 30 minutes post-partum and well over half of both singlets and twins nursed in the first hour.

## III. THE HIDERS VERSUS THE FOLLOWERS

We owe to Walther (1961a, 1964, 1965a, 1968) the development of the concept that there are two distinct forms of integrated maternal-infant behavior in ungulates. These are referred to in German as the 'Ablieger Typ' and the 'Nachfolger Typ'. While various English translations of these terms have been employed I wish to adopt here the simple terminology of 'hiders' and 'followers'. A major goal in this review is to examine the behavioral characteristics of these two social types to determine how well those ungulate species which have been studied fit into this dichotomy and how clearly various behavior patterns may be related to one or the other of these types.

Immediately following parturition mothers and infants of all ungulate species enter into a phase of intensive contact and reciprocal stimulation. Some of the types of contact have already been noted. It is this initial phase, common to all species, that I refer to as the post-partum period. The duration of this period varies considerably from species to species. From the information presented by Walther (1964, 1965a) the period may last for 20 hours in kudu or be as short as 41 minutes in Grant's gazelle; Espmark (1969) indicates 5 hours for roe deer. Among the hider types the mother and the infant then enter into the first of many long periods of separation which typically commences with the infant selecting its own hiding place away from the parturition site. The active role of the infant in this selection process is emphasized by Walther in his reviews of the subject and by Bubenik (1965) in red deer, McCullough (1969) with regard to Tule elk, Jungius (1970) in his study of reedbuck behavior and Schaller (1967) with regard to blackbuck.

The German term 'Abliegen', usually translated as 'lying-out', emphasizes this active role of the infant. Nevertheless, it is clear that we are dealing with an adaptive behavioral complex involving characteristic behavior patterns on the part of both infant and mother. Obviously, not only does the infant in certain species move away to hide but the mother 'permits' it to do so and in fact aids the success of this activity in several ways, i.e. by not attempting to induce following and by maintaining the desirable distance away from the infant. Similarly in follower-type species both mother and infant show specific behaviors which tend to promote early and close following responses.

Furthermore, there appear to be variations or intermediate forms in which the hiding complex is not fully developed. For example, Rudge (1970), although contending that the feral goat is clearly a 'hider', indicates that the mother leads her offspring to a secluded place. Spinage (1969) also describes how the Waterbuck mother leads her calf to a new hiding place. In other cases, to be described later, the infant remains near the birthsite while the mother moves away. For these reasons, I have used the more general term, 'hiders' to refer to those species employing this behavioral complex and reserve the term 'lying-out' to refer specifically to the infant activity of searching out a hiding place.

Walther (1964) describes the characteristics which appear necessary for a desirable 'hiding site' in species such as gazelles. These include the presence of vertical objects and/or depressions. In the wild, cover density seems to be important to many species. Kurt (1968) mentions this with regard to roe deer as does Bubenik (1965) in reference to red deer, Gosling (1969) for Coke's hartebeest and Fichter (this volume) for pronghorn. I have the impression that avoidance of intense light may be involved here, at least this appears to be the case in moose. In moose we have also observed the young infants to actively select a hiding place and to decline to follow or rest near their mothers when they are in the open

The distance maintained by the mother away from the hiding site has been given as 30 to 300 m for Tule elk (McCullough, 1969), 500 m or more for Grant's gazelle (Walther, 1965a) and feral goats (Rudge, 1970), one-fourth to one-half mile (0.4-0.8 km) for pronghorn (Einarson, 1948) and up to 1 km for Defassa Waterbuck (Spinage, 1969).

Maternal behavior traits in hider type species are also characteristic. In general, the mothers of most of these species will not approach and make contact with their infant at its hiding place. Rather, they await its emergence from some distance away. Leuthold (1967) gives this distance as 20 to 40 m for the Uganda kob. According to Walther (1964) the distance is 10 to 15 m in kudu. Hendrichs and Hendrichs (1970) mention a distance of 10 m in the dik-dik. Walther (1964) reports from his observations of animals in captivity that the Sitatunga, although clearly a hider type, moves directly to its calf and makes naso-nasal contact. In this connection it is perhaps worth mentioning the observation by Jobaert (1957) that Sitatunga mothers will frequently lie in a small dry area with their young calves resting between their forelegs.

One or more changes in the location of the hiding site occur during the hiding phase. This has been described in both captive and free ranging subjects. Typically the female initiates such a move but the exact location of the new site depends upon the infant. In mule deer the mother is reported to lead her infant to a new resting site quite regularly after the morning care session (Linsdale and Tomich, 1953).

Generally speaking, the hider type infant acts independently with regard to spatial decisions but not as independently with regard to temporal ones. That is, activity patterns are to a large extent established by the mothers. Nevertheless, as the hiding phase progresses infants will act more and more independently. This is especially evident in studies of cervids. Axis deer (Graf and Nichols, 1967), roe deer (Espmark, 1969), red deer (Bubenik, 1965), and moose young may all call out to their mothers from their hiding place at an early age before they start moving out of these sites on their own. Such independent vocalizations during the hiding phase have not been heard in mule deer (Einarson, 1956) or fallow deer (Gilbert, 1968). Fawns will soon begin to initiate periods of activity independent of their mothers but usually restricted to short distances and not entering into open spaces.

Regular changes in hiding places are also described by Walther (1965a, 1968) for Grant's gazelle. Walther also describes some species that apparently alternate between daytime and night-time hiding spots.

In contrast, the follower species, as exemplified by sheep, caribou, wildebeest and chamois, maintain close and frequent contact between mother and infant. The decline in the frequency of contacts following the post-partum period is not so marked. The follower type mother and infant both are continually responding in a reciprocal fashion to one another's spatial position and tend to be more mobile following the post-partum period. Actual physical contact may occur during resting periods. In general, follower infants are more likely to initiate activities, such as nursing and play, on their own.

A species by species examination of the information presented in Table 1 does not indicate a clear general tendency for followers to be more precocial than hiders.

Certainly the wildebeest is the most precocious of the species for which we have information. On the other hand, caribou calves are by no means more rapid in their development, at least with regard to the three behaviors in question, than are other cervids. In several of the follower types first nursing may be frequently delayed for two to eight hours apparently without detrimental effects (Lent, 1966;Collias in Blauvelt, 1955; Alexander, 1960; Pitzman, 1970; and Kirchshofer, 1963). .

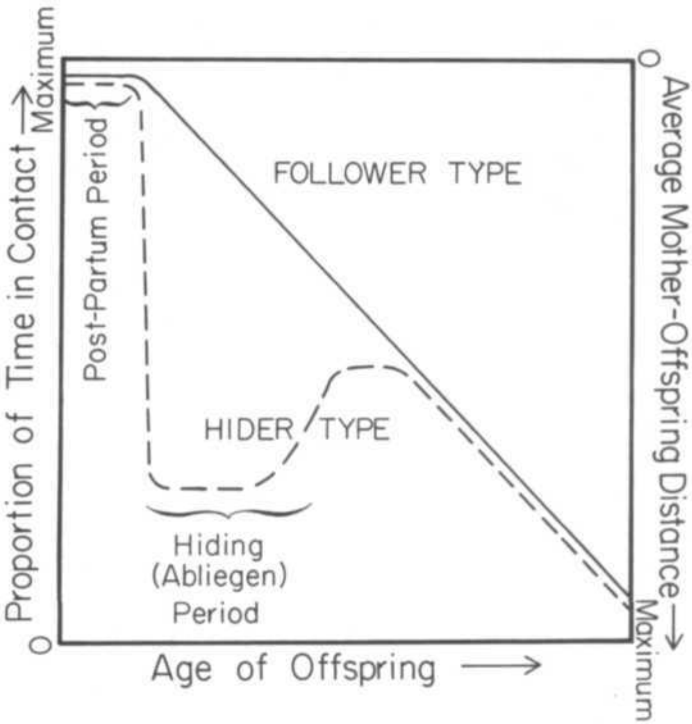

Fig. 4. A schema illustrating the two types of maternal-infant relationships in ungulates

In Fig. 4 I have attempted a schema for illustrating the basic differences in ontogenetic trends between hiders and followers. Two variables are shown on the ordinate axis, total time in contact (per day, for example) and average mother-infant distance, as if one were able to measure this once every minute during a typical day. Species of both types undergo a similar post-partum period, following which we see the most marked divergence of the two categories. Obviously there must exist in the hider species a turn-around point after which interindividual distances again begin to increase and mother-infant contact time decreases. This peak is shown in the 'hider line' after which similar trends associated with weaning and the later breakdown of the mother-infant bond occur in all species. In some ungulates this trend may be prolonged for two years or more and in fact a temporary trend reversal may occur after the first year (see Section VII). Total time in contact has been used in this schema rather than number of contact periods per activity cycle since in many hiders the frequency of contacts also decreases during their hiding phase as it does in similar-age followers, even though total time in contact increases as the hiding phase wanes. Espmark (1969) provides precise quantitative data on this aspect of contact behavior in his study of roe deer. The hiding phase as shown in Fig. 4, is obviously of variable duration in different species. Information on the length of hiding phases is given in Table 2. Walther (1964) in his study of captive greater kudu has described in detail how the hiding phase can wane very gradually. Certain species which have been previously classified among the follower types, particularly the goats, do indeed show hiding periods (see later) and thus in this sense a continum exists with regard to the relative emphasis placed upon hiding behavior.

TABLE 2. DURATION OF HIDING PHASE IN THE ONTOGENY OF YOUNG UNGULATES

| Species | Duration | Captive or Wild | Source |
|---|---|---|---|
| Siberian ibex | 2-3 days | W | Savinov, 1962 |
| Mouflon | 3 days | W | Pfeffer, 1967 |
| Red deer | 3-4 days | W&C | Darling, 1937; Bubenik, 1965 |
| Feral goat | 4 days | W | Rudge, 1970 |
| Axis deer | 7-10 days | W | Graf and Nichols, 1967 |
| Elk | 18-20 days | W | M. Altmann, 1963 |
| Muntjak | 2-3- weeks | C | Dubost, 1971 |
| Roe deer | 2-3 weeks | C & W | Kurt, 1968 |
| Defassa Waterbuck | 2-4 weeks | W | Spinage, 1969 |
| Pronghorn | 2-3 weeks | W | Einarson, 1948; Seton, 1929; Fichter, this volume |
|  | 4-7 days | W | Prenzlow, 1964; Bromley, 1967 |
| Klipspringer | 4 weeks | C | Cuneo, 1965 |
| Dorcas gazelle | 2-6 weeks | C | Walther, 1968 |
| Thomson's gazelle | 2-6 weeks | W | Walther, 1968 |
| Indian blackbuck | 2-6 weeks | C | Walther, 1968 |
| Kudu | 3-7 weeks | C | Walther, 1964 |
| Uganda kob | 2-4 months | W | Leuthold, 1967 |
| Reedbuck | 2-4 months | W | Jungius, 1970 |

Hiding behavior shows its greatest development in certain African antelope species in which it may persist at least partially up until four months. In these same species we see that the initial contacts of the mother with her young are restricted from the start of the hiding phase to two or three sessions per 24 hour cycle. This then is the 'ideal' hider type described by the schema in Fig. 4.

One must be careful not to confuse maternal isolation behavior with 'hiding' behavior. That is, in many species as I have already indicated, the mother may seek isolation for parturition and maintain this isolation for sometime post-partum. During this isolation phase she may well be in close contact with her young. This is the case in the Camargue cattle described by Schloeth (1958), and Marjoribanks-Egerton (1962) apparently misunderstood the situation, since she cites Schloeth to indicate that they hide their calves. Isolation also occurs in the Rocky Mountain goat (Lentfer, 1955; Holroyd, 1967). This may be why Seton (1929) and Hanson (1950) reported that mountain goats in South Dakota hid their infants during the first days of life whereas Klein (1953) and Holroyd agree that the neonate kid follows the mother closely. The matter is similarly unclear with regard to the ibexes. Walther (1961a) describes typical follower-type behavior among European ibex in captivity. Lydekker (1898) and Savinov (1962), however, both refer to hiding behavior in North African and Siberian ibexes. Although the accounts are not detailed this behavior is apparently not simply isolation of mother and young. The numerous observations of European ibex in the wild related by Couturier (1962) suggest plasticity of maternal behavior. When kids are born in areas of extremely rugged terrain movements with their mothers are restricted until a later age. The mothers therefore range farther from them and stay away for some hours. During this time the kids remain quiet. Females may move over 100 m away and return carefully to check up on their offspring. If these are true followers we would expect that the females would always return to rest adjacent to their young. The available information is not explicit on this point.

There is a great need for intra-specific comparative studies of maternal behavior particularly in those species existing in widely differing habitats or whose habitats have been subject to man-made alterations. We know little regarding the extent to which the behavioral traits associated with hiding or following may be traditionally or environmentally influenced, although the work of Walther has shown how clearly these traits are displayed by animals kept in captivity. Perry (1952) believes that the maternal behavior of red deer has altered as the habitat used by this species in Scotland has changed over the past century or two. Rudge (1970) feels that feral goats display hiding traits not seen in domestic forms. However, differences with regard to the development of hiding and related behavior between the genus *Ovis* and the genus *Capra* were noted earlier from studies of domestic animals as discussed by Collias (1956),Herscher *et al.*(1963a) and Hafez and Cairns *et al.* (1969). Walther (1961a) also noted that the following complex is not as strongly developed among the goats in comparison to the sheep.

In summary, the material available at present regarding the maternal behavior of ibexes and goats indicates that in this group there is weak development of hiding type behavior with short hiding phases. Considerable plasticity in behavior is suggested, influenced perhaps by genetic differences, traditions, habitat variables, or some combination of these.

The Suidae represent another problem. My interpretation of the observations of Frädrich (1965, 1967) and Snethlage (1957) is that the period in which the piglets remain in the nest is analogous to the hiding phase. This period is short, after only a few days the young leave the nest and follow the mother. In fact, Frädrich describes young wart hogs at the entrance to their hole on their second day and great weakening of their association with the site by the second week. Frädrich (1965) cites a contrary observation by Verlindern who reported that wild swine mothers remained with their young at the nest for 4 days.

Finally I wish to specifically mention moose. M. Altmann (1956), Geist (1966) and Espmark (1969) all consider the moose to be a follower type. However, my own observations and those of Stringham (unpublished) suggest the existence of certain hider traits. I have already mentioned that young calves will frequently refrain from following the mother and will select resting places independently. Although there is little mobility by the young initially, the mother may range up to 100 m away when they are only a few days old and may be gone for an hour or two. After such separations, reunions may be preceeded by vocal exchanges. Usually the mother rests beside or within a few meters of the offspring.

## IV. THE FOLLOWING RESPONSE AND THE PRONE RESPONSE

Approach and following tendencies are basic to the early behavior of most birds and mammals. In the infant ungulate this following response, or heeling tendency as it has often been called, occurs initially as a generalized response by which the infant attempts to maintain its proximity to objects of an appropriate size range which are moving away from or tangential to it. Walther (1964) lists several other conditions which tend to promote following reactions in infant ungulates. Much more work is required, however, to establish the universality of these promoting factors and their relative importance. As in the young of other vertebrate groups, infant ungulates show a strong following tendency before any alarm or fright response is evident in their behavior. The development of a fright response has been considered to be one of the events leading to termination of the sensitive or 'critical period' for imprinting in birds (Hess, 1959; Sluckin, 1967). My own observations of caribou suggest that the fright response develops first in connection with strange odors, and much later with visual or auditory stimuli. This may occasionally result in a situation where a young calf will approach a human until close olfaction occurs, move away, and then approach again, repeating the cycle. Walther (1969) indicates that bontebok react negatively to strange odors as early as the second day.

Under many circumstances it is important that a following response be induced by the mother. This may require specific behavior patterns as added stimuli, particularly if the infant is an older one or is in a state of satiation or exhaustion. Raising and wagging of the tail is reported to stimulate infant following responses, for example, in Sitatunga (Walther, 1964) and Waterbuck (Spinage, 1969). Caribou mothers use a head bobbing action described by Pruitt (1960) and Lent (1966), which is apparently weakly developed or absent in the domesticated reindeer. Chamois and blesbok employ a similar head motion (Walther, 1966, 1969) In several species occasional naso-nasal contacts by the mother with her infant also appear to strengthen following responses.

Obviously, one of the most important ways in which a mother induces a maximal following response is by pacing, maintaining the optimum speed and most effective distance between herself and her offspring.

Vocalizations are important in strengthening the following reaction in many species, including the camel and dromedary (Pilters, 1956), caribou (Lent, 1966) and elk (M. Altman, 1963. In the latter two species, cohesion calls are used by both mothers and young and occur continually during movements. Among elk these calls will cease during disturbance but among caribou they increase in frequency and intensity. Both these species also produce clicking noises from their feet which may also function to maintain auditory contact between mother and infant during movements. The effectiveness of intermittent auditory and visual stimuli in eliciting approach responses has been the subject of considerable experimental work (see review by Sluckin, 1967).

Walther (1968) suggests that the following response is expressed imperfectly in hider species in that among these species the infants may be frequently seen moving beside or ahead of their mothers. Such behavior is certainly seen in follower types also, but in general perhaps at older ages. In this connection it is interesting that Selous (1890) stated that one method of distinguishing the two species of African rhinoceros was that in the square-lipped rhinoceros the young always ran ahead of the mother whereas with black rhinoceros the calf invariably moves behind the mother. Guggisberg (1966), however, indicated existence of a short hiding phase in this latter species followed by close maternal contact, and Owen-Smith's description (this volume) suggest the white rhino is indeed a follower type.

Following responses directed towards man or other species have been described on numerous occasions. Such events are related for moose (Knorre, 1961), rhinoceros

(Selous, 1890), bison (Garretson, 1938; McHugh, 1958) and red deer (Perry, 1952; Bubenik, 1965), among other species. Couturier (1938) describes chamois one or two months old which showed no fright response even though other individuals only a few days old sometimes reacted to humans with alarm. Krieg (1950) reports following responses in guanacos at even older ages.

Walther (1964) suggests that the replacement of the generalized following response by one restricted to the mother object occurs more rapidly in species such as wild sheep, than in hider types. While it is true that the offspring of the follower species rapidly learn to recognize their mothers and follow them when placed in a choice situation, nevertheless in all the follower species which I have observed the generalized following response persists long after individual recognition has been achieved. The advantages of such a generalized response in gregarious species such as sheep, caribou and wildebeest are evident. In a stress situation, as when chased by predators, the infant will follow the group without hesitation, even though it is unable to locate its mother before fleeing. Reunion of mother and infant can be delayed until the immediate danger is past. Caribou cows and calves, for example, will diligently seek such reunions even when they have been widely separated into different groups after such stress situations. In addition, young who have mastered recognition of the mother will frequently strive to follow and nurse other individuals when they are unable to locate their mothers. This is reported, for example, for bighorn sheep (Geist, 1971a). In short, under any stress situation the generalized response reappears.

The generalized following response is expressed independently of nursing behavior which may rapidly become centered on the mother. The extreme example of this is described by Walther (1964) in which young Sitatunga infants will break off nursing to follow a valent object moving by. Infants of several species have been shown to retain strong human-oriented following responses even though they are fully socialized with the mothers and attempt nursing only from them (Tschanz, 1962; Leuthold, 1967; Waring, 1970). Cairns (1966) found similar possibilities for the formation of separate social and nutritional bonds in experiments with domestic lambs The mother-centered following response in relation to individual recognition is further dealt with in Section VI.

Under certain circumstances young infants of hider species are able to act independently without showing a following response. They will move away from the mother and select a resting place. In such cases the stimulus requirements associated with such sites seem primary.

In addition there is a wide variety of maternal behavior patterns, of particular importance among the hider species, which tend to inhibit or prevent following responses. One method is for the mother to move away quietly and inconspicuously without attracting the infant's attention.

An infantile behavior pattern that has been frequently associated with hider species is 'Sichdrücken', usually referred to in English as 'freezing', 'skulking' or 'lying prone'. This posture differs from the normal sleeping position (Fig. 5) although sleeping postures are frequently employed in similar circumstances. The animal stretches its body out producing the lowest possible profile. In the fullest expression of this behavior the infant remains entirely motionless. Only slight respiratory movements, eye movements or an occasional ear flick indicate the infant is alive. Muscular rigidity is sometimes characteristic of this posture (see, for example, Bubenik, 1965). A caribou in the prone position may go entirely limp when handled, however.

The prone response acts as a cut-off mechanism preventing expression of the following tendency. The response may be induced by the mother in various species by a variety of behavior patterns. The most direct approach is pushing or pressing the infant down. This has been described by M. Altmann (1963) in elk, which use the head, and in red deer, using their forelegs, by Perry (1952) and Bubenik. Roe deer will similarly use their muzzles (Bubenik, 1965). Vocalizations are said to induce a prone response in infant pronghorn (Van Wormer, 1968) and apparently in mule deer (Seton, 1929). Rue (1962) mentions how white-tailed deer mothers will use both voice and physical contact to prevent following by their fawn. Graf and Nichols (1967) also mention that stroking the head will induce lying in axis deer fawns. They describe how

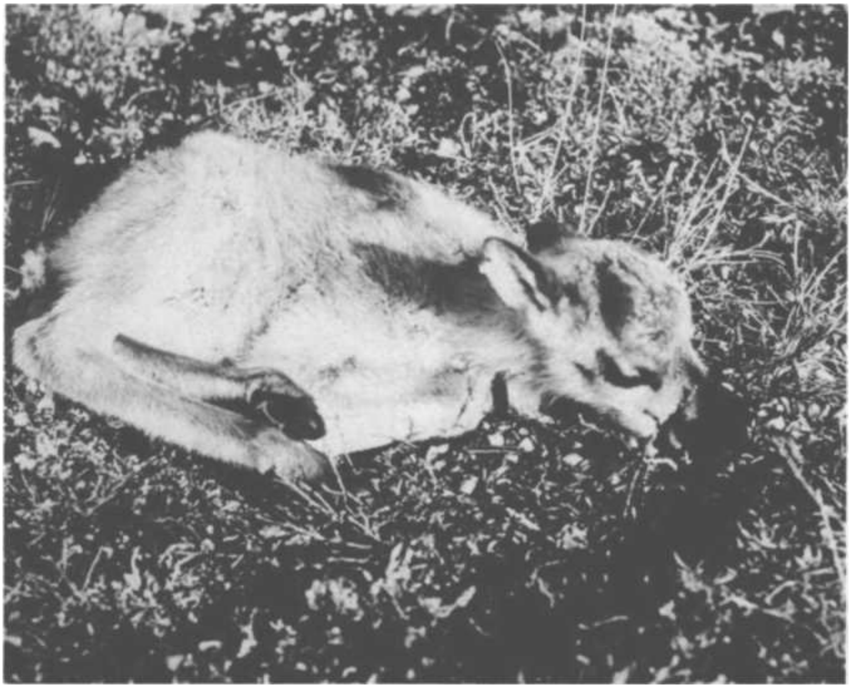

Fig. 5. Caribou calf, approximately 24 hours old, adopts a prone position after being ear-tagged

some fawns will lie prone when their mothers leave but will attempt to flee when approached by humans. High bounding motions by the mother stimulate the prone response in white-tailed deer (Downing and McGinnes, 1969), caribou (Lent, 1966) and mule deer (Linsdale and Tomich, 1953). Such bounding motions are described for other cervid species such as barasingha and sambar (Schaller, 1967).

Non-social disturbances which induce infants to lie prone include sudden, loud noises. Pfeffer (1967) describes how Cypriots fire guns in the air to induce young mouflon lambs to drop. He relates their opinion that this is possible only with very young lambs because such infants have never heard thunder and therefore do not accept loud sounds as being of natural origin! Kurt (1968) describes how young roe deer calves are frequently killed because they lie prone in front of mowing machines. Older calves are not likely to lie prone before hand mowers but will still continue to do so in response to louder machine mowers. Especially among the hiders, the neonate infant frequently adopts this posture without specific external stimulus (Walther, 1964). In all species the tendency to adopt this posture either with or without external stimulus wanes with age. The rapidity of this behavioral change varies considerably between species and these differences are summarized in Table 3. The waning of this behavior is associated with the development of a 'flight response' to alarming stimuli.

The use of this posture as a response to such stimuli is not limited to the hiders, as evidenced by its occurrence in barren-ground caribou (Lent, 1966). However, it has not been described in the follower type bovids nor did Rudge (1970) observe it in feral goats, although Hafez, Cairns *et al.* (1969) mention it with regard to domestic goats. I have not observed it among muskoxen calves. Among free-ranging peccaries the prone response occurs in infants when they are only a few days old, even though such young infants already show a strong following response (Sowls, this volume).

The waning of the prone response is a gradual process and in fact the behavior pattern has been described for yearlings and adults of several species, primarily cervids (Burckhardt, 1958; Kiddie, 1962; Bubenik, 1965; McCullough, 1969), but apparently also in some of the smaller antelope species (Shortridge, 1934). I have not observed it in adult caribou but my former co-worker, Odd Lønø, observed it on rare occasions performed by cows under circumstances of extreme conflict. When attempting to flee and lead their calves away from approaching taggers they were twice observed to lie down oriented towards their calves in a prone position as the taggers approached closely. Immediately afterward they temporarily abandoned their offspring. Bubenik (1965) believes that the prone motor pattern is innate in calves, a statement which is confirmed by all available evidence. He also felt that adults learned to use the behavior to advantage in appropriate circumstances. The widespread occurrence of regression to infantile behavior patterns by adults under stress suggests that learning need not be involved.

TABLE 3 AGE OF WANING OF PRONE RESPONSE TO ALARMING STIMULI ('Schreckliegen')

| Species | Age of Infant | Reference |
|---|---|---|
| Fallow deer | 12-48 hours | Gilbert, 1968 |
| Caribou | 24-48 hours | Lent, 1966 |
| Mouflon | 3-4 days | Pfeffer, 1967 |
| Red deer | 3-4 days | Bubenik, 1965 |
| Moose | 5-7 days | Knorre, 1961 |
| White-tailed deer | 10 days | Downing and McGinnes, 1969 |
| Roe deer | 14 days | Von Raesfeld, 1957 |
| Greater kudu | 14 days | Walther 1964 |
| Dorcas gazelle | 14 days | Walther, 1968 |

## V. NURSING BEHAVIOR

Neonatal sucking motions may occur without contact with any object even before the newborn infant has first arisen (Kirchshofer, 1963; Marjoribanks-Egerton, 1962).

Once limited mobility is gained the neonate will investigate by nosing the ventral surfaces of the mother and poke its head into angles between the limbs and body surfaces. Textural aspects do not seem to be significant at this stage since in captivity the infant will eagerly investigate railings, corners of stalls and other man-made structures. McBride (1963), however, believes the hair patterns on the belly of the sow aid piglets in rapid location of the teats. Most workers are in agreement that the process of locating the mammary glands is accomplished by trial and error learning. I know of no evidence that the unaided neonate is more likely to go to the hind end of the mother than to the forequarters At least in the first hours post-partum, olfaction does not seem to play a role.

Swine receive little aid in locating the teats and yet these species are among the most rapid in time to first successful nursing. First nursing may even start before the umbilical cord is severed (Hafez and Signoret, 1969). The normal reclined position of the mother must certainly make these early efforts easier. The role of the rooting motions of the sow in this connection has been mentioned elsewhere.

The offspring of many species with 'active' type mothers are aided in attaining initial contact with the teats by position shifts of the mother, by maternal crouching as in moose, for example (Stringham, unpublished), and in mountain sheep (Geist, 1971a), or reclining as in roe deer (Bubenik, 1965). Very common is a tendency for the mother to shift the neonate activities towards her hind quarters and to direct it into the reverse parallel position (see below). This is done by the oral and nasal activities of the mother at the infant's anal pole. Such activity is also reported to occur among Camelidae (Pilters, 1956). Alexander and Williams (1964) have carried out experimental work on the facilitory effects of maternal behavior on early nursing of lambs. They demonstrated that, at least under the favorable conditions of confinement, maternal grooming and orientation to the lamb were not necessary for the lamb's survival. Nevertheless, when ewes were restricted from both grooming and orientation to aid their lambs' nursing attempts the offspring showed significantly ($P < .05$) less teat sucking activity and early weight gain.

Information on the frequency and duration of nursing in various ungulate species is compiled in Table 4. Such a compilation is subject to several shortcomings. Information on many wild species is available only from captive individuals in which the enforced proximity of mother and infant may influence nursing behavior. This is suggested with regard to feral swine (see Hafez and Signoret, 1969) and roe deer (Espmark, 1969). There is also great variability in the way in which nursing duration is recorded. Some species nurse in bouts with frequent brief interruptions (loss of contact with teats). In most cases, total bout duration has been reported but various authors do not make it clear which they have measured, bouts or suckling events within bouts. In general, bovinae, especially the hiders, show low nursing frequency and long duration. Long duration suckling is characteristic of the larger bovids such as bison and the Camargue feral cattle (Schloeth, 1961).

The most frequent nursers are apparently to be found in the genus *Ovis*. Dall sheep may nurse in bouts on the average of every 90 minutes during the first days of life (Pitzman, 1970). Young domestic sheep may nurse even more frequently. Porzig *et al.* (1969) cite the work of Sojetado who observed that twin lambs nursed up to 78 times in a 24 hour period. More typically, workers such as Ewbank (1964), Munro (1956) and Munro and Inkson (1957) have reported nursing frequencies up to once per hour. In the reviews of this subject appearing in Porzig *et al.* (1969) and Hafez, Cairns *et al.* (1969), factors cited as influencing nursing frequency include age of lamb (general decrease with age), number of siblings (most studies indicate twins nurse more frequently than singlets), race, and birth weight. With regard to age, data are presented by Porzig *et al.* (1969) based on the work of Czako and Mihalka showing a decrease in frequency from 35 to 45 nursings in the first day of life to 8 to 10 per day by the 28th day. There is a corresponding decrease in the total time spent nursing which is even more marked, being from 80 to 90 minutes in the first day to 10 to 12 minutes total duration by the 28th day. Munro and Inkson (1957) conclude that lambs experimentally restricted to nursing once every four hours received as much milk as those that suckled every hour. Knorre (1961) notes that the optimum nourishment is obtained in hand-reared moose by feeding five times every 24 hours.

The Cervidae tend to show very frequent suckling and care periods initially, with barren-ground caribou representing perhaps the extreme in this family. The duration of suckling tends to be correspondingly lower, although roe deer (Espmark, 1969) and moose (Stringham and Lent, unpublished) are known to sometimes suckle for over 5 minutes. There is a marked decrease in frequency of nursing in all cervid species studied as the offspring age. Caribou calves at 8 to 21 days of age, for example, nurse only one third as frequently in comparison to young calves (Lent, 1966). Roe deer show a change in frequency of similar magnitude after the 6th week (Espmark, 1969). I have described the marked decline in both frequency and duration of nursing bouts in domestic and wild muskox during their first four months (Lent, 1970). Knorre's (1961) work with domestic moose also indicates a marked decline in frequency of nursing by the second and third months.

A further difficulty which may affect the validity of data on nursing frequency is the tendency of many ungulate young to seek their mothers and attempt suckling when disturbed. Schloeth (1961) describes how feral cattle frequently nurse at a change of activities. Walther (1964) describes this type of nursing during disturbance in reference to the genus *Tragelaphus* and refers to it as 'Störungssäugen'. I have observed this most clearly and frequently in caribou, less frequently in muskoxen, impala and tsessebe, and not at all clearly in lechwe. Stringham (unpublished) reports

TABLE 4. DURATION AND FREQUENCY OF NURSING IN SELECTED UNGULATE SPECIES

| Species and Age | Duration | Frequency | Reference |
|---|---|---|---|
| CERVIDAE | | | |
| Pudu | | 3/day | Vanoli, 1967 |
| Red deer | | | |
| First 3-4 weeks | 100 sec. | 6/24 hrs. | Bubenik, 1965 |
| 2 months | | 3/24 hrs. | |
| Roe deer | | | |
| First 40 days | | 6-7/day | Espmark, 1969 |
| After 40 days | | 2/day | |
| Moose | | | |
| Very young | | 10/24 hrs. | Knorre, 1961 |
| 2-3 months | | 2-3/24 hrs. | |
| Caribou | | | |
| First week | 32 sec. | >10/day | Lent, 1966 |
| BOVIDAE | | | |
| Reedbuck | | | |
| First days | 2 1/2-4 1/2 min. | 1-2/day | Jungius, 1970 |
| Defassa Waterbuck | 5 min. | 1-2/day | Spinage, 1969 |
| Uganda kob | | 2/day | Leuthold, 1967 |
| Red lechwe | | | |
| First 3 months | 5 min. | 2-3/day | Lent, 1969 |
| Sitatunga | 2-21 min<br>(10 min.) | 2-4/24 hrs. | Walther, 1964 |
| Greater kudu | 1-18 min.<br>(7 min.) | 3-5/24 hrs. | Walther, 1964 |
| Lesser kudu | 5 min. | 2-3/day | Walther, 1964 |
| Dik-dik | 50-150 sec. | 4/day | Hendrichs and Hendrichs, 1970 |
| Gazelles (Dorcas, Thomson's, Grant's, and Persian) | 30 sec-5 min. | 3-5/day | Walther, 1968 |
| Bison | | | |
| 3 months | 8-10 min. | | KcHugh, 1958 |
| 5 months | 4 min. | | |
| 6 months | 3 min. | | |
| Yearling | 4 min. | | |
| After post-partum period | 6 1/2 min. | 3-4/day | Marjoribanks-Egerton, 1962 |
| Dall sheep | | | |
| First 2 days | 1 1/2 min. | 1/2 hrs. | Pitzman, 1970 |
| Mouflon | | | |
| First days | 2 min. | | Pfeffer, 1967 |
| 6 weeks | 10 sec. | | |
| Muskox | | | |
| Under 6 weeks | 3 min. | 6-8/day | Lent, 1970 & unpubl. |
| Over 2 months | 30 sec. | 2-4/day | |

its occurrence among moose, and Marjoribanks-Egerton (1962) mentions it with regard to bison. Geist (pers. comm.) reports it to be rare in mountain sheep.

Adler *et al.* (1958) refer to the 'Störungssäugen' phenomenon with respect to both goats and humans. They believe the 'pushing syndrome' seen in ungulates is derived from the suckling motor pattern. Fraser (1963), however, disagrees with this interpretation. Adler *et al.* view the phenomenon as evidence for the dual functions of nursing activity, satisfying both nutritive and non-nutritive emotional needs of the young organism. Nevertheless, the disturbed ungulate mother frequently will not permit nursing. I have observed this on many occasions in caribou. There are similar aspects in the alert postures and the nursing invitation postures employed by certain species, namely the stiffening of the legs and the exaggeration of the mother's height. Such use of generalized attention-getting cues is of obvious value, particularly when the mother can more easily communicate further information after close contact is established with her offspring.

The most common nursing position used by ungulate infants is the reverse parallel one in which the body axes of mother and young form an acute angle. This relationship permits access to the anogenital and back regions of the infant by the mother and in many species these are frequently licked or nibbled during nursing. In fact, the activity of the mother may actually induce the infant to take this position (see Blauvelt, 1955: 232). I have shown a statistically significant association between maternal licking and long nursing events in caribou (Lent, 1966). Especially among older infants the angle of suckling varies considerably and angles approaching 90 degrees are occasionally maintained (Fig. 6).

Fig. 6. Caribou calf nursing. Call is approximately one month old

Lying down for nursing by both mother and infant is a general rule among the Suidae (Hediger, 1955; Hafez and Signoret, 1969; Frädrich, 1965), although Frädrich notes exceptions to this, particularly in the Warthog. The mother also typically reclines during nursing in the Tapiridae and the Hippopotamidae; with the latter either on land or in the water, most frequently on land in *Choeropsis.* Reclining while nursing has been frequently reported in white-tailed deer (Severinghaus and Cheatum, 1956), in roe deer with young fawns (Hediger, 1955; Bubenik, 1965; Espmark, 1969), and I have observed it in moose, as did Hediger. Walther (1968 :106) illustrates a Dorcas gazelle nursing her neonate calf in this position and reports (Walther, pers. comm.) this occurring in Mesopotamian fallow deer. Bison calves (Marjoribanks-Egerton, 1962) and other young bovines may frequently gain access to the teats from between the mother's hind legs. This occurs occasionally in red deer (Burckhardt, 1958), pudu (Hick, 1969), mountain sheep (Geist, 1971a) and more frequently in chamois (Kramer, 1969). Caribou make very frequent use of this approach (Lent, 1966) but in both caribou and chamois a higher proportion of unsuccessful suckling attempts are reported when the young employ this tactic. It appears that nursing from the rear is more frequent among the follower types. This may relate to the greater mobility of these species since the mothers are often in motion at the time of the nursing attempt, and, in caribou, the calves may occasionally actually obtain milk while in motion.

Suckling while resting on the carpal joints is especially characteristic of older, larger infants. For example, it is reported by Talbot and Talbot (1963) in wildebeest, Bubenik (1965) in red deer, Hafez, Cairns *et al.* (1969) in sheep, Lent (1966, 1969) in caribou and lechwe, and Geist (1971) in mountain sheep. Hediger (1950) has a plate showing this posture in nilgai twins. In some species, as the young increase in size, pronounced downward curving of the back and neck is observed during suckling. This directs the head upward so that the mouth strikes the teat with correct orientation (Blauvelt, 1955; Hafez *et al.*, 1969).

'Heading-off' or the practice of calves stopping in front of their mothers in order to stop the movement of the mother and permit nursing has been observed in bison by Marjoribanks-Egerton (1962), in Marco Polo sheep by Walther (1961), in greater kudu and Sitatunga (Walther, 1964), in cattle by Schloeth (1958), in Sika deer by Kiddie (1962) and in mountain sheep by Geist (1971a). Marjoribanks-Egerton and Schloeth both described individual infants that developed a propensity for using a specific tactic in suckling to a greater degree than other young in the same herds.

Bunting, the prodding or striking of the udder by the calf with its muzzle, is a universal behavior pattern in ungulates. It is generally more frequent and more vigorous with increased age of the offspring and most workers indicate it functions to induce milk flow or 'let down' (Hafez *et al.* 1969). Folley (1956), Zaks (1962), and Fraser (1968), among others, have reviewed the endocrine and neuronal bases of this phenomenon. The phase in swine nursing frequently referred to as the 'nosing phase' is apparently an analogous activity in the Suidae. Bunting may become so vigorous that it induces the mother to move and/or actually moves the mother by its own activity. In reference to gazelles, Walther (1965a) describes the tendency for mother and infant to pivot ('Säugekreisen') as the infant continues this activity. Continued vigorous bunting frequently appears painful to the mother. Mothers of certain species react to this with threat postures or even blows with their horns or head against their offspring. Other species (fallow deer, for example) may employ biting. Bunting may thus play a role in the weaning process (see later).

The initiation of contact periods which normally include one or more bouts of nursing has already been described with regard to the hiding phase of ungulate ontogeny. The use of vocalization by hider mothers as part of the ceremony preceding nursing-contact periods, that is the 'calling out' of infants, has been described in greater kudu and gazelles (Walther 1964, 1968), moose (Knorre, 1961) musk deer (Flerov, 1954),pronghorn (Prenzlow, 1964), kob (Leuthold, 1967), feral goats (Rudge, 1970) and dik-dik (Hendrichs and Hendrichs, 1970). Certain authors have specifically mentioned a lack of such vocalizations, for example in reedbuck (Jungius, 1970) and Sitatunga (Walther, 1964). Nevertheless such vocalizations may be audible in the wild only under ideal conditions. In non-hider species or in hiding species outside of that phase the mothers may still employ vocalizations to initiate nursing as in ibex and markhor (Walther, 1961a), mountain sheep (Geist, 1971a) and Warthog (Frädrich, 1965); however in other species, caribou for example, this is extremely rare after the post-partum period.

Schuller (1957) reports that a 2 month old domestic calf continued to react to maternal vocalizations by 'udder' searching even though it had been hand raised. Long distance vocal exchanges preceding nursing are described for cattle (Schloeth, 1958,

1961) and muskoxen (Lent, 1970). In the latter, vocalizations of infant and mother are relatively loud and of long duration and thus seem well suited to the loose bond which develops within a few months after birth in this species. Infant vocalizations preceding or associated with nursing are mentioned with regard to llamas (Pilters, 1956), swine (Hafez and Signoret, 1969), markhor (Walther, 1961a), sheep (Haas, 1959), caribou (Lent, 1966) and many other species. Signoret (in Porzig *et al.* 1969) has described how human imitation of infant swine vocalizations will induce more frequent nursing by sows.

Some interesting observations on the vocalizations of cattle-bison hybrid calves are made by Berlioz (1933), Deakin *et al.* (1935) and cattle-wisent hybrids (Krasinska and Pucek, 1968). For a further review of mother-infant vocal communication the reader is referred to Tembrock (1963).

A nursing invitation or udder-presentation posture which I have mentioned previously is employed by mothers of several species as in chamois (Kramer, 1969), roe deer (Kurt, 1968), and moose (Stringham, pers. comm.).

In the chamois it is common for the kid to move to the resting mother and prod her with snout or forehead to induce her to rise and nurse. More rarely, mothers will stimulate their offspring to rise and nurse by use of head or horns or forefeet. Kurt (1968) observed this a few times in roe deer as did Marjoribanks-Egerton (1962) in bison and Espmark (1971) in reindeer). I have seen it occasionally in muskox and rarely (4 out of 137 observations) in caribou.

In the case of neonate ungulates, nursing is almost always terminated by the offspring but in several species a clear-cut trend is evident for increasing frequency of active termination by the mother. Espmark (1969) for example, states that on the first day the infant roe deer always terminates the nursing interaction but by the 17th day the mother always does so. In many cases this termination simply involves a forward movement on the part of the mother, with or without lifting of the hind leg, or, particularly in response to bunting, a swinging of the rear quarters away from the nursling. In other species there is an increasing tendency for mothers to terminate nursing or prevent suckling attempts with agonostic behavior. Kurt (1968) notes the first use of the hind legs in the roe deer at three to five weeks post-partum. Threat gestures involving head presentations are described for kudu but do not occur in sitatunga (Walther, 1964). I have observed similar threat presentations in caribou and lechwe, and with great frequency in muskoxen beginning when the calves are about 2 months old. Such maternal terminations may be viewed as a part of a general trend leading towards total weaning. This subject is dealt with further in section VII.

When siblings are involved, nursing behavior may be altered in comparison to that of singlets. Considerable information is available on this subject with regard to domestic species, Hafez and Lineweaver (1968) found that Hereford twins suckled 11 times a day in comparison to 4 to 6 times daily for singlets. Ewbank (1967) found, as did previous workers cited by him, that twin lambs also suckle more frequently than singlets. Many ewes will not permit suckling until all siblings are present and sows will apparently delay milk letdown until all litter members are in position (Porzig *et al.*, 1969; Hafez and Signoret, 1969). Among sheep fixity of relative position by siblings during nursing does not seem to be as well developed as in swine. However, the literature is conflicting on this point (see Ewbank, 1967).

Ungulate infants frequently attempt to suckle from females other than their own mothers. However, very little information is available on their success rates in this regard, particularly in unconfined wild populations. In the course of several hundred observations of caribou nursing I could only twice confirm that calves briefly suckled from strange cows. After a few seconds they were chased by these females. McCullough (1969) observed such nursing only once in his study of wild Tule elk.

Such suckling was observed to be frequently successful in a captive group of chital reported on by Schaller (1967). In a captive reindeer herd maintained at Cantwell, Alaska, in a small pasture, a 4-month-old calf was found to be obtaining 15 per cent of its milk supply from other cows. This was determined by radio-isotope tagging (Holleman *et al.*, 1971). Espmark (1971) describes in detail the prevalence of what he refers to as 'thief-sucking' in a Swedish reindeer herd. Suckling attempts were susceptible to social facilitation so that up to three calves were observed to suckle simultaneously from the same cow. This phenomenon was most pronounced when the calves were 5 weeks old. One calf specialized in such nursing, accounting for 78% of the 'thief-sucking' in a herd with five calves. An okapi in captivity was also nursed by two cows (Grzimek, 1958). This is extremely rare among gazelles, even in captivity, according to Dittrich (1968) who has observed it only once in the Gazellinae, by a Soemmering's gazelle. This author reports it to be more common in captive greater kudu, Lady Gray Waterbuck, suni, bushbuck, and dik-dik, as well as in the goats and sheep generally. Great maternal tolerance in this respect is also described in captive giraffe by Dagg (1970).

Frärich (1965) describes two captive Warthog mothers sharing the same nest and nursing their young together without discrimination. J. F. Eisenberg (pers. comm.) reports similar observations for wild boars in Ceylon. This communal nursing is similar to that described for certain carnivores and rodents. Sayler and Salmon (1971) have shown that mice raised communally exhibit higher growth rates than those suckling only their own mothers.

Distinct rhythms in nursing activity develop in many species after the post-partum period but seem to be most pronounced in the hider species. Early morning and evening peaks are described in mule deer (Linsdale and Tomich 1953), lechwe (Lent, 1969) and kob (Leuthold 1967). A less distinct three peak rhythm is described for red deer by Bubenik (1965). Mothers with multiple young will frequently not permit suckling unless all offspring are present. Ewes will sometimes call the missing lamb (Ewbank, 1964) and similarly sows call or gather resting members of their litter together for nursing (Hafez and Signoret, 1969).

## VI. INDIVIDUAL RECOGNITION, BOND FORMATION AND IMPRINTING

It has long been known that ungulate mothers and their infants form closed social bonds to the exclusion of other individuals. This occurs even in those species which otherwise maintain open social groupings throughout the year. Frequently the suggestion has been made that precocial mammalian species, ungulates included, rapidly form such bonds through a process similar or identical to imprinting as initially described in birds by Lorenz (1935)(see Grabowski, 1941 and Hess, 1959). Only recently has any experimental work been carried out with ungulates to explore the nature of the mother-infant bonds and the sensory bases for individual recognition.

Circumstantial evidence indicating individual recognition by auditory means has been mentioned with regard to several species, including Dall sheep (Murie, 1944), caribou (Lent, 1966), bison (Marjoribanks-Egerton, 1962) and cattle (Schloeth, 1958). I have unpublished observations indicating similar recognition in both bison and muskox. Reindeer herders may expose neonates to human calls so that they can more effectively call the calves to follow when they are older (Zhigunov, 1961). Markgren (1966) reports that hand-raised moose calves learned to distinguish their keepers' voices from others.

Haas (1959) experimented with playbacks of lamb bleats to Barbary sheep mothers. He noted a general excitation of all mothers with young lambs but no clear cut evidence for individual recognition of the playbacks. Tschanz (1962) carried out similar experiments with mouflon and obtained similar results. Mothers reacted most strongly during the first three days following parturition, which apparently coincides with the hiding phase in this species in the wild (Pfeffer, 1967). With the playback of maternal calls lambs were more likely to respond to their own mother's vocalizations. Smith (1965) reports attracting five ewes to recordings of their own lambs made on their second day of life. Such recordings were effective only when the ewes were standing apart from their offspring. It is not stated how these ewes reacted to recordings of other lambs. Kurt (1968) obtained a positive reaction (alertness and seeking of sound source) from all roe deer mothers in response to playback of their own offsprings' alarm cries but also received positive reactions in the majority of cases to an imitation of the same vocalizations made by blowing on a reed of grass. More recently Espmark (1971 and in press) has performed some playback trials with reindeer cows also indicating ability for individual recognition. Ericson (1971), on the other hand, found no evidence for individual recognition by auditory means in reindeer.

Naturalistic studies have also indicated an important role for olfaction in the process of individual identification especially by the mother. In many species it has been observed that females make nasal contact with the nasal or anogenital areas of offspring. When confusion occurs they will 'test' several successive infants before driving off the strangers or moving off with their own offspring. I have described this process in caribou (Lent, 1966), and M. Altmann (1963) illustrates it with a photograph of two elk mothers and their calves. Tschanz (1962) demonstrated experimentally that mouflon ewes are able to distinguish their own lambs by olfaction as early as 12 hours post-partum. This is accomplished primarily by smelling the anal region. Tschanz suggests that perianal glands are involved.

Working with goats, Klopfer and Gamble (1966) and Klopfer and Klopfer (1968) have performed experiments on the role of olfaction in the formation of permanent mother-kid bonds. Mothers made anosmic by injections of cocaine at the time of parturition later accepted any kid presented to them when they were again rendered anosmic. On the other hand females with unaltered olfaction at birth but which were later cocainized rejected strange young but not their own young when these were presented. Alien kids were accepted if presented for five minutes at the time of parturition. Klopfer and Gamble (1966: 592) concluded that 'an olfactory experience at birth is not a requirement for the manifestation of maternal behavior.' It is however, a requirement for bond formation. They suggested the existence of a sensitive period perhaps having as its hormonal basis the changes in oxytocin levels associated with parturition. Does whose own young were removed shortly after birth reaccepted them if in the meantime an alien kid was available for interaction. Inputs from other senses including gustation were not controlled in these experiments. In later experiments Hemmes (1970) found that oxytocin treatments and vaginal distensions had no statistically significant effect on doe responsiveness following separations. There were subtle effects of the vaginal distension treatment meriting further investigation. Alexander (1960) also found that oxytocin treatments did not reduce desertion or improve maternal behavior among ewes that were poor mothers.

Smith *et al.* (1966) separated ewes from their lambs immediately after birth, collected all fluids and membranes on plastic sheeting, and used other measures to minimize olfactory influences. The ten ewes were kept in isolation for varying periods up to eight hours post-partum. Nine of these accepted their lambs when they were returned. Experiments with seven other ewes involved interchanges of lambs. In each case the first lamb presented after parturition was accepted. A period of 20 to 30 minutes for licking and contact with the lamb seemed sufficient for the establishment of a permanent attachment. Under the experimental conditions, isolation of the lambs for up to 8 hours seemed to have no significant affect on their physical well-being. Techniques for removing and disguising odors and transferring odors to infants for purposes of fostering have long been in use by sheep and goat herders. Some observations on this subject are reviewed by Herscher *et al.* (1963a). Application of a potential foster mother's milk on an infant has proven successful. Smith (1965) mentions that ewes were attracted to clothes soaked with their own amniotic fluid but not to those impregnated with fluids from other females.

Visual recognition is less amenable to experimental minipulation and the information on this subject is correspondingly less precise. Tschanz (1962) reported that lambs correctly identified their own mothers visually in 163 out of 195 events and that mistakes were rare after the 11th day. Whether this identification is based on individual physical characteristics or on perception of specific maternal behavior patterns (such as Schloeth, 1958, describes in the Camargue cattle) is not clear. Smith (1965) stated that vision was of minor importance in recognition of lambs but Lindsay and Fletcher (1968), who experimented with ewes in a T maze, concluded that sight was the only sense essential for recognition under these experimental conditions. With goats it has been noted that substitutions or adoptions are less likely to be successful when the kids are of different coloration (Blauvelt, 1956; Collias, 1956).

The mother's bond with her infant is not absolutely fixed, as evidenced by the occurrence of adoption following the loss of her own infant. There are few data on this subject from studies of animals in the wild. Bubenik (1965) believes that multiparous mothers are more likely to accept strange young than females of monoparous species. More evidence is required to establish the validity of this generalization. Caribou cows, including a few with young of their own, may frequently be seen attempting to lure other calves away from their mothers (Lent, 1966). Pruitt (1960) believes that adoptions are frequent in this species but presents no data to support this. Kurt (1968) found that adoptions were not successful with roe deer if the strange fawn was of a different age from the mother's own offspring. There are numerous references in the literature to yearlings being permitted to nurse if a mother loses her offspring of the year (see section VII).

In another study Herscher *et al.* (1963b) removed the offspring of ewes and does after they had at least two hours of post-partum contact. Alien young of varying ages were later introduced to the mothers. By using stanchions and restraining harnesses to restrict the aggressive behavior of the mothers adoptions were eventually affected. An average of 10 days was required for this.

Long-term fixations of maternal behavior may also be possible. There is an interesting account in Knorre (1961) of a moose cow whose calves were removed each year so that she could be milked by hand. When she was allowed to keep her third offspring she rejected it violently, killing it with her forefeet. She later went to her usual milk-maid, vocalized as moose do when calling-out a calf, and licked the woman's face and hand.

The process of bond formation or imprinting is obviously different for the infant and its mother compared to the mother and her infant. The bond forms very rapidly so far as the mother is concerned. Five minutes may be sufficient for goats and 20 to 30 for sheep. I have estimated that one hour is necessary for formation of a strong bond in caribou so that the mother will diligently seek reunion with her calf after the two are separated for tagging purposes (Lent, 1961, (1966). Prenzlow (1964) suggests that as much as 6 hours may be required for this purpose in pronghorns. Apparently in hider species, such as the pronghorn, the post-partum period of intensive contact serves to develop the bond so that the female responds selectively to her own infant after separations, returns to it, and remembers its location. It seems appropriate to refer to the time span necessary for formation of this bond as the 'critical period'. This should be distinguished from the maximum time period after parturition during which a bond may be formed even though its initiation has been delayed. This sensitive period may be as long as 8 hours in sheep (Smith, 1965; Herscher *et al.*, 1963b).*

In contrast to this rapid formation of the maternal bond, the fixation of the infant's association with its mother is a slower process. Kurt (1968), for example, indicates this critical period extends over 2 or 3 weeks in roe deer and Bubenik (1965) suggests an even longer period. The behavior of infants remains opportunistic and if the mother is not readily available an alternate will be sought, as I have described when dealing with nursing behavior.

Mothers play an active role in strengthening and maintaining maternal-infant bonds by driving away strange infants that approach them. This process has been described for many species, including mountain goats (Lentfer, 1955), red deer (Bubenik, 1965), zebra (Wackernagel, 1965) caribou, Lent, 1966), feral goats (Rudge, 1970) and mountain sheep (Geist, 1971a). In other species it is seen only rarely, as in Barbary sheep (Haas, 1959) and the genus *Tragelaphus* (Walther, 1964). It is apparently unusual for mothers to defend their young, as opposed to the space around their own bodies (Lent, 1966; Kramer, 1969). Ungulate mothers rarely react to intra-specific aggression when their offspring are outside of this sphere of protection. The most frequent exceptions to this statement involve maternal efforts to disrupt play activities of their offspring and other infants. Couturier (1962) describes this in ibex, Pitzman (1970) in Dall sheep, Geist (1971a) for mountain goats and I have frequently observed it in muskoxen.

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* See Sluckin (1970) for a discussion of the terms 'critical period' and 'sensitive period'.

There is considerable confusion in the literature, both technical and popular, regarding the terms 'following response' and 'imprinting'. Frequently the two have been used as equivalents (Forrester and Hoffmann, 1963, for example). An observation that a young ungulate follows a moving man or other object (such as those cited in Section IV) is not sufficient evidence for imprinting. It is the strong innate tendency to follow which aids the formation of a bond, that is, among ungulates, the generalized following response leads to the formation of an object-specific following response. Hess (1959) has suggested that the strength of the imprinting process is proportional to the amount of effort expended in following the object of imprinting. While such effort may facilitate the process it is not essential. Cairns and Johnson (1965) and Cairns (1966) described the formation of bonds between lambs and dogs under conditions of confinement where neither following nor physical contact were possible Such bonds of association were found to be reversible. Four lambs which had formed bonds with dogs were then placed with sheep for 4 months. After this period when placed in a choice situation they chose to associate with conspecifics rather than with the dogs in 93% of 30 trials. However, these lambs had been initially exposed to their mothers before being placed in association with dogs. The irreversibility of imprinting in birds has also been questioned (Salzen and Meyer, 1968).

## VII. WEANING AND THE BREAKDOWN OF MATERNAL-INFANT BONDS

In comparison to the experimental studies and many detailed observations that have been made on the subject of ungulate parturition and bond formation, there is available almost nothing on the weakening of the mother-infant bond and the weaning process. What little is known is mainly based on captive animals and thus extremely questionable, or based on chance rather than systematic observations. The opportunities for further work in this field are enormous.

One indication of the start of weakening of maternal-infant relationships is the formation of peer groups or creches. Murie (1944) mentions the occurrence of such groups in elk, M. Altmann (1960) in bison, Bubenik (1965) in red deer, Harper *et al.* (1967) in elk, Schenkel (1967) and Fraser (1968) in impala, and Geist (1971a) in mountain sheep. Although communal sharing of maternal duties has been suggested for some of these species, the actual events involved in these cases have not been adequately described. From an early age muskox calves spend much of their active time with peers and away from their mothers in spite of the fact that they are extremely contact-prone animals, with offspring, mothers and even other adults often resting in contact or very close proximity. I have never had the impression that one female was 'guarding' these peer groups, nor did Geist observe this in sheep. The factors leading to the formation of such peer groups requires further investigation. In the red lechwe, calves have a very loose association with their mother from an early age yet such groups are rarely seen (Lent, 1969).

The weaning process involves gradual and reciprocal changes in the behavior, anatomy and physiology of both mother and offspring, as has been described so well in studies of the domestic cat (see Schneirla *et al.* 1963).

As I have already described, the infant behavior pattern of bunting is associated with weaning in ungulate species. Presumably this activity is an indicator of the reciprocal changes taking place in both mother and infant. As the infant develops in capacity and motor ability it apparently draws out milk with increasing rapidity. At the same time the mother's milk production may be dwindling. The infant seeks to obtain more milk by vigorous efforts which in many species appear to result in discomfort and even pain to the mother. The result is aggression towards the offspring or, at very least, withdrawal with increasing regularity.

Among domestic sheep weaning is said to be completed when the young are between 3 and 6 months old, according to Fraser (1968), but his cited references do not seem to substantiate this. Similarly, Couturier (1962) states that ibex are frequently weaned by three months. Geist (1971) states that suckling was rarely observed in November among Canadian mountain sheep. This suggests weaning occurs at four to five months. Bubenik (1965) believes that weaning of red deer is complete by mid-October. Severinghaus and Cheatum (1956) give November as the normal end of nursing in white-tailed deer. Hanson (1958) cites Einarson's conclusion that mule deer fawns are weaned by 5 months but he observed a nursing attempt by a 9 month old fawn. Four to five months is considered the end of the nursing period in axis deer by Graf and Nichols (1967). Weaning occurs between 6 and 8 months after birth in Defassa Waterbuck (Spinage, 1969). In smaller ungulates suckling may cease at an earlier age, especially in those that may breed twice annually. Hendrichs and Hendrichs (1970) report that dik-diks nurse little, if at all, after the sixth week. On the other hand, I have observed and filmed caribou calves nursing as late as March (nearly 10 months old), Tener (1965) suggests that prolonged lactation in muskoxen (he believes it may continue for 15 months) is a behavioral adaptation for Arctic survival. However the introduced muskox on Nunivak Island Alaska appear to be weaned much earlier and females there may be having calves in consecutive years (Spencer and Lensink, 1970; Lent, in press). Among desert ungulates, the dromedary in particular, Pilters (1956) has observed lactation prolonged for 24 months or more. On the other hand, Couturier (1962) believes that observations of ibex calves suckling through the winter are most common in winters with better than average grazing conditions. There is a great need for further information regarding winter nursing and environmental effects on lactation. We also need to know the minimum amount of suckling required to maintain lactation. Darling in the 1956 edition of his 1937 book adds this comment:

> "... such few December milk hinds as I have examined have certainly had milk and many stalkers have supported this finding. I have known mares living out with no more adventitious food than hay to lactate from foal to foal, an interval of a year. The quantity of milk may be very small, and in the case of the mares, I know it was very small, but I believe it has a value for the young animal quite out of proportion to quantity.'

Suckling by yearlings has been described in a wide variety of species, especially cervids. Hanson (1958) reports a one month old fawn and a yearling simultaneously being nursed by a mule deer mother, and Perry (1952) describes a similar episode in red deer. Observations of this nature are unusual and most commonly nursing by yearlings occurs only after loss of the offspring of the year (Altmann, 1960; Couturier, 1938, 1962; Bubenik, 1965, Lent, 1966; Geist, 1971a).

Differences in weaning age and duration of the mother-infant bond relatable to the sex of offspring are described for several species including black-tailed deer (Dasmann and Taber, 1956), wildebeest (Talbot and Talbot, 1963), red deer (Eygenraam, 1963), roe deer (Bubenik, 1965; Kurt, 1968) and impala (Fraser, 1968). I have suggested (Lent, 1966) that such a sex-dependent differential may be responsible for the fact that few adult male caribou complete the traditional spring migrations and enter the calving areas.

While there is probably a general tendency for young males to show stronger exploratory behavior, attitudes of mature males may also be more likely to drive male offspring away from females at breeding time. In addition, precocial mounting and sexual play by young males generate maternal antagonism, as Eygenraam (1963) has described. In his review of mounting behavior by infant ruminants Sambrous (1970) found a general tendency for males to perform such activities more frequently than females. However, M. Altmann (1963), among others, reported such activity to be performed equally by both sexes. She believed mounting attempts function to attract maternal attention to the offspring. In red lechwe such mounting always evoked maternal withdrawal or aggression. Kurt (1968) believed that maternal aggression was not a significant factor in bond breakdown because such aggression was directed with four times greater frequency towards female fawns. Nevertheless, these remained with the mother far longer.

Weaning and bond breakdown are not synonymous. Close, functional social relationships between mothers and their offspring continue far beyond the time of weaning. Darling (1937) believed that matriarchal groups exist in red deer which may contain four generations of females. In other species in which these associations exist (see Gosling, 1969, for example), they do not include more than three generations so far as is known. Such lasting bonds between females may be disrupted at parturition time but renewed later (M. Altmann, 1963; Dasmann and Taber, 1956; Pfeffer, 1967; Kurt, 1968; Rudge, 1970).

## VIII. FUNCTIONAL AND EVOLUTIONARY ASPECTS OF MATERNAL BEHAVIOR

The most obvious benefit to the infant that we associate with maternal care is the nutritional one. Closely related to this, during the first days of infancy at least, is the provision of passive immunity which in ruminants and most other ungulates can be obtained only post-partum through the colostrum and milk (Brambell, 1958). The role of the mother in aiding neonate thermoregulation either directly by contact or indirectly by licking and drying has already been discussed. An active role by the mother in assisting her neonate in traversing difficult terrain has been described by Couturier (1938, 1962) in the chamois and ibex, and Pitzman (1970) in Dall sheep. Hediger (1965) relates the observation of C.G. Manuel that the Mindoro tamarau will lift and carry its infant. While this requires confirmation, there have been many observations of lifting attempts among elephants (Winter, 1964, for example). This also recalls to mind the observation related by Pallas (1781) that Siberian reindeer moved in such concentrated and enormous herds that the fawns were able to move on top—from back to back!

Predation is a major force which has molded maternal behavior and social behavior in general in ungulates. I am currently putting together a more complete review on the subject of ungulate responses to predators. Here I wish only to cite a few of the many observations of successful maternal defense of offspring against mammalian predators: Dixon, 1928 (mule deer v. coyote), Seton, 1929 (elk v. coyote: coyote killed), Murie, 1944 (Dall sheep v. wolves, moose v. sled dogs), Tener, 1954 (muskox v. wolves), Geist, 1963 (moose v. black bear), Mech, 1966 (moose v. wolves: several times), Estes and Goddard, 1967, and Lawick-Goodall, 1970 (zebra and wildebeest v. hunting dogs), Haber, 1968 (moose v. wolves), Woolf and O'Shea, 1968 (bighorn sheep v. coyotes), Van Wormer, 1968 (pronghorn v. coyote), Hornocker, 1969 (bighorn sheep v. bobcat), Anon., 1969 (zebra v. hyena and impala v. jackal), and Eaton, 1970 (warthog v. cheetah).

Observations of such active defensive measures are only the part of the iceberg above water. Much more important but less easily evaluated are the efforts of mothers to hide their offspring and lure predators away or confuse potential predators by distraction (M. Altmann, 1963; Walther, 1965a, 1968).

Wide spacing of young siblings (Bubenik, 1965; Espmark, 1969; Van Wormer, 1968) and relative lack of odor in infants (Severinghaus and Cheatum, 1956; Graf and Nichols, 1967; Van Wormer, 1968; McCullough, 1969) have both been mentioned as adaptations promoting survival of hider type young. Related to the latter aspect of odor is the associated maternal tendency to devour the placenta and the neonate's feces. This tendency is absent or only weakly developed in follower types.

I view the behavior complexes of hiding and following as two grand strategies for the protection of infant ungulates. The hiders take advantage of dense cover and topography to seclude the infant and minimize the chances for contact with both predators and conspecifics. The species-typical distances which are maintained between the mother and her offspring during this phase presumably represent compromises between the advantages of close contact and maternal care and the advantages of separation, the latter particularly in reference to minimizing predation.

Among the Cervidae the hiding behavior is nearly universal, the single important exception being the caribou (and reindeer). Among red deer there appears to be a definite shortening of the hiding phase and weakening of associated traits in comparison to closely related species. The moose also represents an interesting case with some flexibility in behavior as I have already mentioned. When the moose calves are very young the mother, when disturbed, may elect to remain apart from them and give no clue as to their location (Flerov, 1952; LeResche, 1966). I have observed a moose cow repeatedly frightened by helicopter overflights. The cow left her young calves without hesitation and remained away for several minutes after each disturbance. The calves made no attempt to follow her. When they are older however, the survival of the calves is clearly aided by extremely close following and contact with the mother (Murie, 1944; Geist, 1963; Mech, 1966).

The hiding phase may also serve to protect the infant from intraspecific encounters until it has reached a desirable level of development. Such a function could be expected to be most important in those species, such as dik-diks and duikers, which maintain family groups on territories defended by the male. Such protection might be most critical in species where mating occurs soon after parturition. The Malayan chevrotain is an example of such a species. Davis (1965) and Tubb (1968) report all copulations in captivity occurred 48 hours after parturition. Later the male frequently rests near the fawn.

Sowls (1966) cites literature on the post-partum heat in domestic sows and mentions a captive collared peccary that was mated 12 days after farrowing. Morrison and Buechner (1971) report post-partum estrus in the Uganda kob. Dubost (1971) observed mating attempts by muntjak two days after parturition and successful copulation on the fourth day post-partum. Gardner (1971) describes a post-partum estrus in the red brocket deer. I suspect that post-partum breeding may be far more widespread than has been reported, especially in the smaller, 'primitive' tropical forest ungulates, among which the hiding behavior must have originated.

The follower type is associated with open alpine, steppe, tundra or savannah habitats. Even such nominally open habitat can provide considerable cover, especially for the smaller ungulate species. Larger species are not only less able to utilize low cover but they are also more effective in providing defense, especially against the smaller secondary predators. Infant ungulates in open alpine habitat are particularly vulnerable to large avian predators. The effectiveness of close contact between the mother and her infant in such cases had been well documented (Murie, 1944; Perry, 1952; Couturier, 1962; Kramer, 1969; Pitzman, 1970; Geist, 1971).

Mobility is another quality that is associated with follower species. This may be either a distinct migratory pattern or a more variable movement which takes advantage of localized greening of vegetation, as with wildebeest (Talbot and Talbot, 1963). Altitudinal movements soon after birth are important in alpine species (Couturier, 1938). There must be strong selection for rapid development and frequent reinforcement of close mother-infant contact in such species. Formosov (1966) has described this type of social behavior among the highly mobile ungulate species of the Asian Steppes.

The importance for northern species of a mother-infant bond that extends through the winter months has been suggested by many authors (for example, Couturier, 1938; Denniston, 1956; M. Altmann, 1958; Espmark, 1964). Except for the data of Baskin (1970), no statistics are available from any study to provide concrete support for such contentions. Bromley and O'Gara (1967) found no winter mortality among orphaned pronghorns.

There is little evidence indicating that the chances for survival of ungulate young are increased by maternal instruction; even learning through imitation is difficult to establish although it has been suggested to be important in developing feeding preferences (Fraser, 1968). Transmission of traditions presumably occurs but here again concrete evidence is lacking.

What the ungulate mother appears to provide is the optimum environment for rapid development and learning. By this I mean that the infant is exposed to optimum levels of stimulation by the care-giving activities of the mother on the one hand and by the behavior patterns which shield the infant from extremes of social and non-social stimuli. A similar conclusion is reached by Harper (1970) in his recent review of mammalian parent-offspring relationships.

Much of the early behavior of infant ungulates can be interpreted as a seeking of optimum levels of stimulation. As I have discussed in a previous paper (Lent, 1966), the theoretical framework advanced by Schneirla (1959, 1965) for dealing with the early ontogeny of behavior in organisms seems especially useful in understanding the early maternal-infant interaction in ungulates. Schneirla divides early responses into two classes, 'approach' and 'withdrawal'. Approach tendencies are evoked by stimuli of relatively low intensity and withdrawal responses by stimuli of high intensity. This does not imply that the infant is merely a passive body nor does it imply that all will respond similarly to a given stimulus. Each species obviously responds differently in accordance with its own genetic attributes, sensory and other. Maternal behavior patterns promoting approach responses such as licking, soft vocalizations, head-bobbing and moderate movement presumably provide optimal stimulus levels in contrast to those which elicit withdrawal type responses such as loud vocalizations (or other noises, see page (47)) and sudden bounding motions. Experimental work with other mammals has established the effectiveness of optimal stimulus complexity in promoting approach responses (for example, Sales, 1968).

Ungulates are particularly responsive to movement in the visual field, as any predator, human or otherwise, knows. There is quite likely to be a genetically determined basis for this (Johnson *et al.*, 1969). The effectiveness of motion in maternal (and infant) behavior thus provides an unconditioned basis of great importance for later behavior and for maintaining approach responses, as has been described for other vertebrate groups (James, 1959).

In the precocial ungulate, learning processes very rapidly build upon the innate base. There is a massive body of experimental and theoretical information demonstrating the importance of optimal levels of stimulation in promoting rapid learning (Leuba, 1955; Gewirtz, 1961; Rheingold, 1961; Ambrose, 1969). Gewirtz in particular provides a cogent discussion of the importance of early following responses and subsequent fear-flight responses in promoting learning processes.

There are several references to abnormal social behavior in maternally deprived ungulates but in all cases it is impossible to separate effects of maternal deprivation from other forms of social deprivation. This is particularly so because almost all relevant material is based on follower types which normally enter into social interactions with conspecifics soon after birth.

Lemmon and Patterson (1968) have reported a positive relationship between maternal presence and performance of lambs in visual cliff experiments. Liddell (1958) and Moore (1958) found that maternal presence minimized the traumatic effects of training experiments on young lambs. Hemmes (1970) reported significant differences in 'open-field' tests with kids separated from their mothers for 2 1/2 hours postpartum.

Scott (1945) states that a lamb isolated for 9 days post-partum failed to develop fully normal social behavior. Gilbert (1968 and this volume) reports that hand-reared fallow deer exhibited abnormalities in their social behavior. Rossdale (1968) relates the occurrence of fear toward conspecifics in a hand-raised foal and D. McConnell (pers. comm.) has described the same result with a hand-reared muskox calf initially rejected by its mother. A hand-reared group of caribou calves showed initial signs of imprinting to humans but has now formed a successfully breeding wild population (Jones, 1966).

It might seem strange to conclude this section with a paragraph on the role of paternal behavior, however, I believe the subject has been neglected. There are several species in which males are indicated as playing a role in defense of their offspring. This paternal behavior occurs in mobile species which nevertheless maintain long-term familial organizations such as the vicuna (Pilters, 1956; Koford, 1957), the kulan (Formosov, 1966), the zebras (Klingel, 1967; Lawick-Goodall, 1970), and apparently the feral horse (Ryden, 1970). Paternal defense of offspring or territory directed towards both conspecifics and other species is also evident in the behavior of species which maintain long-term family bonds on fixed home ranges as has been described for klipspringer (Cuneo, 1965), dik-dik (Hendrichs and Hendrichs, 1970) and probably occurs in other species in which the father associates closely with his offspring, such as pudu (Vanoli, 1967), muskdeer (Egorov, 1965) and the Asiatic tapir (Seitz, 1970). The abnormal conditions of confinement are apparently responsible for the disdirection of paternal defense in zebras resulting in attacks of the offspring (Hediger, 1955; Walther, 1961b).

## IX. APPLIED ASPECTS

The many applications of behavioral knowledge regarding maternal-infant interactions in the livestock industry are discussed by Alexander (1960, 1961), Rowley (1970) and by several contributors in the volumes edited by Fox (1968), Hafez (1969), and Porzig *et al.* (1969). The proper management of animals in zoological gardens also requires an understanding of maternal behavior, as demonstrated by Hediger (1955) and Walther (1961b, 1965b) among others.

Application of such behavioral knowledge to the management of wild species is only beginning. Leuthold (1969) and Geist (1971b) have provided valuable summaries of this topic, but the game biologist is in great need of further information. For example, the effects of manipulations of young animals, as for tagging purposes, cannot be fully understood until we have a more precise understanding of the critical periods and related phenomena in many species. We are particularly lacking in understanding of the importance of maternal infant bonds later in ontogeny. The hunting of females is an increasingly common practice in North American big game management, yet there has been no systematic study of the effects of such hunting on orphaned offspring. Our Unit has just begun such a study with orphaned moose calves on the Kenai Peninsula. We are also examining the effects of man-made barriers on cow-calf bonds in caribou and reindeer, a study which Mr. Child describes elsewhere in this symposium.

Increasing human use pressure in wild lands will bring increasing needs for management of such use based on behavioral data as well as for proper habituation of ungulates to man in certain cases, as Geist (1971b) has suggested. For example tourist pressure in East African reserves may reach a point where significant neonatal mortality occurs simply from accidental disturbance. Lawick-Goodall (1970) has described the occurrence of such incidents involving zebra and wildebeest. The young of hider species are not exempt either. Kurt (1968) has described the high mortality among roe deer fawns in Switzerland caused by mowing machines. Recently travellers in East Africa have been warned against buying Thomson's gazelle calves being offered for sale. Most of these are captured during the hiding phase.

In Alaska we badly need more information of the effects of 'all-terrain' vehicles, snowmachines and aircraft on pregnant animals and infants. The muskox calf appears to be particularly susceptible to desertion caused by disturbance and a long critical period is indicated in this species (Lent, 1971). All our Arctic ungulates are especially prone to disturbance by helicopters. Noise pollution is becoming a very real problem and finding the solutions will require better understanding of behavior, both human and ungulate.

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## APPENDIX

| Common name | Scientific name | Common name | Scientific name |
|---|---|---|---|
| African Buffalo | *Syncerus caffer* | Lechwe | *Kobus leche* |
| Asiatic tapir | *Tapirus indicus* | Lesser kudu | *Tragelaphus imberbis* |
| Axis deer | *Axis axis* | Malayan chevrotain | *Tragulus javanicus* |
| Barasingha | *Cervus duvauceli* | Marco Polo sheep | *Ovis ammon* |
| Barbary sheep | *Ammdtragus lervia* | Markhor | *Capra falconeri* |
| Bighorn sheep | *Ovis canadensis* | Moose | *Alces alces* |
| Bison | *Bison bison* | Mouflon | *Ovis musimon* |
| Blackbuck | *Antilope cervicapra* | Mountain goat | *Oreamnos americanus* |
| Black rhinoceros | *Diceros bicornis* | Mule deer | *Odocoileus hemionus* |
| Black-tailed deer | *Odocoileus hemionus* | Muntjak | *Muntiacus muntjak* |
| Bontebok | *Damaliscus dorcas dorcas* | Musk deer | *Moschus moschiferus* |
| Brocket deer | *Mazama americana* | Muskox | *Ovibos moschatus* |
| Bushbuck | *Tragelaphus scriptus* | Nilgai | *Boselaphus tragocamelus* |
| Camargue cattle | *Bos taurus* | Okapi | *Okapia johnstoni* |
| Camel | *Camelus bactrianus* | Pere David's deer | *Elaphurus davidianus* |
| Caribou | *Rangifer tarandus groenlandicus* | Pronghorn | *Antilocapra americana* |
| | | Pudu | *Pudu pudu* |
| Cattle | *Bos taurus* | Red deer | *Cervus elaphus* |
| Chamois | *Rupicapra rupicapra* | Red Lechwe | *Kobus leche* |
| Chital | *Axis axis* | Reedbuck | *Redunca redunca* |
| Collared peccary | *Tayassu tajacu* | Reindeer | *Rangifer tarandus tarandus* |
| Dall sheep | *Ovis dalli* | Rocky Mountain goat | *Oreamnos americanus* |

| | |
|---|---|
| Defassa Waterbuck | *Kobus defassa* |
| Dik-dik | *Madoqua kirki* |
| Domestic mares | *Equus caballus* |
| Domestic ewes | *Ovis aries* |
| Dorcas gazelle | *Gazella dorcas* |
| Dromedary | *Camelus dromedarius* |
| Duiker | *Cephalophus sp.* |
| Elk | *Cervus canadensis* |
| European ibex | *Capra hircus ibex* |
| Ewes | *Ovis aries* |
| Fallow deer | *Dama dama* |
| Giraffe | *Giraffa camelopardalis* |
| Goat | *Capra hircus* |
| Grant's gazelle | *Gazella granti* |
| Greater kudu | *Tragelaphus strepsiceros* |
| Guanaco | *Lama guanicoe* |
| Ibex | *Capra hircus ibex* |
| Impala | *Aepyceros melampus* |
| Klipspringer | *Oreotragus oreotragus* |
| Kob | *Adenota kob* |
| Kudu | *Tragelaphus sp.* |
| Kulan | *Equus hemionus* |
| Lady Gray's Waterbuck | *Kobus megaceros* |
| Llama | *Lama peruana* |
| Roe deer | *Capreolus capreolus* |
| Saiga | *Saiga tatarica* |
| Sambar | *Cervus aristotelis* |
| Sheep | *Ovis aries* |
| Sika deer | *Cervus nippon* |
| Sitatunga | *Tragelaphus spekii* |
| Soemmering's gazelle | *Gazella soemmeringi* |
| Square-lipped rhinoceros | *Ceratotherium simum* |
| Steenbuck (steenbok) | *Raphicerus campestris* |
| Suni | *Nesotragus moschatus* |
| Swine | *Sus scrofa* |
| Tamarau | *Anoa mindorensis* |
| Thomson's gazelle | *Gazella thomsonii* |
| Tsessebe | *Damaliscus lunatus lunatus* |
| Tule elk | *Cervus canadensis nannodes* |
| Uganda Kob | *Adenota kob* |
| Vicuna | *Vicugna vicugna* |
| Warthog | *Phacochoerus aethiopicus* |
| Waterbuck | *Kobus ellipsiprymnus* |
| White-tailed deer | *Odocoileus virginiana* |
| Wildebeest | *Connochaetes taurinus* |
| Wisent | *Bison bonasus* |
| Zebra | *Equus burchelli* |

Paper No. 2

# Some Reflections on Expressive Behaviour in Combats and Courtship of Certain Horned Ungulates

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## ABSTRACT

The importance of expressive behaviour in its theoretical and practical aspects as well as some problems of definition, classification and certain theoretical conceptions are discussed. The following operational definition is suggested:

Expressions which function in social communication, are the outward manifestations of an animal's momentary psycho-somatic state. They are addressed to an actual partner (usually a conspecific) and are aimed at releasing adequate responses above the level of contagious effects, without influencing the partner mechanically and without the performer leaving the partner's vicinity.

The paper is focused on postures and gestures and, within this realm, on major coordinations. Under the heading of intraspecific aggression and sexuality, it is suggested that expressive behaviour be classified into threat displays, dominance displays, courtship displays, submissive displays, displays of space claim, and excitement activities. The discussion of these displays presents the phenomena, their meanings, the effects upon the recipients, and the social and biological functions.

Most of the phenomena can be interpreted as ritualized intention movements and symbolic actions. The body orientation towards the partner seems to be an original and basic component in many expressive postures and gestures. Especially difficult and interesting problems arise in respect to behaviour patterns which apparently have changed their meaning and their function during phylogenetic evolution.

In order to determine the meaning of an expressive behaviour, one has to investigate its connections and relations to other behaviour. This means that one has to be familiar with the entire behaviour inventory of the species under discussion and sometimes also with the behaviour of related species. The effects upon the recipient become obvious from a study of the partner's responses. Insight into the social functions can be obtained by analysing the releasing situations under which a given expressive behaviour may occur. Since all three aspects are related to one another, it is possible to test the correctness of one of these points (e.g., the meaning) with the help of the other two (e.g., the effects and the functions).

In this way, it becomes evident that each expressive behaviour has basically only one meaning, usually two (dichotomous) effects, but multiple social functions. These multiple functions determine the importance of expressive behaviour in the social life of the bovids.

## INTRODUCTION

Many ungulate species are gregarious. Certainly, a knowledge of their social life is very important for a better understanding of the biology of these animals. However, there are also some social interactions, for example fighting, mating and nursing the young, in more solitary living species. Social life is always based on the communication between the partners. In the animals under discussion, expressive behaviour is one of the most important factors in social communication. Thus, the study of expressive behaviour is fundamental to any investigation of the social behaviour of these species.

With expressive behaviour the animal indicates what it is going to do next and what it expects the partner to do. Therefore, knowledge and observation of expressive behaviour becomes important for predicting the actions of an individual or a group. Predicting what an animal will do in the next moment, is often of practical importance.

Such knowledge of expressive behaviour requires patient and thorough observing. The latter point is essential in the training of every person who has to deal with wildlife. Only in this way can he become familiar with the animals, learn to understand them, and know when to keep his hands off and when to take necessary action. I dare say that an ethologist, a conservationist, a game warden or a zoo keeper (to name only some of the professions concerned) is only as familiar with his animals as his knowledge of their expressive behaviour goes.

Finally, the expressive displays of animals are often of great aesthetic appeal. Their description and presentation is a very good way to raise and to keep the public's interest and sympathy in animal conservation.

## SOME THEORETICAL CONSTOERATIONS

Having pointed out briefly why I think that research and knowledge of expressive behaviour is important for scientific and practical purposes, I wish to discuss a few theoretical problems.

The first problem is to find an operational definition that allows us to determine which behaviour pattern is of direct concern to our study, and which behaviour is outside the realm of our immediate interest. Such a definition is also the first step towards a classification of behaviour which is needed to avoid an almost Babylonian confusion of terms in the behavioural sciences where often the same words are used for phenomena on very different levels of integration.

As Leyhausen (1967) has pointed out, expressive behaviour is not restricted to social life but is a more general phenomenon. Taking into consideration only those definitions which are applicable to animal behaviour, there have been two heroic attempts by outstanding scientists to define expression in its general sense. Hediger (1954, English edition 1968) defined expression to be 'all the variable, non-pathological phenomena of the animal which help to an understanding of its situation'. Leyhausen (1967) said: 'Expressions are those changes in the effector system of an organism which are brought about by those of the tendencies involved which are in the minority.' ('Ausdruck sind jene Veränderungen im effektorischen System eines Organismus, welche die jeweils in der Minorität befindlichen Tendenzen hervorrufen.') Used in such a broad sense, the term 'expression' becomes more or less synonymous with "behaviour'. Regardless of their merits, these two definitions are too broad, especially when one has an approach towards a classification of behaviour in mind.

Other authors tried to restrict the term 'expression' to social life. Schenkel (1947) defined expression as being '... the function of structures whose biological meaning is to contribute to communication in social life by influencing the mood or by releasing a reaction.' ('Ausdruck ist die Funktion von Strukturen, deren biologischer Sinn es ist, durch Stimmungsübertragung bzw. Reaktionsauslösung an der Steuerung sozialen Zusammenlebens mitzuwirken.') Eibl-Eibesfeldt (1957) rightly criticized this definition as still too broad because it included all those behaviour patterns which may occasionally have contagious effects. In part, this is linked with the problem that expression may be a phenomenon (a special posture, gesture, sound, etc.) but it also may be an epiphenomenon. In the latter case, it is not the behaviour pattern *per se* that is bearer of the expression but the mode in which it is performed. Since this may happen with almost any behaviour, the suggestion to restrict the discussion primarily to the phenomena is very understandable. Taking this aspect into account, Lorenz (1951) and after him Eibl-Eibesfeldt (1957), suggested 'to speak about expression only when a behaviour serving co-ordination in social life has become differentiated; this demonstrates its essential importance for this particular social function'. ('... nur dann von Ausdruck zu sprechen, wenn ein Verhalten im Dienste der Koordination sozialen Gemeinschaftslebens besondere Differenzierungen bekommen hat; denn diese beweisen, dass die soziale Funktion die wesentliche Leistung der fraglichen Bewegung 1st.') In short, all these authors tried to restrict the term expression to the social life of animals. When one is interested primarily or exclusively in social problems it is absolutely necessary to make such a restriction. However, one has to be aware that: (a) the expressive behaviour functioning in social communication is only a section of expressive behaviour and that there are transitions between social and non-social expression, and (b) the mention of the function, necessary as it may be, does not make the definition. A subject *and* its function are two different matters. First of all, one has to define the subject, then one may add some remarks on its function for a more detailed explanation.

Taking this principle into account, we must say that all the definitions mentioned above have failed. Moreover, not one of them enables us to make a distinction between expressive behaviour and non-expressive behaviour in the social realm, but all of them are applicable to non-expressive behaviour as well, such as fighting, sexual mounting, nursing and cleaning the young, etc.

In trying to approach an operational definition for that section of expressive behaviour which is of special importance in social life, I would like to combine parts of Hediger's and Schenkel's definition with some of my own ideas (Walther, 1958b and 1968a). I suggest:

Expressions which function in social communication, are the outward manifestations of an animal's momentary psycho-somatic situation. They are addressed to an actual partner (usually a conspecific) and are aimed at releasing adequate responses above the level of contagious effects, without influencing the partner mechanically and without the performer leaving the partner's sphere of action.

Unfortunately, nowadays we live in such a confusion of terms that it would not be a luxury to explain and to justify the use of each single word in this definition to avoid misunderstandings. At least, I will interpret two phases.

'Outward manifestation' is meant to be synonymous with phenomenon in the original meaning of this word. It is something which appears outside, at the surface of the animal's body, and it can be seen, heard, smelled, or touched in the intact animal.

With respect to its function in social life, the mention of this outward manifestation must be completed by the statement that the effect upon the partner is brought about 'without influencing him mechanically'. A phenomenon is anything which appears and can be observed. For example, a fighting movement is also a phenomenon; however, it is not an expressive behaviour. It is a characteristic of expressive behaviour (e.g., a threat) that it has the same or very similar effects as a non-expressive behaviour (e.g., a fight) but without influencing the other mechanically. Admittedly, we may run into difficulties when applying this part of the definition to tactile expression; however, tactile expression is so poorly understood that we are obliged to exclude it from the discussion at present.

Unfortunately, the classification of expressive behaviour is as difficult as the definition of expression itself. It is an old and good rule to name the behaviour patterns according to the phenomena, but not according to their functions because the latter already include interpretations. Relatively easily one can apply this principle to the fixed action patterns. Then, however, under the headline 'expressive behaviour', we have a collection of rather heterogenous fixed action patterns which obviously need some tighter classification. Unfortunately, there have been only two approaches towards classifying these important behavioural intermedium categories: von Uexküll's (1921) functional circles (Funktionskreise) and Tinbergen's (1951) major instincts. These hypotheses have been held up to now with some additions and modifications, and so we may talk about the functional circles or major instincts of sexuality, territoriality, behaviour against predators, parental care, etc. Certainly, these functional circles may bring a certain order into a chaos of phenomenea, and they may give the titles for papers, books, or chapters in a book. On the other hand, they may lead us into confusion because it is quite common for one and the same behaviour pattern to serve two or more functions and thus it may show up in several, different functional circles. As a result, there have been many arguments as to which functional circle or major instinct, respectively, gave rise to a given behaviour, which often resulted in rather questionable conclusions. Perhaps the situation may improve somewhat when we establish functional categories other than the classical functional circles which either may replace them or may be taken as sub-categories of them.

At present, such a classification would suffer from the confusion in the literature over an expressive behaviour's meaning, its effect upon the receiver, and its function in social life. One could say that the meaning is the function of the expressive behaviour, that the effect upon the addressee is the function of this meaning, and the resulting consequence in the social life may be called the function of both. Thus, it is possible to use the same word, 'function', for three completely different levels.

Under the heading of intraspecific aggression and sexuality, I suggest that expressive behaviour be classified into threat displays (Drohverhalten), dominance displays (Imponierverhalten), courtship displays (Werbeverhalten), displays of space claim (Raumanspruchsverhalten), submissive displays (Demuthaltungen), and excitement activities (Erregungshandlungen).

On the present paper, aside from the restrictions given by our operational definition, I will focus the discussion on postures and gestures, and largely neglect acoustic, olfactorial and tactile expressive behaviour. There is not too much known about these latter three and/or some of them require a rather special presentation. Furthermore, not all the movements in question are equivalent. Tembrock (1963) distinguished between major' coordinations (Grundkoordinationen) and accessory coordinations (Rahmenhandlungen). I consider movements and postures of the body, the neck, the head, and the legs to be major coordinations, and I will focus the presentation on them, while I will neglect largely the accessory coordinations which may occur in combination with them (e.g., movements of the eyes, the ears, the mouth, the nostrils, the tail, etc.).

Finally, it seems advisable to add some remarks on certain, in my opinion, erroneous conceptions which still influence the ethological literature on expressive behaviour. These conceptions go back more or less directly to the displacement hypothesis (Tinbergen, 1940). It in turn was based on the hypothesis of the functional circles which, at least in its strict and literal sense, has become somewhat dubious, as discussed above. Secondly, it envisioned an energy model as the underlying physiological mechanism. This model has become increasingly dubious during the last 20 years, and as Hinde (1966) states, '... for casual analysis, the term (displacement activity) can no longer be used.' On the other hand, this author and with him apparently a good many other ethologists, think that '... for the field worker, concerned with the initial descriptive phase of behaviour..., it will undoubtedly continue to be useful.' I disagree with this opinion because (a) the use of the term 'displacement' brings us back to the functional circles again and again, and (b) this term is not descriptive at all, but is clearly derived from the mentioned energy model. Moreover, the decision as to which behaviour pattern has to be considered as a displacement activity does not only depend on the observer's immediate, subjective impression—in case of a qualified observer, I would still be ready to accept this—but on his reflections and theoretical belief. Practically, this means that everybody who sees a behaviour and finds it difficult to interpret may declare it to be a displacement activity. As a result, the ethological literature is loaded with 'displacement activities' (e.g., in ungulates: grooming, scratching, wallowing, pawing the ground, lying down, grazing, alarm signals, turning the head sideward, lowering the head, and mounting in combat situations as well as the kick with the foreleg in courtship).

On the basis of this displacement hypothesis, Tinbergen and other ethologists developed the further hypothesis that displacement activities played.a very important role in expressive behaviour. They even believed that expressive behaviour in general is necessarily brought about by a conflict of antagonistic tendencies. They restricted the discussion almost exclusively to threat and courtship displays, and declared it to be a principle that in any hostile encounter the antagonists experience conflicting desires to attack and to escape (Tinbergen, 1952). For example, they concluded from this principle that generally threat display result from an inhibition of aggression by escape tendencies, and they argued that a threatening animal has to be inhibited by fear to some extent, otherwise it would not threaten but attack.

In ungulates, however, the most common threat displays cannot be derived from displacement activities but are clearly intention movements for fighting. In the phenotypical appearance, usually no other tendency than aggression is recognizable; and in cases where another tendency could be involved, it is often not clear whether this is fear. The most important dominance and certain courtship displays can be interpreted as having evolved from phylogenetically old aggressive actions (Walther, 1960a). Other courtship displays are apparently intention movements for mounting.

I will not deny that sometimes an animal may be in a conflict between aggression and fear in a hostile encounter; however, this is not a general principle. There are many situations where the rivals walk straight towards each other, either threatening all the time during the approach, or starting the threat display as soon as they are close enough. There is nothing in the behaviour of the opponents which would justify the assumption of a conflict between aggression and escape tendencies. Applied generally, the 'principle' that in a hostile encounter the animal is in a conflict between aggression and flight simply because it is in a hostile encounter, comes unpleasantly close to a dogma.

In the assumptions that an uninhibited animal would not threaten but attack, and that this inhibition of the aggression would be a constitutional factor for all threat displays, apparently exclusion is mistaken for inhibition. When an animal walks, it cannot gallop at the same time, and *vice versa,* since walk and gallop are different modes of locomotion which exclude each other. This, however, does not mean that an animal would walk only when it is inhibited to gallop. Correspondingly, threat and attack are different and mutually exclusive modes of aggression, but this does not mean that an animal would threaten only when fighting is inhibited.

The facts point towards the conclusion that in principle each expressive behaviour pattern represents only one tendency. In some cases, of course, two or more tendencies may occur in combination; and in special cases, they may even be in competition. In such cases which are very likely modifications, analysis is only possible under the presupposition that each single feature is indicative of only one particular tendency.

Having pointed out some of the difficult theoretical problems, I will now present several concrete examples which will permit discussion of some further ideas on expressive behaviour in bovids.

## THREAT DISPLAYS

Threat behaviour always indicates the readiness for fighting and it, so to speak, anticipates the fight. Therefore, threat can only be understood and interpreted when one knows the fighting techniques of a given species. In some species the fighting behaviour is different in attack and in defense. Correspondingly, we have offensive threat displays indicating the readiness to attack and defensive threat displays indicating the readiness to ward off the opponent's attack (Walther, 1958a and 1966a; Geist, 1965 and 1971).

In the Bovidae the horns, as the major weapons, are the basis of the most important fighting techniques. According to the differing sizes and shapes of the horns and to certain phylogenetically determined behavioural particularities of their use, fighting techniques vary in the different species. Even within one species the animals may use several fighting techniques. Correspondingly, there are differences in the threat displays. Fortunately, this variability does not preclude the establishment of some general rules. On the other hand, the high degree of variability must always be taken into account. In some extreme cases very similar behaviour patterns may have rather different meanings in two or more different species.

For example, in the oryx antelope (*Oryx gazella*) one fighting technique is the heavy downward blow with the frontal side of the long horns. Correspondingly, the erected-neck-posture as the upswinging movement (Ausholbewegung) for this blow, is a very serious and offensive threat in this species (Walther, 1958a). In order to parry this blow from above, the opponent may lower his neck and head, shielding the body behind his long horns. Correspondingly, there is a head-low posture in this species which is a more defensive threat and thus a somewhat milder form of threatening than the erected posture. When an oryx responds with the head-low posture to the challenger's erected-neck threat, this comes close to an inferiority behaviour (note Fig. 10). With the head-low posture the animal does not react by an equivalent offensive counter-display. It is not ready to go into an attack with heavy downward blows but it expresses only its readiness to ward off such blows in case of the other's attack. On the other hand, in species in which the rivals do not fight with downward blows but always bring their horns together close to the ground, e.g. in Gray's Waterbuck (*Onotragus megaceros*) (Fig. 1 c and d), or push with their horns upward from below e.g., in the chamois (*Rupicapra rupicapra*), a head-low posture (Walther, 1960b; Kramer, 1969), very similar to that of the oryx, may mean a rather offensive threat.

Even the hornless females of some species may fight with their bare heads in a similar way as the males do with their horns. In this case, the threatening behaviour of males and females is very similar or even identical. On the other hand, horn fighting is not the only fighting method found in horned ungulates. In some species the opponents try to wrestle down one another by means of their necks ('Halskampf, Walther, 1958a), or by throwing their body against the rival's in a jump (in which the hindlegs do not leave the ground). They may also snap, or push with closed mouth. Correspondingly, there are threat displays which are related to these fighting techniques. Such fighting methods and threatening movements are often more pronounced and frequent in the hornless females than in the horn-bearing males.

In many species, the rivals stand in a more or less frontal position before and during a fight. In any case, they have to come together for a fight. Therefore, already a pronounced frontal approach may sometimes express hostile intentions. This approach can be emphasized by a ritualized retardation, often combined with a striking prancing gait. On the other hand, an animal may rush at full speed towards the opponent, without even showing any particular threatening gesture but often uttering special sounds (e.g., in gazelles a relatively loud, repeated snoring). Chasing the opponent may follow after the complete defeat of a rival. Therefore, in running straight into the other at a full gallop without any previous fighting, the aggressor, so to speak, anticipates victory. This behaviour is used predominantly by superior animals (e.g., territorial males) against inferior opponents (e.g., non-territorial males, and especially against subadult and adolescent males). In such a case, usually the inferior animal flees as fast as it can. If the opponent is not inferior at the onset of the interaction, he may stand and await the aggressor's approach. Then, both may crash together in a fight, or the aggressor may stop some distance from the opponent (feint attack).

These aimed and emphasized approaches and even more the flight anticipating chases and the feint attacks lead us into a category of expressive behaviour which I wish to term symbolic actions (Symbolhandlungen). The essential point seems to be that the sender performs the full action, without touching the addressee and sometimes at a distance from which he cannot possibly touch him. In other words, it is an action performed in the air. The clearest cases of this kind in horned ungulates are the symbolic butting with head and horns, and, apparently closely related to it, the head-nodding (Figs. 2 and 3) and the in certain species very striking head-shaking, the symbolic jump with the forelegs thrusting the anterior part of the body in the direction of the opponent, the symbolic snapping movement, and the symbolic pushing movement with the snout ('Schnauzenstoss', Walther, 1958a). Species which rise on their hindlegs (Fig. 5b) or other species which drop on their 'knees' in fighting (Fig. 5a), may also use these behaviour patterns symbolically as means of threat.

Up to now we have discussed symbolic actions as being directed towards the opponents, and this is true in many cases. However, sometimes symbolic movements are addressed, but not directed, towards a partner, especially when the addressee is superior to the sender. This leads us to the so-called redirected aggression (Moynihan, 1955) in which, according to the principle of a symbolic action, the animal performs the full movement (beating, butting, pushing, etc.). In social situations, the behaviour may clearly be released by a conspecific but it is directed against a substitute. This substitute may be either a weaker and/or inferior animal ('Radfahrer-Reaktion', Grzimek, 1949), or an inanimate object such as a tree, a bush, a bunch of high grass, or the ground. In some bovid species butting at grass or the ground with the horns alternately to the right and the left has become ritualized into a rhythmical weaving (Fig. 4). In the horned ungulates, neither the motivation, nor the effects upon the receiver, nor the social functions of the redirected aggressions are completely clear. Certainly, there are cases in which this behaviour has nothing to do with expression in the restricted sense of our definition. Rather, it seems to be simply an outlet for surplus energy, and sometimes may involve play with inanimate objects. In other cases, such redirected aggressions may be related to marking behaviour (Walther, 1964b). Finally, the redirected aggression can also be addressed to a prospective opponent. To the human observer, this behaviour is usually rather striking and one would assume that it is a very effective means of threat. Strangely enough, this is often not true. I saw situations in which the addressee reacted in the expected manner but, at least as often, the addressee only watched the sender's action or even ignored it completely. This happened even in cases in which the addressee was clearly inferior, and the sender attacked him later. In short, the effect of redirected aggression upon the receiver is often poor in the bovids, and the redirected aggression seems to be at the border of that realm of behaviour which serves a communicative function in social life.

The opposite is true for those threatening gestures or postures which are usually described as intention movements (Heinroth, 1911). For the human observer, they are often not as striking as the redirected aggressions, but their effects upon the conspecific receivers are incomparably stronger. Certainly, they are the most important and common kinds of threatening behaviour in bovids. In contrast to the symbolic movements, the animal does not perform the entire action, but just the initial movement. In threatening bovids, these intention movements refer predominantly to the use of the horns. Either the animal brings its head and horns into a position from which it can go into immediate action according to the species-specific fighting methods, or it swings out with head and neck for an intensified blow. One can see the same movements when a fight starts. Used as expressive behaviour, these movements are 'frozen' into postures which are held from a few seconds up to a minute, occasionally even for several minutes. These initial movements are sometimes (but not necessarily.' ) demonstrated at a distance, from which the animal cannot possibly fight its opponent. Furthermore, the presentation of the horns is often somewhat exaggerated (ritualized) (See figs. 13 and 14). Especially when performed in an erected-neck posture, features of threatening behaviour and features of dominance displays appear combined ('Droh-Imponieren'). On the other hand, there are also some relations to symbolic butting and even to redirected aggressions. The latter is probably true for the downward sweep of the horns, a behaviour which Schaller (1967) found especially pronounced in the Indian blackbuck (*Antilope cervicapra*), Burckhardt (in Walther 1964a) reported it for nyala (*Tragelaphus angasi*), and I found it very pronounced in Grant's gazelle (*Gazella granti*).

Besides such connections and transitions, there are three main forms of horn threat according to the different types of intention movements for fighting: sideward-angling the horns (when the sender stands in a broadside position, and does not face in the direction of the opponent), presenting the horns towards the opponent, and the head-low posture in which the horns point upward. The presentation of the horns is especially common and can be performed in three different ways: presentation of the horns more or less parallel and close to the ground (low presentation), presentation of the horns with erected neck (high presentation), and presentation of the horns on body level (medial presentation) (Fig. 1). Sometimes all three forms may appear within the same species. On the other hand, there are quantitative species-specific differences, with species showing one or two forms far more frequently than the third one. In some species, one of the forms may be completely absent.

Probably the most common form is the medial presentation (body level) which ontogenetically may develop from fighting 'with an air cushion'. This later is a special kind of fight in which the rivals stand in frontal position and perform attacking and parrying manoeuvres without touching one another. It looks as though there is an invisible cushion between the horns of the two fighters. The high presentation of horns, apparently the most ritualized form, may be understood as a somewhat exaggerated preparation for a heavy downward blow, and the low presentation as the preparation for a upward thrust. The low presentation corresponds to the habit of many species of bringing the horns together close to the ground in fighting. In some species this posture shows gliding transitions to the head-low posture, and from both, the head-low posture and the low presentation of horns, the animal may change into grazing, obviously a transitional activity (Lind, 1959).

Finally, as with symbolic actions, sometimes these horn threats may be addressed to, but not directed at the partner. For example, in the mating ritual of the Thomson's gazelle (*Gazella thomsoni*) occasionally the males kick with the foreleg ('Laufschlag', Walther 1958a) or mounting may release medial presentation of the horns or symbolic butting in the female (Fig. 3b). However, facing in the same direction as the male and standing or moving in front of him, she threatens in the exact opposite direction to the male. If she meets or passes another female at this moment, she may direct the threat against this other female, in which case it more or less becomes a redirected aggression.

Although the threat displays related to the initial movements of horn fighting are the most important and common ones, there are some further ones in certain species of bovids. In species which rise on their hindlegs when fighting, the intention movement for this raising may also serve as a means of threat. The animal stands with stiffly stretched forelegs, the neck as erect as possible according to the species-specific anatomical constitution, and the nose usually lifted in an angle of about 45° to an (imagined) horizontal line. This posture also occurs in species which do not rise on their hindlegs when fighting (see below).

Similar aspects are valid for the head-and-neck-stretched-forward posture (e.g., the 'Überstrecken' in the tragelaphines, Walther, 1958a, or the 'low stretch' in the sheep, Geist, 1968a) which is a common expressive behaviour in horned ungulates (Fig. 18a). Obviously, the meaning indicated is not the same in all the species which use this posture, and the meaning is not always completely clear. It may be that in some species it is no more than an intensification of the approach which also may constitute a threat, as discussed above. In greater kudu (*Tragelaphus strepsiceros*), lesser kudu (*Tragelaphus imberbis*), sitatunga (*Tragelaphus spekei*), bushbuck (*Tragelaphus scriptus*), and nyala, it can be interpreted as an intention movement for the neck fight which, in a ritualized form, is a very typical courtship behaviour in these tragelaphine species (Walther 1958a, 1964a) (Fig. 17b and c). In the related nilgai antelope (*Boselaphus tragocamelus*), however (Fig. 17a), the neck fight occurs as a true fighting method and thus, the corresponding expressive behaviour may be said to be a threat display in the strict sense. This head-and-neck-stretched-forward posture will be further discussed in the section on courtship displays.

Having mentioned the most common kinds of threatening behaviour in horned ungulates and some aspects of their origin and meaning, we should comment on their effects and functions. In principle, threatening may have two different effects upon the addressee: challenge or intimidation. The alternatives depend to a large extent on the sex, age and social status of the partners. Certain results (a preliminary evaluation of somewhat larger samples) of a quantitative study on threatening behaviour of Thomson's gazelle in the Serengeti National Park may serve as an example (Table 1a-c).

According to Table 1a, there is always a strong preponderance either of the challenging effect, resulting in a fight, or of the intimidating effect, resulting in an inferior behaviour of the one partner. The intimidating effect is highest, and the challenging effect lowest when two unequal partners are involved such as 'te♂ : ad♂' and 'ad♂ : jv♂'. Somewhat higher but still relatively low is the challenging effect when the opponents are two adult, non-territorial animals such as 'ad♂ : ad♂' and 'ad♀ : ad♀'. In the categories 'te♂ : te♂' and jv♂ : jv♂', however, the challenging-effect clearly outweighs the intimidating effect.

A further insight is given by the distribution of the one-sided and the two-sided threat encounters (Tables 1b and 1c). The percentages of two-sided threat encounters (Table 1b) agree strikingly with the percentages of threat encounters ending with a fight (Table 1a) in all the categories, and, as shown in Table 1c, more two-sided encounters end with a fight than do one-sided encounters. Whether the addressee simply 'obeys' the sender's threat, or responds by a counter-display, depends upon sex, age and social classes. This is easy to understand in the case of unequal partners. In 90.9% of the encounters in which a territorial buck threatened a non-territorial, adult male, the bachelor did not react by a counter-display. In 90. 6% of the cases in which an adult buck threatened a juvenile male, the youngster did not show a counter-display. In other words, very often the inferior opponent does not 'dare' to respond with a counter-display. If he does, the superior rival will fight him immediately. This is especially clear in the relationship te♂ : ad♂ where one-sided threats of bachelors against territorial bucks were not observed, and 95. 5% of the (infrequent) two-sided threat encounters ended with a fight. In the case of equal opponents, the readiness

*[text continued on p. 65].*

TABLE 1. EFFECTS OF THREAT DISPLAYS IN THOMSON'S GAZELLE

| | te♂ :te♂ | te♂ :ad♂ | ad♂ :ad♂ | ad♂ : jv♂ | jv♂ : jv♂ | ad♀ :ad♀ |
|---|---|---|---|---|---|---|
| n threat encounters | 244 | 242 | 1141 | 235 | 169 | 80 |
| Table 1a | | | | | | |
| % ending with fight | 95.1 | 8.7 | 18.5 | 6.0 | 65.7 | 12.5 |
| % ending with inferiority behaviour | 1.2 | 85.1 | 74.2 | 88.9 | 29.0 | 78.8 |
| % ending in another way | 3.7 | 6.2 | 7.3 | 5.1 | 5.3 | 8.8 |
| Table 1b | | | | | | |
| % two-sided threat enc. | 97.5 | 9.1 | 26.4 | 9.4 | 68.6 | 12.5 |
| % one-sided threat enc. | 2.5 | 90.9 | 73.6 | 90.6 | 31.4 | 87.5 |
| Table 1c | | | | | | |
| % ending with fight | | | | | | |
| two-sided threat enc. | 95.4 | 95.5 | 68.8 | 63.6 | 90.5 | (5)† |
| one-sided threat enc. | (6)* | 0.0 | 0.5 | 0.0 | 11.3 | 7.1 |

* out of 6 cases †out of 10 cases

**Table 1—Explanatory comments**

Only the horn threats (high presentation, medial presentation, transitional forms between these two, symbolic butting, and in this species the relatively rare low presentation and the downward sweep of the horns) are counted as threat behaviour in these tables. By 'threat encounter' I mean any encounter in which threatening was observed. In a 'one sided threat encounter' only one partner threatened the other. In a 'two-sided threat encounter' both opponents threatened.

There are six categories according to the partners involved: 'te♂: te♂ ' (te♂ = territorial male), 'te♂ : ad♂' (ad♂ = non-territorial, adult male), 'ad♂ : ad♂', 'ad♂ : jv♂' (jv♂ = juvenile male, i.e., subadult or adolescent), 'jv♂ : jv♂', and 'ad♀ : ad♀' (ad♀ = adult female). Fawns are not mentioned in these tables because, with little exaggeration, one may say that fawns do not threaten. Threatening encounters between males and females were rare (except the non-directed threatening of females during the courtship ritual mentioned above), and also threatening of females against fawns was infrequently seen. Threatening of juvenile males against territorial males was not observed at all, and the latter used horn threats against juvenile males only very exceptionally. Usually they chased them away by rushing towards them. Furthermore, excluded from this presentation are the rather rare cases in which a juvenile male threatened an adult male without the latter reacting by a counter-display. Thus, in the category 'ad♂; jv♂' the adult buck always threatened the juvenile one in the one-sided threat encounters. *Mutatis mutandis* the same is true for the category 'te♂:ad♂', i.e. one-sided threatening by a non-territorial adult male of a territorial male was not observed.

The effects of the threat displays are indicated by the ends of these encounters (Table 1a): 'ending with fight' (including fighting with an air cushion—no distinction is made between 'sparring' and 'fighting'), 'ending with inferiority behaviour' (i.e., withdrawal, flight, or submissive behaviour—of course, only on the part of one partner; in case of 'te♂ : ad♂', this was always the non-territorial, adult male; in case of 'ad♂ : jv♂', it was always the juvenile male.), and 'ending in another way' (i.e., cases in which the addressee did not react to the sender's threat, or in which the two opponents were disturbed by a third buck, etc.).

**Table 1—Explanatory comments—***cont.*

Table 1b shows the percentages of two-sided and one-sided threat encounters in the different categories (te♂ : te♂, te♂: ad♂, etc.), and Table 1c shows the percentages of two-sided and one-sided encounters ending with a fight. Thus, Table 1c reads the following way: according to Table 1b e.g., 97.5% of the (244) threat encounters between te♂♂ were two-sided threat encounters; of these two-sided encounters (97.5% of 244 = 238) 95.4% ended with a fight, etc. One-sided encounters between te♂♂ and two-sided encounters between ad♀♀ ending with a fight were so rare that the absolute numbers rather than percentages are given (in parenthesis).

The differences between the single categories in Table 1a were tested with Chi-square. The differences between 'ad♂; ad♂' and 'ad♀ : ad♀', between 'te♂: ad♂' and 'ad♂: jv♂', and between 'te♂: ad♂' and 'ad♀: ad♀' were not found to be significant ($p > 20\%$). All the other differences were significant ($p < 0.1\%$).

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'to obey' the initiator's threat 'without any objections' is not as high. Here there is an interesting difference between the adult females and the non-territorial adult males on the one side, and the juvenile males and the territorial bucks on the other. The non-territorial adult animals—males and females—are much more 'tolerant' than the two other classes. In the young males, the higher readiness to react to a threat by a counter-display and/or a fight is probably due to the generally higher excitability of juvenile animals. With respect to the challenging effect of threatening behaviour, the territorial bucks are closest to the young males; the number of threat encounters finding with a fight is even significantly higher in the territorial males (Table 1a). This is not because the two-sided encounters of young males would end without fighting more often than in the territorial bucks (Table 1c), but because two-sided encounters are more frequent in territorial males (Table 1b). In other words, the territorial bucks are most intolerant of threats and react immediately with a counter-display (if not with an attack). When both opponents are territorial, in a two-sided threat encounter neither gives in, and this frequently results in fighting. This is probably true for every species in which, as in Thomson's gazelle, the territories are relatively small and adjacent to another, and in which the animals rely predominantly on the horn threat rather than a highly ritualized dominance display.

As mentioned above, non-territorial adult animals are much more 'tolerant' and 'obedient', with no significant difference between males and females. However, these similar results are brought about in different ways. In the females, the number of two-sided threat encounters (Table 1b) is significantly ($p < 1\%$) smaller than in adult bachelors. Obviously, the females do not react as readily with a counter-display. In the non-territorial males, however, many two-sided threat encounters end without a fight. The opponents threaten and 'wait' until one ceases threatening. The same is true for the category 'ad♂: jv♂'. In this regard the adult males do not make a distinction between partners of the same or a younger age.

As to the biological functions of threatening behaviour, it enables these animals to settle a good number of hostile encounters without a fight. The threat displays especially help in avoiding fights between unequal partners. This fight-saving function is the result of the intimidating effect, which has often been emphasized in ethological literature. As far as I know, however, not very much has been said about the challenging effect of threat behaviour which appears as important as the intimidating effect. By the challenge one partner becomes aware of the other's aggressive intentions and, although a fight is not avoided, the probability of a surprise attack is diminished considerably. Undoubtedly, the surprise attack is the most dangerous form of aggression, and the probability of serious or fatal injuries decreases when both opponents are prepared for fighting.

For the discussion of social functions let me stay with my example of Thomson's gazelle. If threatening behaviour, and aggressive behaviour in general, does serve particular functions in social life, one expects it to appear in the corresponding social situations. In other words, the aggression releasing situations which can be observed directly permit some conclusions on the social functions of this behaviour. I analysed the releasing situations for more than 2000 threat encounters in this species. The quantitative results will be presented in a later publication. Here I will only give the conclusions drawn from the qualitative results.

In the territorial bucks 'everything revolves around the boundary' of the territory. In particular, threatening behaviour, and at least in qualitative aspects also any other kind of aggressive behaviour, serves to: (a) establish the boundaries and later to confirm their position between territorial neighbours; (b) possibly change or maintain that position when a territorial male tries to extend his territory into an area occupied by another male; and (c) prevent other males, especially non-territorial bachelors, from crossing the boundaries and entering the territory.

In non-territorial adult males and in adult females, one of the functions of threat is to maintain the individual distance. In adult males the individual distance is somewhat higher than in the females, and in grazing it is greater and apparently more important than in any other activity. Sometimes this may lead to the defence of a very small and temporary feeding place. On the other hand, sometimes grazing males enlarge the distance around themselves and between one another, far above the usual individual distance and without any direct relation to the food. This stage often preceeds the establishing of territories.

Furthermore, especially in the non-territorial adult males, the aggressive behaviour and above all the horn threats are the most important means for coordinating the activity of a group. In particular, threatening may serve to: (a) speed up the change from one activity to another, as from resting to grazing or moving; (b) determine the direction and order of a move; and (c) keep the group going during migration. For these purposes, adult males almost exclusively use the threatening behaviour against each other. Thomson's gazelle males usually do not threaten females with their horns. They communicate with the females in another way (see below). One may say that the non-territorial adult males are the motors of migration in this species. In such non-territorial adult males, threatening in relation to coordination of group activity makes up the greatest portion of all threat behaviour. This explains why the adult males are relatively tolerant and obedient of each other's threats, as shown above. According to their activity rhythm all are more or less in the same mood (e.g., to switch from resting to moving, at a definite time of the day). In this situation a resting animal is quite ready to stand up and move when threatened by another animal already on its feet since the addressee would have risen soon anyway in accordance with his own mood.

In the females, threatening, besides other aggressive behaviour, may serve to repel the sucking attempts of strange young, but also of their own young when the latter solicit milk at the wrong time. Furthermore, it is used sometimes to repel sexual approaches of young (adolescent) males. In many species threat behaviour serves the same or very similar social functions as for Thomson's gazelle. In other bovid species, there may be other or additional functions such as establishment and maintainance of a social hierarchy, defence of a harem, and defence of the young against other conspecifics.

## DOMINANCE DISPLAYS

In discussing the dominance displays, we encounter a language problem. In German we say 'Imponierverhalten'. The translation often used in English literature is 'display behaviour'. However, the meaning of the word 'display' is broader than that of 'Imponieren' which implies that the behaviour in question has a very strong effect upon the receiver. The kind of behaviour discussed here, is always and exclusively 'Imponierverhalten', for which I suggest the translation 'dominance display', as giving approximately the right meaning (Lent, 1969, and Geist, 1965 and 1971, have used the translations 'display threat', 'present threat', and 'bravado display'.)

Another problem is produced by the subject itself. Heinroth (1911) was the first one to speak about 'Imponierverhalten' in animals, and he and later Eibl-Eibesfeldt (1957) considered it to be some kind of threatening behaviour which also acts a role in courtship ('Imponieren ist Drohen und Werben zugleich'). That means, it depends on the sex of the addressee whether one and the same behaviour pattern intimidates (the challenging effect was not taken into consideration) or attracts the partner. Obviously this principle was difficult to apply to all the behaviour patterns in question, and so Eibl-Eibesfeldt (1957) expressed the opinion, with special reference to mammalian behaviour, that it would not be possible to distinguish between dominance displays and threat displays. These views and uncertainties seem to be typical results of a definition based exclusively on functional aspects and not distinguishing properly between the different levels of the 'functions'. Of course, dominance displays do show connections and transitions to threat displays and sometimes also to sexual behaviour, and certain dominance displays may be used in both hostile encounters and in courtship. However, connections and transitions are found almost everywhere in behaviour and, as we just discussed in the example of threat displays, one and the same expressive behaviour may often serve several social functions. Thus inspite of some difficulties arising from these connections and transitions, I think that in principle one should make a distinction between threat and dominance displays, simply because there is a difference.

In dominance displays, animals do not demonstrate their readiness for immediate attack or defense as in threat displays, nor do these displays refer to the weapons. Rather the animals display their height and breadth demonstratively, and they may present striking structures such as colour patterns, manes, beards, and odour producing glands. Thus, the most typical and most common dominance displays are erected postures and broadside presentations. The animal exposes its body to a possible attack by the opponent in the dominance displays far more than in the offensive threats and completely in contrast to the defensive threats. Although it is a somewhat primitive technique, it sometimes contributes to better understanding when one tries to 'translate' the meaning of an expressive behaviour in terms of human language. The translation for a threat display would be 'I am ready to fight you', whereas that of a dominance display is 'I am the greatest'.

Standing in a broadside position an animal may block another's path and in so doing, may force him to deviate from his original course or even to retreat, without, however, —and this is important—direct fighting intentions. This blocking the way definitely does occur in horned ungulates. In a non-ritualized form it plays a very important role in the social life of some species, e.g. when a territorial male of Grant's gazelle tries to keep females inside his territory. In other species such as kongoni (*Alcelaphus buselaphus*), this blocking the way is used by territorial bulls against intruders in hostile encounters. In such cases the sender is in a right angle position to the addressee. In other species and/or in other situations, the challenger may circle around his opponent. When both partners display the broadside presentation simultaneously, they automatically come into a parallel or, more frequently, into a reverse-parallel position. When both of them move during the encounter, they circle around each other with the flank kept towards the rival.

In these two-sided dominance displays another factor may appear. In the mountain goat (*Oreamnos americanus*), Geist (1965) found that fights may develop by the delivery of horn blows from the reverse-parallel position. Thus, in this species the broadside position is a threat display. Geist (1966) argues convincingly that this fighting in reverse-parallel position might be a primitive type of fighting behaviour in horned ungulates. Fighting in a broadside position is also found in barbary sheep (*Ammotragus lervia*), where the rivals, standing in reverse-parallel position, may hook with one horn over the other's back and try to wrestle down the opponent with it; and in yet other species the broadside posture can be combined with sideward-angling of the horns (towards the opponent). Thus, one can assume that the reverse-parallel position might have originated from special but relatively primitive fighting techniques: it also would not seem to me out of place to take pushing with the shoulders or the rump into consideration. These two hypothesis—the broadside presentation having originated from blocking the way, and the broadside display having originated from a fighting technique—are not mutually exclusive. However, if such a connection between fighting behaviour and broadside display has existed in phylogeny, it has disappeared in some, probably even most of the recent bovid species which show the broadside presentation. With Grant's gazelle in the wild, and in captivity with oryx, eland (*Taurotragus oryx*), lesser kudu, and with a tame greater kudu bull—where I acted the role of the opponent and could even force the situation experimentally (Walther, 1964a and 1966a)—, I have frequently observed that no attack is made directly from the broadside position. Sometimes they may move from a broadside display into a fight, thereby giving up the broadside presentation. They start threatening with a sideways angling or presentation of the horns, and in so doing turn into a frontal position for fighting.

In short, in some species the broadside display can be considered a dominance display, but in other species a threat display. This is not surprising when we assume that dominance displays have evolved from phylogenetically old fighting methods which in some species have disappeared completely from the fighting repertoire in the course of evolution, whereas in some other species, less advanced in this regard, the old fighting methods are still kept (Walther, 1960a).

In most bovid species there are additional behavioural components in this broadside presentation. The most common one—which may also occur in threat and dominance displays other than the broadside presentation—is a sideways inclination of the head away from the opponent (Fig. 12). In this case, as well as in the full sideway turn of the head (see below), we should remember that the eyes of these animals are located laterally on the head. Thus, this inclining or even turning of the head is not necessarily a 'facing away' and 'losing eye-contact' as it would be in humans or in certain other animals whose eyes are located more frontally.

In the mountain goat (Geist, 1965), some bovines, and also in the chamois and the markhor goat (*Capra falconeri*), the broadside presentation is often performed in an arched-back posture (Walther 1960a and b). Almost all of the possible expressive neck postures—neck downward, upward, forward, and bent—may occur in combination with this arched posture either within the same or in different species. The head-and-neck-forward/downward posture—as it was found in gaur (*Bibos gaurus*) and gayal (Antonius, 1939), greater kudu (Fig. 17c) and nyala—seems to be in the best phenotypical accordance with the arched-back posture of the body. In these species, the arched-back posture is accentuated or even dependent upon placing the hindfeet more forward than usual under the body.

However, the broadside presentation need not be performed in an arched-back posture. Greater kudu can display with or without arching the back, and other species such as lesser kudu. Grant's gazelle, gerenuk (*Litocranius walleri*), Indian blackbuck, and oryx antelope do not arch the back at all. In these species, the hindlegs are in a 'normal' position, the forelegs are kept a little stiffer than usual, the neck is as highly erected as possible, and the head is often lifted. In some species this may result in a nose-upward posture. This nose-upward movement may lead to an almost vertical positioning of the head (Figs. 9 and 20b). This posture differs in meaning, and probably also in origin for different species. In Thomson's gazelle, Grant's gazelle, and Indian blackbuck, it is obviously an exaggerated form of lifting the head—a dominance display. In lesser kudu and some other species it seems to be more closely related to defensive behaviour.

Although it often occurs in combination with the broadside presentation, the erected posture described above is an independent dominance display. It may also occur when the animal is standing in a frontal position to the partner. The broadside presentation makes the displaying animal appear as broad as possible, the erected posture makes it appear as tall as possible. When an animal stands in broadside presentation with erected neck, the effects of both displays summate—more or less according to the rule of heterogenous summation (Seitz, 1940). In looking for the origin of the erected posture, two aspects must be considered. In some cases it can be an intention movement for a heavy downward blow with the horns, as found in the oryx antelope. In certain other species such as Marco Polo sheep (*Ovis ammon*), the erected posture is obviously an intention movement for raising on the hindlegs (Fig. 7), and it may still be considered related to the species-specific fighting technique and with it to a threat display. This, however, is not true for other species which show the erected posture combined with lifting the nose as a non-expressive behaviour only before rising on the hindlegs for browsing or sexual mounting. Thus, the corresponding expressive posture may still be taken as an intention movement for rising on the hindlegs but without a direct relation to the recent, species-specific fighting methods. In some species which show the erected display in hostile encounters, mounting occasionally follows. In Grant's gazelle, in a sample of 132 dominance displays between males, mounting the rival occurred in 12% of the cases (Walther. 1965a). It is noteworthy that whenever an adult male was mounted he always turned and attacked the opponent immediately. At present, we must leave open the question of whether the erected posture in hostile encounters is directly related to sexual mounting in these species, or whether this intention movement is some kind of phylogenetic relict from jumping at the rival during ancestral fighting. I admit that I am in favour of the second alternative. In any event, there are species in which the erect display has no connection with recent fighting methods, and thus one cannot say that the erected posture is a threat display in these cases.

When offered in a frontal position, the erected-neck posture may sometimes be combined with an approximate 90° sideways-turn of the head (Fig. 13). As mentioned above, I do not think that this is necessarily an intention movement for facing away, giving up and withdrawal or flight. In special cases this may be true, especially when the animal turns its head through almost 180°, facing in the opposite direction to its rival, or when the animal turns its head without adopting the erected posture or any other kind of dominance or threat display. Although there may be cases in which it is difficult to make a clear distinction, I think that these postures are different from the head-turn of about 90°. Geist (1971) interpreted the sideward inclination of the head and the 90°-head-turn as an emphasized ignoring of the opponent. I had the impression (Walther, 1965a) that it is a lurking watch and/or a ritualized swing-out movement (Ausholbewegung) for turning towards the rival. Sometimes one may even think of some kind of an abbreviation of a broadside display. These views do not necessarily exclude one another; possibly they may even complete each other.

There seem to be quantitative, species-specific differences in the relationship of the erected posture and the head-turn. In some species (e.g., lesser and greater kudu) they are occasionally combined with each other. In other species such as Uganda kob (*Adenota kob*) (Buechner and Leuthold, pers, comm.), and in impala (*Aepyceros melampus*), this combination is apparently far more frequent, and often occurs before a fight, in pauses during a fight, or in lieu of a fight An unique variation is found in the dominance display of Grant's gazelle (Walther, 1965a; Estes, 1967). It starts with an erected posture with lifted head, as is not uncommon in other species. Then a slight sideward inclination of the head away from the opponent follows, as also known from other species (swing-out movement, lurking watch, emphasized ignoring, see above). However, the displaying animal then turns its nose towards the addressee in a sudden, vehement movement. This has not been described for any other bovid species to date. This display is rarely shown when the sender stands in a more or less frontal position to the addressee, but is usually delivered from a broadside position (discussion of the few but very informative exceptions in Walther, 1965a). Due to the opponent's lateral orientation, this head turn (head-flagging) is only physiologically a sidewards movement. Actually the displaying Grant's gazelle turns its nose *towards* the rival (Fig. 14). Apparently, this display is highly ritualized in Grant's gazelle. It occurs in the same situations as fighting (Walther 1965a), it can substitute for a fight and thus may prevent fighting in a considerable number of encounters between adult

TABLE 2. FIGHTS AND DOMINANCE DISPLAYS IN GRANT'S GAZELLE

| | adult ♂♂ | subadult ♂♂ |
|---|---|---|
| Numbers of animals seen in encounters | 271 | 146 |
| % in dominance displays | 72.8 | 5.5 |
| % in fights | 27.2 | 94.5 |

This table is based on data taken in the Ngorongoro Crater during 74 observation hours within one week. It does not give the numbers of encounters but the numbers of fighting and displaying animals, i.e., two in case of a flight or a two-sided dominance encounter but only one in case of a one-sided dominance encounter.

The same results were presented in another form in Walther, 1965.

bucks (Table 2). Younger males do not show this behaviour as often as adults do, and probably for this reason they fight more often

In general, dominance displays mature relatively late in the ontogeny. For example, in bighorn sheep, they may mature fully between six to eight years (Geist, 1968b) Even after having matured in young animals, their appearance may be suppressed by superior adult conspecifics (Walther, 1961; Geist, 1971). This may be the reason why these displays are seen predominantly in adult males. Females usually do not lack the species-specific dominance displays but, as with threats and fights, they perform them far less frequently than males.

In principle, dominance displays have very similar effects upon the recipient, and they serve very similar social functions as threat displays However, there are some important differences in the details. As pointed out above, threat displays are much closer to fighting than dominance displays. In case of a threat encounter, if the addressee reacts with an equal counter-display, there is a high probability that a fight will follow. This is not true for dominance displays. Even after an intensive two-sided dominance encounter between equal opponents, the probability that it will end without a fight is rather high. An exception from this general rule occurs in those cases where the opponents move from the dominance display into a position suitable for fighting. Occasionally, this may happen in all the species which show dominance displays In the mountain sheep it even occurs rather frequently (Geist, 1971) In the two-sided threat displays, the rivals are in postures from which they can go into an immediate fighting action. In the majority of the species and cases, the combatants stand in a frontal position where each step forward brings them closer together and increases the probability of a fight. In dominance displays, however, the opponents are not ready for an immediate attack or defense. Frequently, they stand in a reverse-parallel position, so each step forward takes them away from one another and contributes toward ending the encounter without fighting. Thus, although the dominance displays are not principally different from threat displays in regard to the effects and functions, they are milder forms of aggressiveness and favour the peaceful solution of encounters. This is also the basis for a function of some of the dominance displays in courtship.

An interesting question lies in whether or not the horns may also play a part in certain dominance displays. I emphasized that the horns are presented in threat displays in such a way that the animals can go immediately into a fight from these postures. However, when an old bighorn ram (*Ovis canadensis*) approaches an opponent in the 'low stretch' (Geist, 1966) and rotates the head about its median axis, this may be linked with a presentation of the sideward expanding horns, but it is not a posture from which the animal can go into an immediate horn attack. Thus, in principle it is possible that the horns can also play a role in certain dominance displays (see also Geist, 1971).

*[text continued on p. 83*

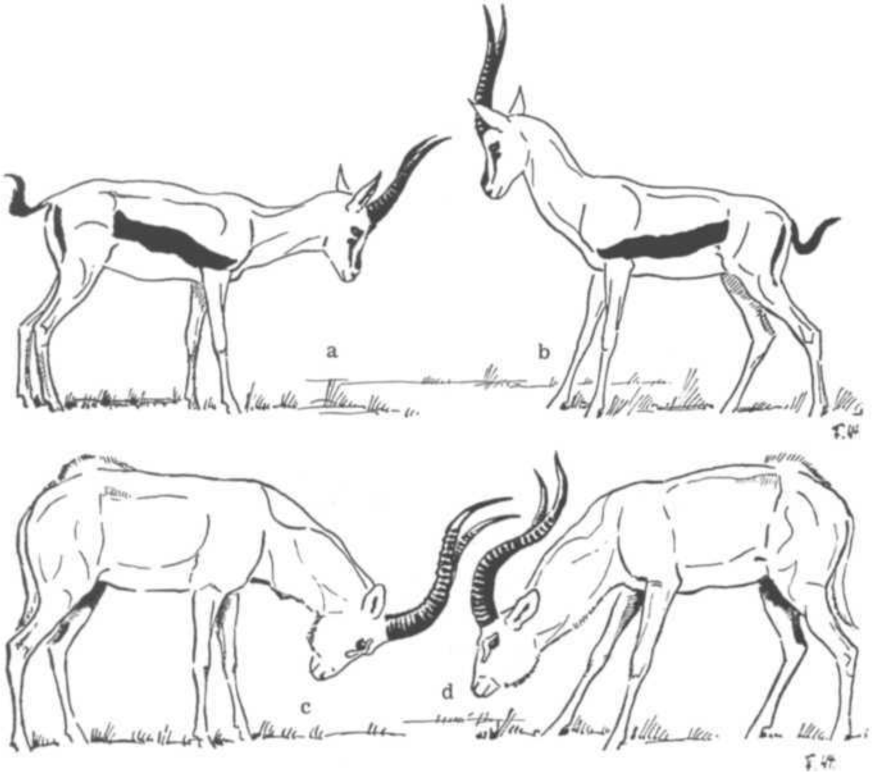

Fig. 1.

Thomson's gazelle
a. Medial presentation of horns
b. High presentation of horns

Gray's Waterbuck
c. Low presentation of horns
d. Head-low posture

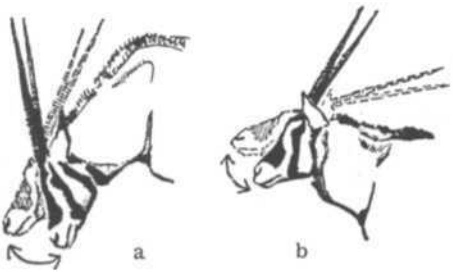

Fig. 2.

Oryx
a. Head-nodding in head-low posture
b. Head-nodding in erected posture

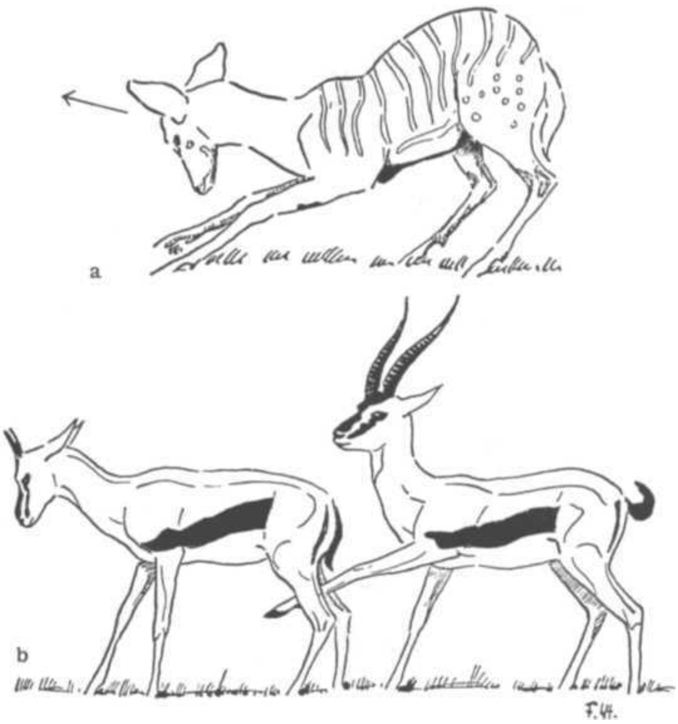

Fig. 3

a. Symbolic butting—combined here with lowering of the anterior part of the body (female Sitatunga)
b. Undirected symbolic butting as response by the female to the male's kick with the foreleg (Thomson's gazelle)

Fig. 4 Beating the grass with the horns ('weaving'—Grant's gazelle)

Fig. 5

a. Symbolic dropping to the 'knees' (wildebeest—after photo of R. D. Estes)
b. Symbolic rising on the hindlegs (ibex)

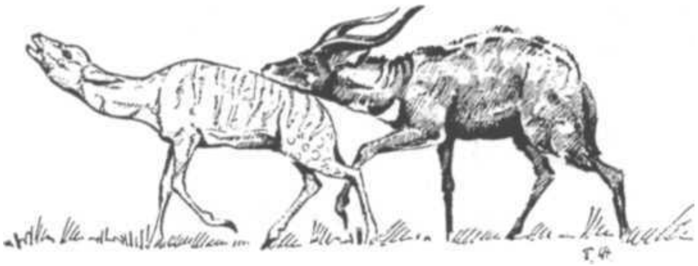

Fig. 6 Undirected symbolic snapping as a response by the female to the male's sexual approach (Sitatunga)

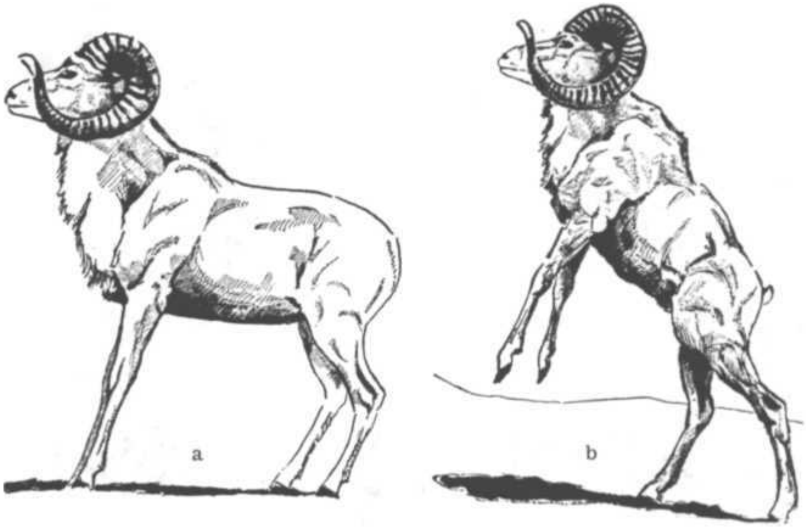

Fig. 7

a. Erected posture as an intention movement prior to rising on the hindlegs
b. Rising on the hindlegs (Marco Polo sheep)

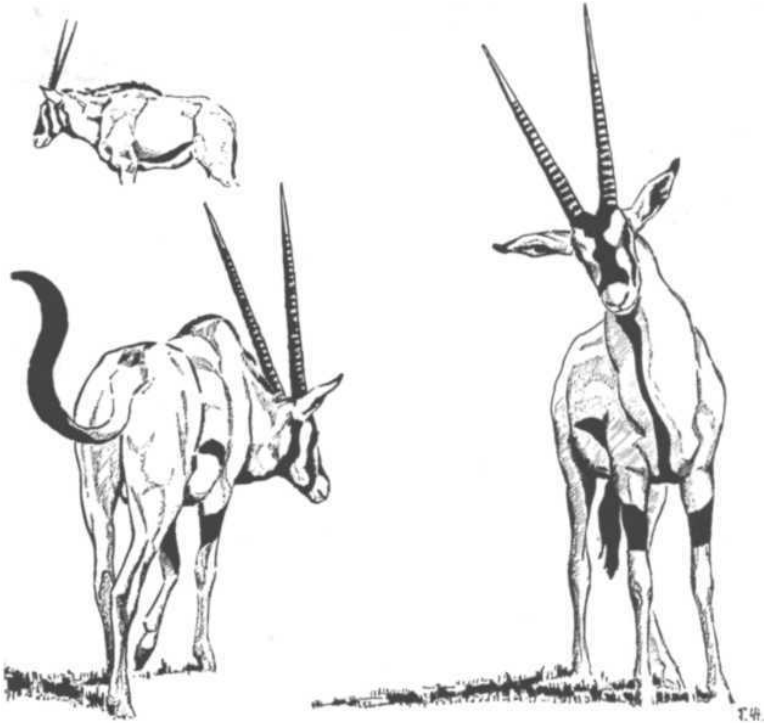

Fig. 8. Horns angled in erected posture and broadside position on part of the superior opponent (right). Intention for head-low posture on part of the inferior opponent (left). Above left: Normal posture for comparison (oryx)

Fig. 9. Nose-upward posture as a response by the female to the male's erected posture (lesser kudu)

Fig. 10. Head-low posture by the female as a response to the male's courtship displays in mating-whirl-around (oryx)

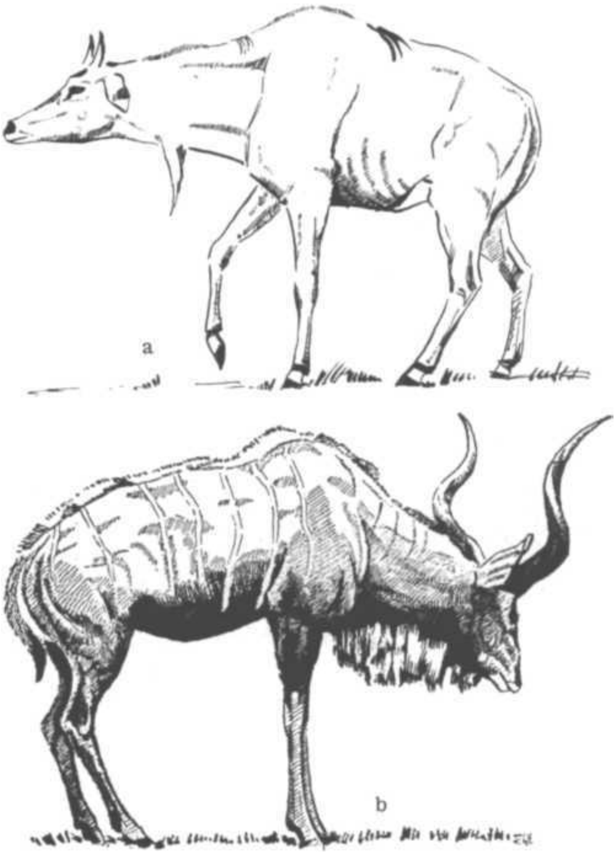

Fig. 11a. Broadside display with head-and-neck-stretched-forward posture (nilgai)
b. Broadside display with head-low posture (greater kudu)

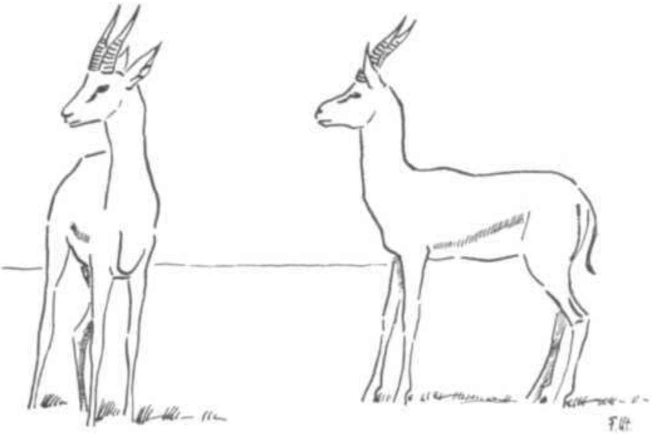

Fig. 12. Broadside posture with sidewards inclination of the head (mountain gazelle)

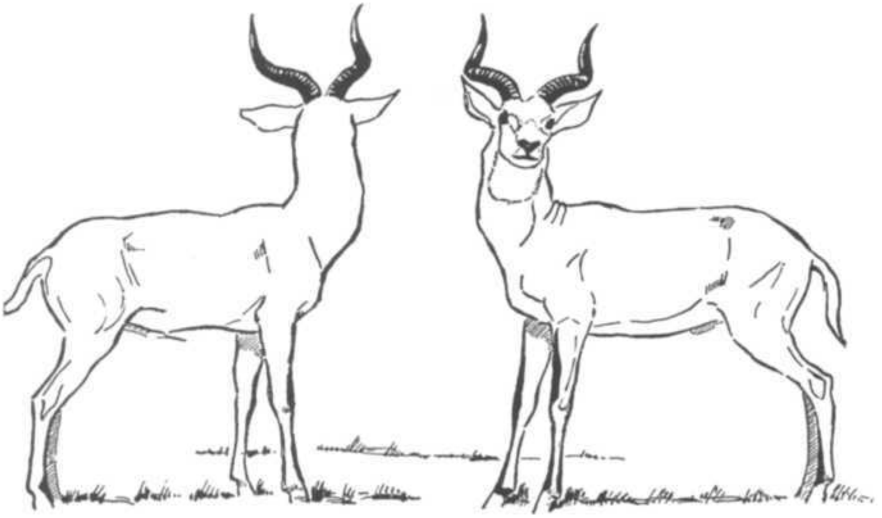

Fig. 13. Head-turning in the erected posture in frontal position (Uganda kob—after photo of W. Leuthold in which the opponents were somewhat farther apart than shown in this sketch)

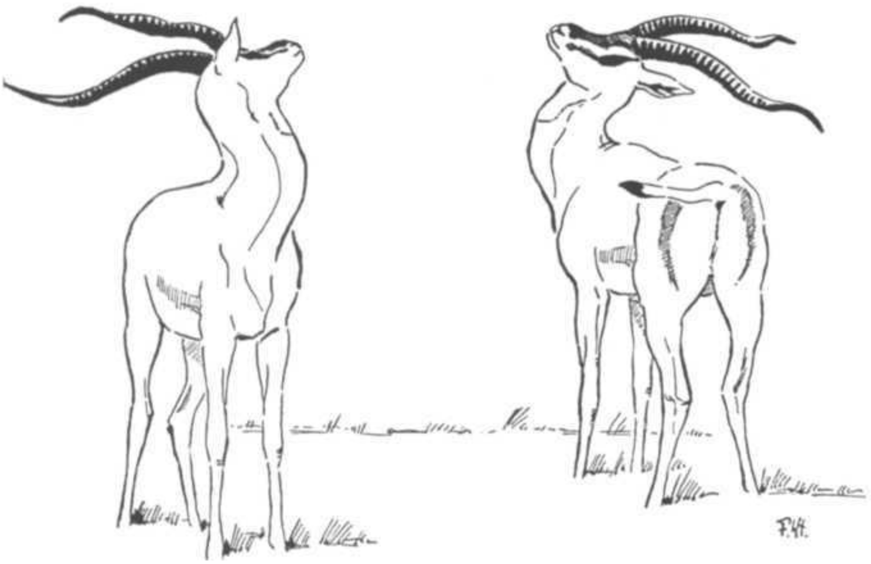

Fig. 14. Head-flagging from the erected lifted-head posture in broadside position (Grant's gazelle)

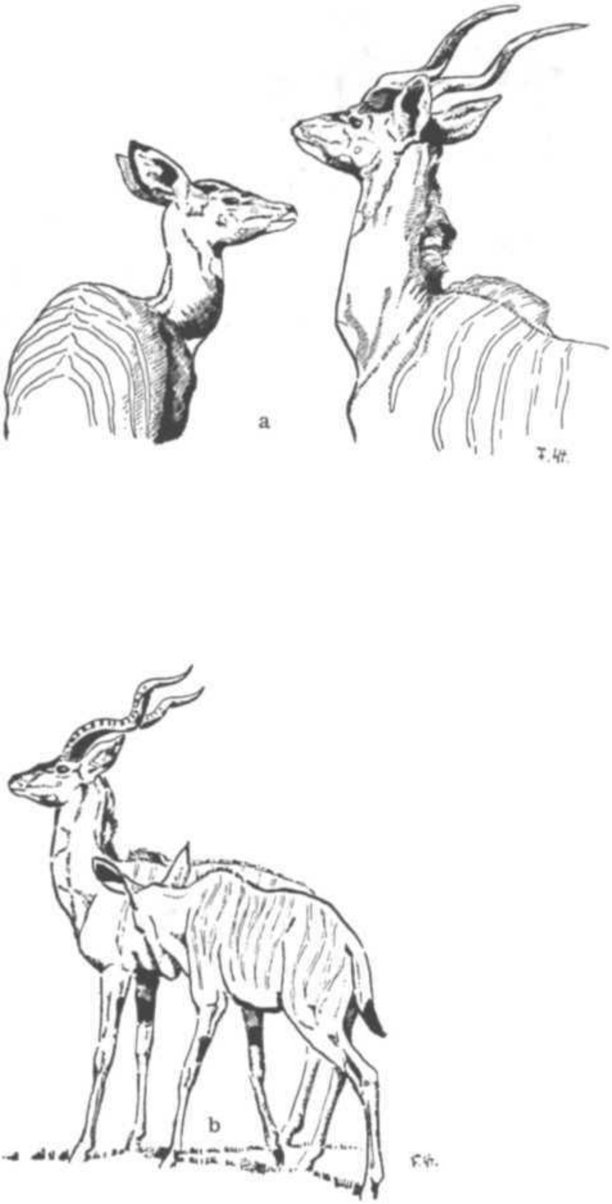

Fig. 15.

Lesser Kudu

a. Lifted-head posture in the erected posture on part of the male (right). Intention for pushing with mouth shut on part of the female.

b. Attack by the female against the male in broadside display

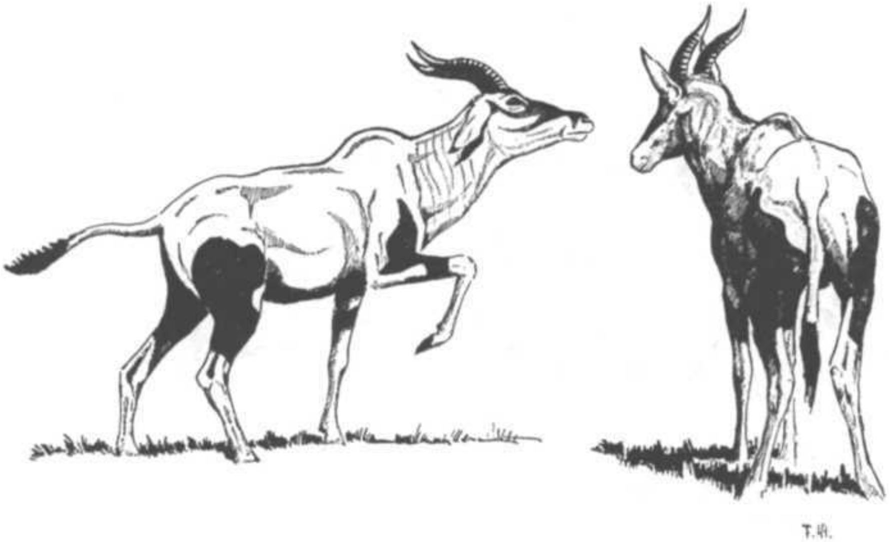

Fig. 16. Lifted-head posture combined with ear-drop and prancing during courtship (topi)

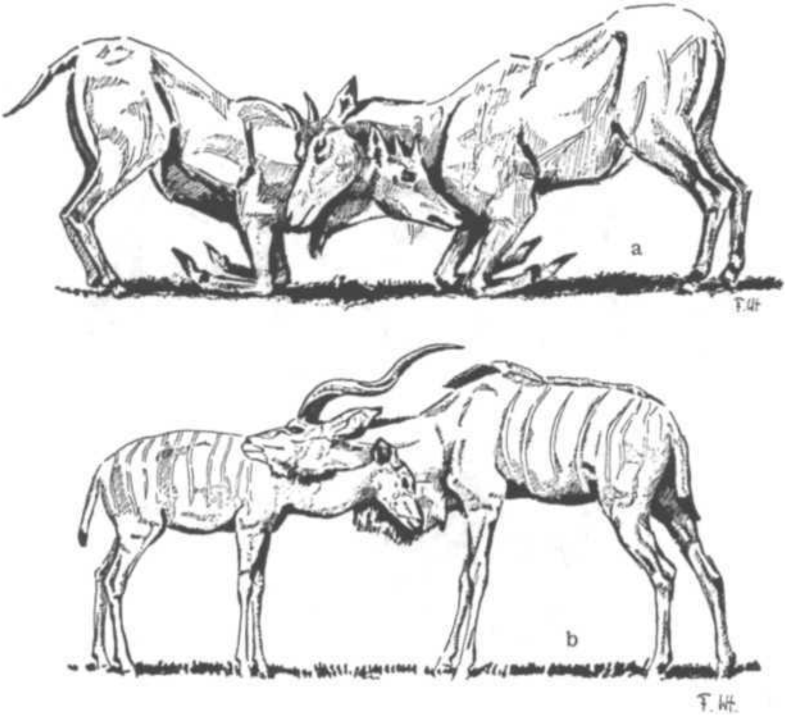

Fig. 17.

Nilgai
a. Neck-fighting of an adult bull with a subadult bull (nilgai)

Greater Kudu
b. Ritualized neck-fight between male and female

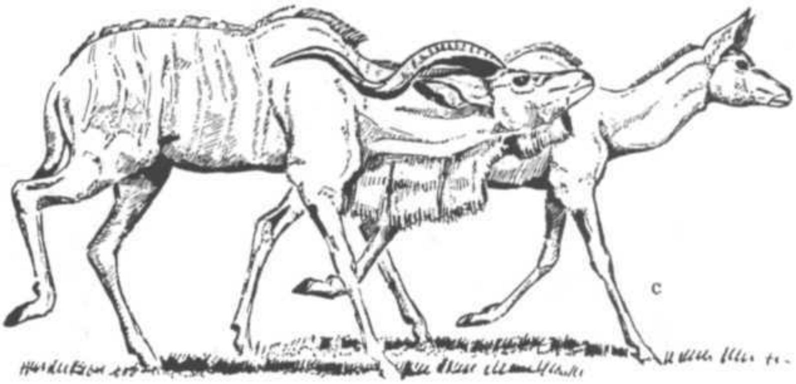

Fig. 17—*cont.*

c. Head-and-neck-stretched-forward posture (Überstrecken) during lateral escort

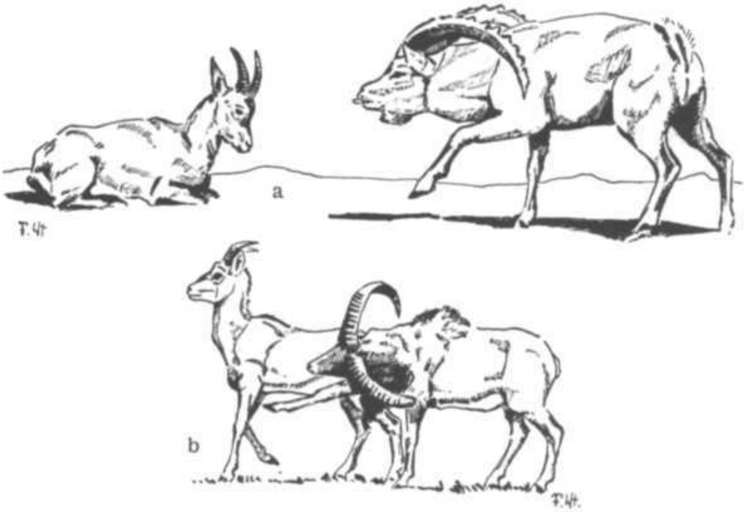

Fig.18

a. Symbolic kick with the foreleg (Laufschlag) combined with head-and-neck-stretched-forward posture—here shown in a frontal approach; female is defending with horn presentation (ibex)

b. Laufschlag combined with low-stretch and twist of the head during lateral escort (urial)

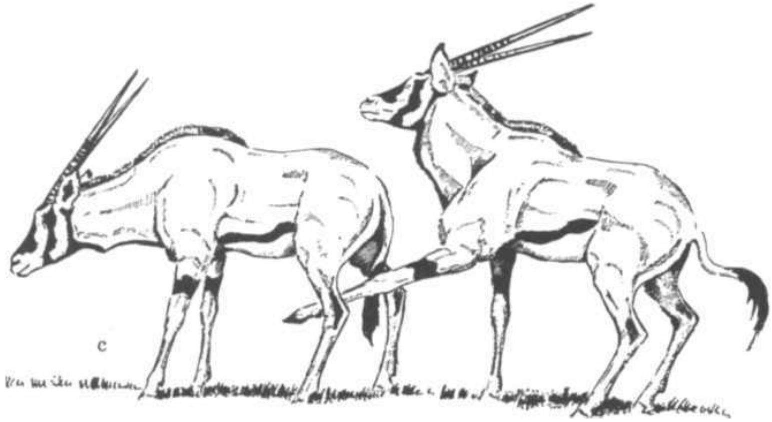

Fig. 18–*cont.*

c. Laufschlag combined with erected posture and intention movements for mounting (oryx)

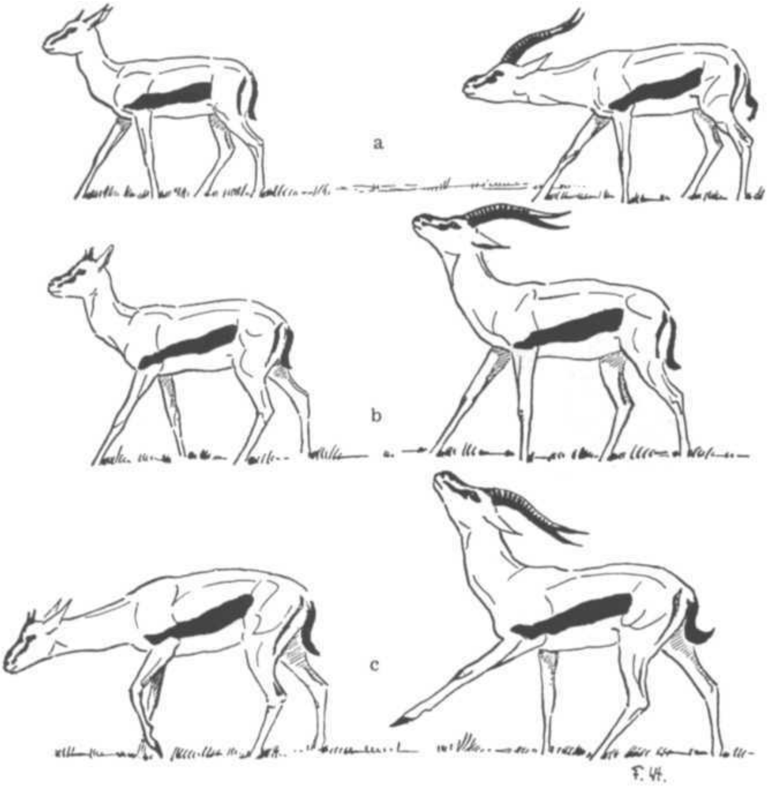

Fig. 19.

Thomson's gazelle
a. Head-and-neck-stretched-forward posture
b. Lifted-head posture
c. Symbolic Laufschlag combined with lifted head posture

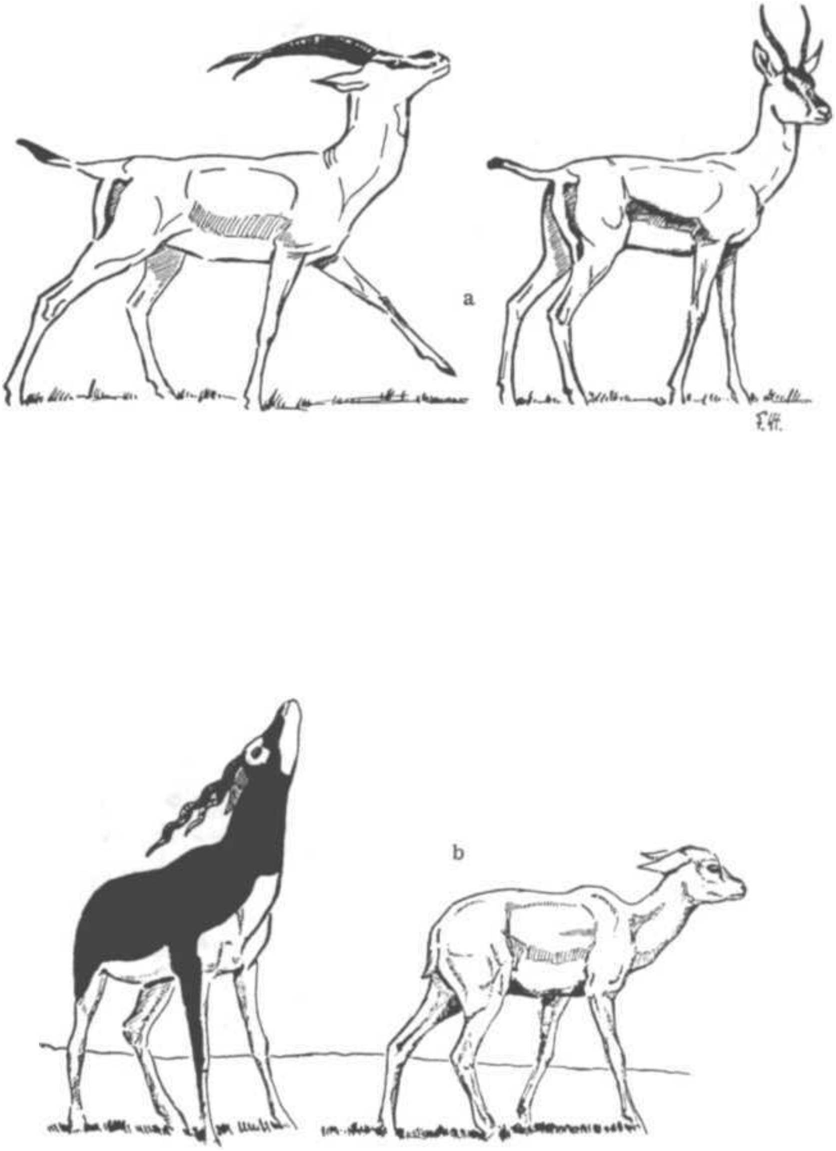

Fig. 20a. Lifted-head posture with Laufschlag-relic (Grant's gazelle)
b. Nose-upward posture as exaggeration of the erected lifted-nose posture (Indian blackbuck)

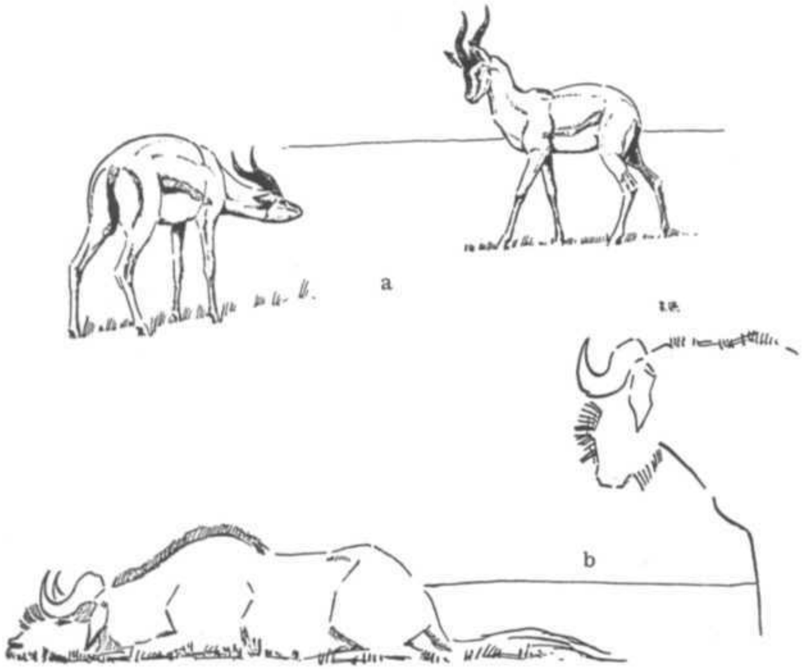

Fig. 21a. Submissive posture (left) as response to the threat of a superior opponent (dorcas gazelle)
b. Submissive lying down in front of the superior opponent (black wildebeest)

## COURTSHIP DISPLAYS

Admittedly, the word 'courtship display' is not a very good term but it is at least brief. To be more precise they are displays related to dominance displays but used by males exclusively or predominantly toward females. Females rarely show these displays. The displays usually shown by females during the courtship ritual are either sexual behaviour patterns in the strict sense (e.g., lifting the tail before copulation) or 'tool-activities' ('Werkzeug-Aktivitäten', Lorenz, 1963—e.g., walking in front of the male), or the species-specific (defensive) threat displays, rarely dominance displays, or often submissive displays, as they also occur in encounters with opponents of the same sex.

As mentioned above, the transition between dominance and courtship displays is a continuum. In certain species some dominance displays may be used against partners of either sex. As an example of such a case we can stay with the just described display of Grant's gazelle. Usually head-flagging is not shown by the buck in courtship probably because the male follows behind the female in the mating ritual of this species. Occasionally they may come into a reverse-parallel position, and then sometimes the male head-turn occurs also in the courtship ritual; however, this is rather exceptional. On the other hand, the erected posture with lifted nose which regularly preceeds head-flagging, and sometimes may even occur without it in hostile encounters, corresponds precisely to the posture almost permanently displayed by the buck during courtship. Furthermore, females may also show the erected posture and head-flagging in agonistic encounters, although not as frequently as the adult males. Relatively often in courtship, a female may perform the erected posture and head-flagging symbolically 'into the air', since she is standing or walking in front of the male and facing in the same direction as he is, when she obviously has reached the highpoint of the heat. Almost regularly, the driving buck responds by mounting (challenging effect ?). Thus the erected-neck, the lifted-head posture and, to a lesser extent, even the head-flagging in Grant's gazelle may be taken as examples of displays used in aggressive encounters as well as courtship.

For a better understanding of courtship displays in the strict sense, it seems advisable to start out with a discussion of their effects and functions, and to describe the phenomena later.

Hediger (1941) pointed out the importance of individual distance in an animal's life. Furthermore, in general a gregarious animal always seems to try to act as dominantly as the situation allows. In copulation, however, the individual distance between male and female has necessarily to be become zero, and the female has to literally act the role of the 'subordinate' partner. Thus, the behavioural problems of courtship are: (a) the male—who usually makes the approach—has to overcome the female's reaction (aggression or flight) to his close approach; (b) he has to manoeuver her into the (subordinate) posture and position necessary for copulation; and (c) the female has to overcome the male's aggressiveness and, despite her inferior role, has to prevent him from treating her as a defeated conspecific. Seen in this light, courtship is a rather delicate biological problem.

Pure offensive threats from the male would be suitable only in that they may release submissive behaviour on part of the female. On the other hand, they may release counter-display and fight, strong defence, withdrawal, or even flight. These responses do not assist mating. The few offensive threats which are shown in the courtship of certain species, are typically forms which show transitions to, or combinations with, features of dominance displays. Space claims (see below) are also not suitable because the sexual partners have to be close together. Defensive threats are possible but usually only on the part of the female in order to prevent the male from becoming too aggressive. If both partners were to rely predominantly on defensive threats, the very necessary approach would never be made. Dominance displays as milder forms of aggressiveness are not completely out of place and, as mentioned above, some dominance displays are actually used in the courtship rituals of certain species. In other species, however, they do not seem to be a perfect solution; sometimes because, although milder in form than the threats, they still may be mistaken for indications of hostile intentions, sometimes because not all species have developed dominance displays. Thus, displays are 'required' which intimidate or possibly also challenge the partner to some extent without releasing strong escape reactions, severe defence, or attack.

I have mentioned several times in this paper the possibility of phylogenetic relicts in expressive behaviour. An expressive behaviour having originated from a form of aggression which is no longer used in the hostile encounters of a recent species, would possibly fulfill the requirements of a courtship display. It is an aggressive behaviour by origin and therefore may still have some intimidating or challenging effect upon the receiver. On the other hand, it is unmistakably different from all the recent forms of aggression so these effects are not strong. We do not, of course, know anything about the behaviour of the extinct ancestors of our recent bovids. However, we know from paleontological evidence that they did not have horns. Nevertheless, they presumably had their fights which were somewhat different from those of the recent horned ungulates. The study of the fighting behaviour of recent species similar to bovids but lacking horns may suggest possible fighting techniques for the hornless ancestors of recent bovids. Possible candidates for this study are hornless artiodactyl species (such as llamas), species which have antlers only temporarily usable as weapons (cervids), and hornless female bovids. When we find corresponding behaviour patterns in recent bovids and when the addressee still shows reactions which agree with the possible origin of these displays from fighting techniques, the probability that evolution may have taken this course is as high as it can be in the circumstances.

It is surprising how many more or less different fighting techniques have been found in 'unarmed' artiodactyls such as tylopods (Gauthier-Pilters, 1954 and 1956). The rivals rise on their hindlegs and jump at each other. To counteract this aggressive jump the opponent may keep its neck steeply erected with the nose pointing upward and may press against the rival with neck and chest. Sometimes this may also occur as a fighting technique on its own. Biting is very common, and the llamas also push strongly with their mouth shut. They try to force the rival down with their muscular neck, or they lower the neck in order to bite the opponent's legs. Sometimes, although infrequently, they may push against each other with the sides of their bodies, and finally they may kick with their forelegs and hindlegs. A good number of the behaviour patterns mentioned may also be used in combination, and for many of these fighting methods there are more or less ritualized intention movements in llamas which act as threat displays.

Except for kicking with the hindlegs, all these fighting techniques, or their corresponding intention movements, do occur in the courtship of recent bovids.

We have discussed how the erected-neck posture and the lifted-nose posture can be interpreted as intention movements for rising on the hindlegs in bovids. Fighting llamas show these postures immediately before jumping against each other. In the mating ritual of llamas the same behaviour may occur when the male jumps on the female from behind in order to bring her down (in tylopods, copulation takes place in a lying posture). Furthermore, as discussed earlier, the broadside display may possibly have originated from pushing with the shoulder or the rump, as occasionally found in fighting llamas.

Biting still occurs in the fights between hornless females of certain bovid species and also in species with very short horns (duikers). The corresponding expressive behaviour of symbolic snapping (Fig. 6a) is shown as a female threat display in a good number of bovid species (Walther, 1964a). Real and symbolic pushing with shut mouth is even more common (Fig. 15a). With respect to male courtship displays, we have already mentioned the head-and-neck-stretched-forward posture, which is a wide-spread courtship behaviour in bovids. Possibly the origin of this posture may be an intention movement for biting. This is likely for all those species in which the male directs its mouth towards the female and 'twists' his head, as is typical for biting species. Interestingly enough, all the recent Caprinae species, as well as a few others, perform flicking movements with the tongue in the low-stretch posture. This would indicate that there is (still?) some nervous excitation taking place in the mouth organs simultaneously with stretching the head and neck forward. In the tragelaphines this posture ('Überstrecken') is clearly an intention movement for neck fighting which is a fighting technique in the llamas, and which occurs in the courtship behaviour of the greater kudu in a slightly ritualized form (Fig. 17b). In other tragelaphine species the males at least lay their head and neck on the female's back in mounting. The assumed origins of the head-and-neck-stretched-forward posture from the neck fight and from biting do not exclude one another since in fighting llamas both behaviour patterns are often combined.

Erecting the neck steeply with the nose pointing upward (counter-acting the aggressive jump in llamas) is a gesture of the female's defense, found in lesser kudu, Sitatunga, bushbuck, etc. (Fig. 9). In other species such as the Indian blackbuck, a very similar posture is typical in the male's courtship (Fig. 20b). Although it does not occur frequently, it is interesting that at least occasionally the courting male blackbuck may push the female with his chest and the lower part of the neck—precisely what fighting llamas or hornless female nilgai do.

As a last example I would like to mention the kick with the foreleg ('Laufschlag', Walther 1958a). This is a wide-spread male courtship behaviour in bovids, especially common in the Antilopinae, Hippotraginae, Reduncinae, Neotraginae, Cephalophinae, and Caprinae (Walther, 1960c), and also found in the non-bovid okapi (*Okapia johnstoni*). In most of the species, the Laufschlag actually touches the female's body, predominantly her hindlegs, but besides this, a symbolic performance is not unusual. In Grant's gazelle and Indian blackbuck, this behaviour has apparently undergone a process of ritualized diminution. It is only a big and emphasized, stiff-legged step with one foreleg so the male does not touch the female at all (Fig. 20a).

In discussions with colleagues, I find that they generally agree with the derivation of the head-and-neck-stretched-forward posture from neck fighting, at least in the tragelaphines. However, not all of them share my opinion about the origin of the Laufschlag from an ancestrial aggressive behaviour. They argue that other interpretations would be possible such as an intention movement for mounting (see Fig.

18c), an infantile behaviour, a ritualized form of scratching the ground, an exaggerated kind of walking, or an expression of a general approach tendency. I have given much thought to these possible objections; however, I have found that each of them applies to only a few of the species which show this behaviour or to a few of the situations in which it may occur or to only a few of the variations and combinations which can be observed. However, if one considers all these different aspects—and I think one has to do so—only the hypothesis of an origin from aggressive behaviour remains in accordance with the facts, i.e., in quite a number of cases it fits very well, and in other cases, it is, at least, a possible explanation.

Everybody who knows the behaviour of fighting tylopods or antlerless cervids, will also know that the behaviour patterns under discussion may often occur in combination with one another. If some of the courtship and dominance displays of recent bovids have evolved from these original fighting techniques, we may expect that corresponding combinations may also occur in the courtship behaviour of the bovids. This happens so frequently that I will mention only a few examples.

Fighting llamas may raise on their hindlegs *and* try to push each other down with their necks at the same time. Correspondingly, mounting and pressing head and neck on the female's back are combined in the male tragelaphines. Interestingly enough, in species which also show the head-and-neck-stretched-forward posture (e.g., certain Antilopinae and Caprinae) but lack the ritualized neck fight in mating, the mounting posture is different, i.e., these animals do not lay head and neck on the female's back in mounting.

Fighting cervids rise on their hindfeet *and* beat with the forelegs simultaneously. In certain bovids such as topi and oryx antelope, the Laufschlag is frequently combined with clear intention movements for mounting (Fig. 18c). As discussed elsewhere (Walther, 1960a), this is different in other species in which Laufschlag and mounting usually occur separated from each other. However, for example in gerenuk, Thomson's gazelle, Indian blackbuck, etc., the Laufschlag is frequently combined with lifting the head, an intention movement for rising on the hindlegs; and/or the nose-upward posture becomes strikingly pronounced at the moment when the animal performs the Laufschlag (Fig. 19b & c).

In horses and red deer the aggressive kick with the foreleg sometimes may be performed *simultaneously* with biting. In this case, of course, the animal must stretch head and neck straight forward to reach the opponent. Correspondingly, in the courtship of the Caprinae the low stretch and the Laufschlag may be combined (Walther, 1960b).

Perhaps these latter two cases may be taken as a little demonstration for our previous discussion on the origin of the Laufschlag. As pointed out, it is possible in the Antilopinae to interpret the Laufschlag and the lifted-head posture as well as their occurrence in combination by mutual origin from aggressive behaviour. On the other hand, in *this* case, the derivation from sexual behaviour could also be taken into consideration (provided one does not care that the stiff-legged rising of the foreleg, so typical and common in Laufschlag, is difficult to derive from mounting). However, as soon as one looks at the combination of the Laufschlag with the low stretch in the Caprinae, the hypothesis of a mutual origin from mounting has to be dropped; on the other hand the hypothesis of a mutual origin from aggressive behaviour can be applied and can also make the combination of the two behaviour patterns understandable.

Obviously the original aggressive component of courtship displays is still recognized by the conspecific partners and they react to it. Again I can bring only a few examples in the space available and, since the courtship displays are predominantly performed by the males, I will restrict the discussion to the examples of female responses.

In certain circumstances, misinterpretations of the male's courtship displays do occur, i.e., the female reacts by true withdrawal or flight as for a threat. This is especially common for females not yet at the peak of estrus. Even when the female is in heat, over-intensive or too frequent displays of the male may release the same responses.

It also happens, although less frequently, that the female may react with a dominance display or a threat which may even result in a fight between male and female. This takes place in some species rather regularly when the male is too young, but in Grant's gazelle it even happens occasionally with a fully adult male. In Thomson's gazelle, the female may sometimes react to the male's Laufschlag by symbolic butting in the air, and in the Sitatunga a female responds rather regularly with symbolic neck-fight movements and snapping into the air when the male touches her with head and neck stretched forward (Fig. 6). Thus, the two most important effects of a threat display—intimidation and challenge—may also show up as effects of courtship displays in certain species and/or in special situations.

Besides such special cases, in many species the female responds to the male's courtship display by an only moderately ritualized withdrawal; she walks in front of him and he follows her, as in pursuit of an inferior opponent. In several species the female may even show a ritualized flight with the male pursuing her at a gallop, as an obligatory or facultative phase of the mating ritual.

In other species, the mating march is reduced to a minimum or may be lacking completely, and the animals remain more or less at the same place during courtship. In the oryx and its relatives, the female reacts to the male's approach and courtship display with a pronounced and permanently held head-low posture, a defensive threat or even a submissive display, as it is also shown by an inferior male in a hostile encounter. Then, the bull and the cow circle around each other in reverse-parallel position, a mating-whirl-around ('Paarungskreisen', Walther, 1958a), again an almost identical figure to the circling as it occurs in a threat encounter between a very superior and a very inferior male in this species (Fig. 10).

In many bovid species the female's posture during copulation is related to a defensive threat or even a submissive behaviour (lowered head), and the most common position of the female immediately before copulation, with her hindquarters towards the male, coincides with the turning of the rear end towards the superior opponent in submissive behaviour. As mentioned above, it seems to be one of the functions of the male's courtship display to manoeuvre the female into such a posture and/or position.

Usually we can distinguish several phases in the mating ritual of bovids. The first phases(s) are characterized by pronounced courtship displays of the males for which the females react by only moderately ritualized withdrawal or flight or by submissive displays or by defensive behaviour. Then often follows a phase in which no special displays are shown—in gazelles, the relatively quiet mating march, in oryx standing in reverse-parallel position, etc. In the phase immediately before mounting, the males often once again show an increase of courtship displays, sometimes the same as in the initial phase(s), or sometimes different ones. In certain species the Laufschlag now acts an especially important role, in some species the head-and-neck-stretched-forward posture, in others the combination of both, etc. In this progressive phase of the courtship ritual the female does not react very much to the male's displays, and the latter may be interpreted as 'last inquiries'. When the female does not react to them she has reached a state in which she is ready to tolerate the male's approach and mounting, without defence or escape reactions. To bring her into this state, is the other function of courtship displays.

Some 'courtship' displays also occur in other situations than mating. Especially behaviour patterns belonging to the first phase(s) of the mating ritual are often used when males herd females within their territories which is not a sexual behaviour in the strict sense. The same and some further courtship displays are also used by the males to make resting females stand up. In this situation sometimes the Laufschlag changes into scratching the female's back. In the mountain gazelle (*Gazella gazella*), even *females* were observed using the Laufschlag when rousing a conspecific from rest (Grau, pers. comm.). In the genus *Ovis,* the Laufschlag occurs in courtship as well as in hostile encounters between rams (Geist, 1966; Walther 1960a.).

The most interesting aspects of functions of courtship displays compared to the functions of threat displays occur in species such as Thomson's gazelle where the males have a completely different behaviour inventory for fellow males and for females. I have described how the bucks threaten each other with their horns when the herd changes the activity, when the direction of a move is not yet determined, or when the migration slows down. In migratory herds, where males and females run together, the males use the head-and-neck-stretched-forward posture and the lifted-head posture against females in precisely the same situations in which they threaten the other males with their horns. In other words, in these situations, these 'courtship' displays have the same effects upon the females as the threat displays have upon other males, and very obviously both of them serve the same function.

## SPACE CLAIM DISPLAYS

In hostile encounters further behaviour patterns may occur which are somewhat related to threat or dominance displays but are, on the other hand, obviously different. One could even doubt whether they belong to expressive behaviour with a function in social communication as defined, since they often do not have a clear effect upon the addressee. They seem to be connected to behaviour used in relation to space, the environment or the ground. They are not restricted to hostile encounters but they may also or even primarily show up in other situations.

In animals which mark by means of special glands—herein the preorbital glands seem to be especially important in certain bovids—and/or by urine and feces, such marking activities frequently occur in connection with hostile encounters. In the case of territorial animals, this marking may serve to make the boundaries and other important points of a territory better recognizable for other conspecifics and the owner himself. I even think the latter is the primary function, it being important for the owner's spatial orientation. In hostile encounters—we will not discuss here other functions of marking, or marking in other situations—this means that the owner can retreat to the marked area if necessary, as this is his territory into which no opponent will follow easily. If the animal is not territorial, it may create a starting point by marking to which it also may retreat in a pause during the fight—comparable to the 'corner' in the boxing ring.

Furthermore, by marking in hostile encounters the animal claims occupancy—literally in case of a territorial animal, symbolically and only temporarily in the case of a non-territorial animal. This may have intimidating effect upon a conspecific which has no 'rights' on this particular place. When two rivals mark simultaneously, each of them claims the same or the adjacent place for himself. This can be interpreted as a challenge. Thus, in hostile encounters marking may have rather similar effects and functions as a threat.

Very similar aspects are true for pawing the ground with the foreleg which in some species precedes urination and defecation. The function of this behaviour is not completely clear; it may be that the animal deposits a secretion from the interdigital glands in this way, or that the scratches on the ground act as a visual mark, but there are even more theoretical possibilities. In some cattle species and in the wildebeest (*Connochaetes taurinus*), pawing the ground seems to be more related to rolling on the ground (Schloeth, 1958). By pawing the ground, often followed by digging the ground with horns, in these species, the animal may prepare the place for wallowing. Territorial wildebeest bulls have often a definite wallowing place within their territories. With respect to cattle Schloeth (1961) has developed the interesting hypothesis that it may be some kind of social privilege of high-ranking members of a group to use a wallow before others do. Possibly also wallowing *per se,* e.g. in bison (*Bison bison*), in the presence of a rival may belong to this category of behaviour. Thus, again there seem to be connections with the use of space and 'claims' of space, respectively.

When we compare this pawing the ground as a possible agonistic display in a number of bovid species, there is apparently a tendency of this behaviour to become independent from its connections with urination, defecation or wallowing. In territorial Thomson's gazelle, pawing the ground precedes urination and defecation, and it may occur in both combat situations and non-combat situations; however, it seems that the frequency is higher in hostile encounters. There are also rare but clear cases in which the gazelles paw the ground before or during a fight without urinating and defecating after doing so. Similar things are also true for some other species. With respect to these relatively rare cases, one could still argue tht the animal has urination and defecation 'in mind' after pawing the ground but did not get around to doing so because of the pressure of the situation. However, in oryx antelope pawing the ground without defecation precedes a fight so frequently that this argument can hardly be held for this species. So, in some species, a separation of this behaviour from defecation is rather obvious and, in this way pawing the ground comes even closer to a threat behaviour. It may be that this is a recurrent development, and that pawing the ground has evolved as a kind of symbolic or redirected aggression from beating with the forelegs during a fight.

In this respect, but also in regard to its close connection with pawing the ground in some species, digging the ground with the horns or fighting an inanimate object, or weaving as a ritualized form (Fig. 4), may be related. We have discussed this behaviour when talking about redirected aggression in threat displays but we also stated that it is not quite equivalent to other threatening behaviour and that its effects and functions are not as clear. We may further add that there are also resemblances to marking behaviour.

As a last behaviour possibly belonging to the category of space claims I would like to mention agonistic grazing. Grazing in hostile encounters is very common in horned ungulates and probably has somewhat different meanings, functions and possibly also origins in different species. One point seems to be shared by all variations: in fighting as well as in certain threat postures and also in certain submissive displays, many ungulates lower the head. Thus, they are in a posture which is also proper for grazing. According to the mechanism of transitional activity (Lind, 1959), they may easily switch to grazing. In other words, the sometimes variable meaning of agonistic grazing is linked with the problems of the head-low posture, the meaning of which varies according to its position in the entire behaviour inventory of different species, and even within one and the same species this posture may show transitions between an aggressive and a submissive behaviour.

The most detailed analysis of agonistic grazing up to now, has been given by Estes (1969) with respect to the combats of territorial wildebeest bulls. He discussed it as a possible displacement activity, a transitional activity, a neutral activity, as related to submissive behaviour, and as a means of reassurance from fear, and he emphasized generally the basically non-aggressive character of agonistic grazing. I doubt this last point. The other statements may be taken as an indication that the agonistic grazing is a rather complex behaviour and not easy to interpret in wildebeest and in certain other species. In case of such a wide-spread behaviour, however, it should be possible to find some species in which this behaviour is somewhat simpler and easier to analyse. This in turn, may help to a better understanding of more complex and complicated situations in other species.

Apparently in some species such as Grant's gazelle and oryx antelope, the meaning of agonistic grazing is clearer in that it occurs predominantly as the reaction of an inferior animal to the dominance or threat displays of a superior opponent; in these species it is very closely related to a defensive threat or even a submissive behaviour.

On the other hand, in the Thomson's gazelle a grazing ritual is found (Walther, 1968a) the meaning of which seems to be opposite that of grazing in combat situations in Grant's gazelle and oryx. This grazing ritual is exhibited exclusively by adult males, predominantly by territorial males. It rarely precedes a fight. Incomplete attempts at starting a grazing ritual are frequent during pauses in a fight, but the complete and pronounced ritual is seen only after the end of a fight or in place of a fight. It is always performed by both opponents, and the striking point—which makes me use the work 'ritual'—is a very pronounced and predictable change of the positions between the rivals. Grazing almost uninterruptedly, they go through a frontal position, a parallel or reverse-parallel position, and an opposite position—hindquarters to hindquarters. These three changes in the positions of the combatants are the minimum, and sometimes the opponents may graze side by side along the entire neighbouring boundary of their territories and back again; or from the parallel or reverse-parallel position one of the combatants may turn again into a frontal position towards the rival, and the other may turn in the same direction grazing now with his hindquarters towards the opponent, in front of him. Following, while still grazing, the first buck 'grazes back' the opponent in the direction of the centre of the withdrawing rival's territory until the latter turns, uninterruptedly grazing, from a broadside into a frontal position. Now the intruder may turn 180° and graze back to the starting point, followed by the grazing opponent. Then they may continue, again, grazing parallel along the boundary, etc., till finally both animals turn—still grazing—into opposite directions, and each of them grazes back to the centre of its territory. Such a grazing ritual may last from a few minutes (when after a fight the rivals merely go through the obligatory frontal, broadside and opposite position) up to half an hour and longer when they exercise around the boundary in the manner described.

As mentioned above, the opponents often come up to a true grazing ritual only after several incomplete trials in which they change from grazing back to fighting. This happens only very exceptionally from grazing in an opposite position, occasionally from grazing in a broadside position, but very frequently from grazing in frontal position. In the latter case, the grazing posture and the fighting posture are so similar that, under slightly unfavourable observation conditions, I sometimes had difficulty in distinguishing whether they were still fighting or already grazing, or *vice versa.* Thus, in this species, agonistic grazing is rather closely connected with fighting, and one may now understand better my scepticism with respect to the 'basically non-aggressive character' of this behaviour.

Furthermore, as mentioned in the discussion on threat and dominance displays, in certain bovid species the hornless females snap actually or symbolically in hostile encounters, besides pushing with their bare fronts and other fighting techniques. In greater kudu, lesser kudu, and Sitatunga I observed clearly snapping movements with the mouth into the air simultaneous with pushing of the opponent with the front. In grazing the animal performs movements with the mouth which are similar or even identical with biting. It has been shown in certain fishes that a significant connection between feeding and aggressive biting is possible (Albrecht, 1966). In combination with the observation of aggressive snapping in certain bovids, one could speculate that agonistic grazing may be related to the—in these animals, phylogenetically old-aggressive biting. This hypothesis would explain why grazing occurs so often in hostile encounters in ungulates, and it seems reasonable to assume that in some species this phylogenetically old aggressive behaviour is still more closely related to fighting than in others where it has been replaced by more recent fighting techniques and thus, as with certain defensive threats, comes close to being a submissive behaviour when performed as a response to the opponent's acute horn threat or dominance display.

When grazing in a frontal position after a clash, Thomson's gazelle bucks immediately enlarge the distance between one another by stepping backwards. In this species, as apparently in most, possibly all ungulates, the individual distance has not a constant size, but it depends on age, sex and activity. It reaches its largest extent in adult males and in grazing. When the animals clash together in a fight, the individual distance is zero. By simultaneous grazing immediately after the fight the opponents signal a return to the (large) grazing distance to one another. Used in a frontal position the grazing posture allows the gazelle to go immediately into fighting action again, if necessary. The parallel or reverse-parallel broadside position has probably the same origin and basic meaning as other broadside displays—blocking the way—, as is rather obvious in grazing along the boundary. Finally in the opposite—hindquarters to hindquarters—position, agonistic grazing, according to its possible connection with a phylogenetically old fighting behaviour, may allow an exit without 'losing face'. This last point is very important to a territorial animal since here a clearly inferior behaviour would mean the loss of a part of the territory or even of the territorial status, as Estes (1969) has convincingly pointed out.

In short, at least in Thomson's gazelle, the grazing ritual seems to belong to that category of expressive behaviour which is connected with space relations.

## EXCITEMENT ACTIVITIES

As mentioned earlier, I do not like the term 'displacement activities' since one cannot use it without buying a whole theory. For a few behaviour patterns which are usually described under this heading, I use the term 'excitement activities' because, at least in ungulates, they are not restricted to social encounters, such as combat or courtship, but they also occur in many other and different situations (Walther, 1969b), and they indicate rather generally and unspecifically that the animal is restless. In favour of the old conceptions, one could perhaps assume that this excitement may be linked with an inner conflict, but then this conflict boils down to the very general formula 'Better to stay or better to go ?', and 'to go' does not necessarily mean an escape reaction.

In horned ungulates, such behaviour patterns are predominantly grooming, scratching, shaking, the volte (stepping around in a narrow circle), sometimes a vertical jump on the spot, and perhaps also stamping. I am not quite sure about the latter since I do not have many comparative observations on it.

Probably due to their very general and unspecific meaning, these behaviour patterns usually do not release striking responses above the level of occasional contagion. Thus, if they should have any importance in social communication at all, it is not clear at present. Probably these behaviour patterns give a certain relief to the performer.

## SUBMISSIVE DISPLAYS

The submissive behaviour in ungulates appears to be performed predominantly on the principle of being the opposite to dominance and offensive threat displays. In certain features, submissive displays are related to hiding or flight behaviour. On the other hand, sometimes connections to aggressive behaviour (defensive threat displays) are given, as mentioned above. When submissive behaviour is mainly the opposite to offensive threat and dominance display, submissive displays will show species-specific differences corresponding to the species-specific differences in threats and dominance displays.

Generalizing my observations on some bovid species, submission is predominantly expressed (a) by lowering the neck which is opposite to the wide-spread erected postures in offensive threats and dominance displays; (b) by holding the head downward-forward and laying the horns back on the neck, a posture which is opposite to the wide-spread presentation of the horns in threatening (Fig. 21a); (c) by turning the hindquarters towards the opponent which is opposite to the wide-spread frontal approach in aggression, and which is also opposite to the broadside presentation, since in the latter a bovid appears as broad as possible while from the rear it appears as small as possible; and (d) by lying down flat (Fig. 21b), by which the animal, so to speak, blends into the ground, which is opposite to the self-exposure especially in the dominance displays. In a completely submissive animal these behaviour patterns occur in the sequence mentioned above, which expresses a gradual increase in the intensity of submission. One exception is relatively common: an animal may lie down without previously having turned its hindquarters towards the opponent. When the submission is not as complete, the animal may show only the first phase(s) of this sequence. In the *Alcelaphus* and *Damaliscus* species, the submissive posture deviates from this general scheme. Here the submissive animal holds its head in a posture similar to the medial horn presentation of other species. Gosling (pers. comm.) observed even moderate butting from this posture against the superior opponent. Thus, an aggressive (defensive ?) component seems to be in it. Maybe, in evolutionary terms, it is an originally aggressive behaviour 'on its way' towards a submissive display. As some threatening behaviour patterns anticipate the fight or even the victory, so these submissive postures anticipate defeat.

Because the submissive displays lack the features which could challenge an opponent and release his aggression, the effect is that he calms down and may even stop the aggression completely as there is nothing left with which to fight.

In some cases, these postures, gestures and positions are similar or even identical with behaviour patterns typical for young animals or for females in the mating rituals. So the question arises whether an inferior animal—including an inferior male—in a submissive display mimics the female or a juvenile animal, or whether, *vice versa*, the young animal or the female in estrus behaves like an inferior partner in a hostile encounter. In some cases, this is difficult to determine. In bighorn sheep, Geist (1968a, 1968b, 1971) found that the inferior ram in a hostile encounter uses the same behaviour patterns with the same relative frequencies as a female in estrus, and that the superior opponent also treats the inferior one like a female. In some African 'antelopes', I had occasion to study, this was by no means so clear. In certain cases such as the described mating-whirl-around of oryx antelope, I am even convinced that it is the other way around, i.e., that the female in the courtship ritual behaves like an inferior opponent in a hostile encounter. Thus, at present, it seems that we have to take both possibilities into consideration in different species.

In regard to infantile behaviour, the special question is whether a behaviour shown by a young animal, e.g., in the mother-offspring relation, is always a genuine infantile behaviour. Since usually the mother is the first social partner of a young mammal, naturally certain behaviour patterns of social life may be shown for the first time in the mother-offspring relation. This, however, does not prove that they are infantile behaviour patterns. With respect to lying down flat in submissive behaviour, it is, of course, tempting to assume a connection with the infantile lying-out behaviour (Burckhardt, 1958); however, lying down in extreme submission was also found, e.g., in the black wildebeest (*Connochaetes gnou;* Fig. 21b), a species where the young do not stay put (Walther, 1966b).

On the other hand, there are cases in which apparently typical female behaviour assumes the role of submissive behaviour. In species where females fight or threaten by snapping (among other forms of aggression) but adult males do not do so, the female may respond to the dominance or courtship display of the male by symbolic snapping. The same may also occur without any display by the male when a female passes close to him in a group (observed in Waterbuck *Kobus ellipsiprymnus*, eland and Sitatunga). In this latter case one may get the impression that the female emphasizes that she is a female by this behaviour and not an equivalent opponent for an adult male.

I should mention, however, that there are other inferiority or appeasement behaviour patterns, which either do not belong to expressive behaviour (e.g., withdrawal or flight), or of which it is dubious whether or not they should be considered to be expressive behaviour in the terms of our definition, e.g., social grooming (tactile expression ?).

Finally, we may consider the social functions of submissive displays. When comparing the submissive displays of zoo animals and of animals in the wild, I have not found any differences in principle,—the same applies to all behaviour patterns on the level of the fixed action patterns—, but I have found differences in intensity and frequency. In gazelles, I have seen the most intensive form, lying down, rather frequently in captivity but very seldom in the wild; in general, submissive behaviour was observed more frequently in captivity in these and some other species. This difference in quantity and intensity between zoo animals and free-ranging animals seems to be important with respect to function. In the wild an inferior animal very often can retreat from the influence of a superior one simply by withdrawal or, if necessary, by flight. This possibility is diminished in captivity. Thus, the submissive behaviour occurs when the inferior animal is not able or not ready to go some distance away. In other words, the submissive displays enable an inferior animal to remain at a definite place and/or with a definite group despite the presence and the agressiveness of superior conspecifics. Because of the spatial limitations in captivity, such situations occur here more often and are more pronounced than in the wild. However, submissive displays are not completely lacking in the wild, and they can also be observed in free-ranging animals when the corresponding situations are given: for example, if a female during a mating ritual is driven too violently by the male, if a male sexually approaches a female which is not truly in heat, if a female which has just given birth is bothered by a superior conspecific but is not ready to withdraw because of her young, if an adolescent male is attacked or threatened by an adult male and the youngster is not ready to leave the group, possibly because of a still existing bond with his mother, etc.

An extremely interesting demonstration of the function of submissive behaviour occurred during a small study (Walther, 1968b) of the territorial behaviour of Kirk's dikdik (*Rhynchotragus kirki*). A pair had their territory around my bungalow in

Serengeti, and when a fawn was born its preferred lying-out place was right under that bungalow. Since it was growing rather fast, at about five months the fawn was recognizable as a young male, and the father began to treat it as a such. When the young male approached his mother—probably still with 'infantile intentions'—the old male frequently interfered by rushing towards the fawn with a fast spurt, the long hairs of his front ruffled up like a little crown. The young male regularly responded by immediately lowering the head and lying down flat on the ground. The father always stopped his attack one to five yards in front of the submissive fawn and returned to the female. I saw this more than fifty times during one night (so we even have to be careful with the statement that submissive behaviour occurs more frequently in captivity than in the wild: it depends completely on the situation). In this way the young male dikdik managed to stay in the parental territory for several more weeks despite his father's aggressiveness. One may speculate that this prolonged stay in. a familiar area contributes to the survival chances of the young in this species.

## SOME FINAL CONCLUSIONS

I have tried to approach the problems of expressive behaviour by determining its (indicated) meaning, its effects upon the receiver, and its social functions. In some cases, the biological functions (survival value, consequences for the population, etc.) may also be taken into consideration. The latter, however, remain always somewhat speculative.

In methodological terms, the determination of the meaning seems to be the most difficult problem. One has to investigate the relations and connections of the expressive behaviour under discussion with other behaviour. For this reason, it is often necessary to know the entire behaviour inventory of a given species or, at least, large portions of it. In certain cases, even this is not sufficient but one has to compare several —sometimes even many—different species, trying to reconstruct the possible phylogenetic evolution of an expressive behaviour in this way. The determination of the effects and of the social functions is comparatively simple. The effects become obvious from the responses of the recipients. Insight into the social functions can be obtained by analysing the releasing situations under which a given expressive behaviour occurs. Fortunately, all three aspects are connected with one another. It is possible, therefore, to test the correctness of one of these points (e.g., the meaning) with the help of the two others (e.g., the effect and the social function.)

Threat displays always indicate the readiness for immediate fighting. Most of them can be interpreted as intention movements for fighting according to the—sometimes rather different—species-specific fighting techniques. Usually, each species has several threat displays indicative of different degrees of severity of the threat. Some of them are predominantly used by males, others by females. In certain species, there are differences between offensive threats ('I am going to attack you—so you had better step away!') and defensive threats ('I am ready to defend myself—so you had better keep off!'). Offensive threats are sometimes related to dominance displays; defensive threats often show connections and transitions to submissive displays. It is assumed that certain submissive displays have evolved from defensive threat displays. The effects of threat displays upon the addressee are intimidation or challenge, this alternative depending on the sex, age and social status of the opponents. The main social functions are the establishment and maintenance of territories, the maintenance or enlargement of individual distance, the coordination of activities within a group, the determination of the direction and duration of a move (sometimes also of the marching order), the repulse by females of suckling attempts or sexual approaches, the establishment and maintenance of a social hierarchy, and the defense of 'objects of value' such as food, resting places, young, sexual partners, etc. With respect to the biological functions, the two most important points seem to be the avoidance of fights between unequivalent rivals and of surprise attacks between equal opponents.

In contrast to the threat displays, dominance displays do not show connections to recent fighting techniques. Commonly, the animal tries to impress the opponent by height and/or breadth. Thus, the meaning of these displays is the claim of superiority over the opponent, however, without expressing the readiness for immediate aggression ('I am the greatest!'). In these postures and positions the displaying animal exposes itself to possible attacks much more than in threat displays. The broadside presentation has probably evolved from blocking the opponent's path and/or from (phylogenetically old) fighting in parallel or reverse-parallel position. The erected posture seems to have evolved as an intention movement for raising on the hindlegs but it is a debatable question whether this is more closely related to sexual mounting or to the (phylogenetically old) aggressive jump. Dominance displays mature relatively late in the ontogeny, and play a greater role in the encounters between adult animals than in subadults and adolescents, resulting in relatively more frequent fighting in the latter two age classes. Furthermore, dominance displays are more frequent in males than in females. Basically, dominance displays have the same effects upon the addressee as threat displays. They are, however, a milder form of intimidation or challenge. Apparently, this is the reason permitting some of them to be used also in courtship. Otherwise, their social functions are the same as those of threat displays, but their realm is more restricted. Since females and juvenile animals show them infrequently or not at all, they are not used by females for the repulse of suckling attempts and sexual approaches, nor do they show up in mother-offspring relations; also in the defence of 'objects of value' they appear more infrequently than threat displays. Their major biological function is the settling of hostile encounters without fighting and, in this respect, they apparently work even more effectively than threat displays.

Besides threat and dominance displays, certain behaviour patterns may show up in combat situations which obviously are connected to behaviour used in relation to space. From this it follows that they are not restricted to hostile encounters but also and even primarily occur in other situations. The most likely interpretation of the occurrence of these displays in combats seems to be that the animal claims occupancy of a definite place, literally or symbolically ("This is my place—you had better keep out!') Thus, they also may have a certain intimidating or challenging effect.

Often, however, these effects upon the addressee are less pronounced compared to those of threat and dominance displays, and also the functions are often not as clear, and their range is not as broad. In particular, they are not used for coordination of the activity of a group, they are seldom used by females and juveniles, and they also are not seen in courtship. On the other hand, they may occur in the defence of 'objects of value'.

Courtship displays can be interpreted as special kinds of dominance displays—in the majority of the species they are used by males toward females. Their meaning is a claim of superiority combined with an inquiry of the female whether or not she is ready to accept the male's close approach. Their origin from phylogenetically old aggressive behaviour is likely. The effects upon the partner are similar to those of dominance displays, i.e. mildly intimidating (releasing a ritualized withdrawal or flight or another form of inferior behaviour in the female) or very mildly challenging (releasing defensive threatening in the female). These relatively moderate responses, however, are predominantly shown by females in estrus or close to estrus. A non-estrus female may run at full speed when approached by a male in courtship display, or—although more rarely and usually only when the male is clearly younger than the female—she may defend herself seriously. In mating, the functions of courtship displays are to prepare the female for her inferior role in copulation, and to overcome the consequences of the reduction in the individual distance, i.e. so that the female tolerates the male's close approach to touch her, eventually, without flight or aggressive reactions. Furthermore, certain courtship displays are used for herding females without any direct sexual significance. In species in which the males have a completely different behaviour inventory for females and males, certain courtship displays are used towards females in precisely the same situations as threats against other males, as for the coordination of the group activity, the determination and duration of a move, etc. Exceptionally, male courtship displays are even shown by females in these situations. In certain species, the young solicit milk by such gestures. In a very few species, behaviour patterns which are courtship displays in the majority of the other bovid species also appear in hostile encounters with opponents of the same sex, apparently with very similar effects and serving about the same functions as dominance displays.

The excitement activities indicate rather unspecifically that the animal is more than usually excited. They are not restricted to hostile or sexual encounters, but may occur in many different situations having in common only that the animal is under a certain situational stress and perhaps in an inner conflict. Except for occasional contagion, no effects upon the partner are known at present, nor is much known of their social functions. Probably these behaviour patterns give a certain relief to the performer.

Usually, submissive displays in horned ungulates are in every way the opposite to dominance and offensive threat displays. As mentioned above, sometimes there are connections with certain defensive threats. The meaning of submissive displays is the acceptance of the inferior role. They anticipate defeat and lack features which could possibly challenge an opponent and release his aggression. Correspondingly, their effect is that the challenger calms down and may cease his aggression completely or at least diminish its intensity. In certain situations, some submissive displays may also have the effect that the challenger switches from aggression to sexual behaviour. The social function of the submissive displays is that an inferior animal does not have to withdraw when threatened by a superior one, but it can stay within the group or at a given place. This also plays a role in mating where the female often responds to the male's dominance or courtship displays by submissive behaviour, accepting the male's approach in this way. In certain species, submissive displays enable the young animal to stay together with its mother for a longer while or to remain in the parental territory even after it has reached an age at which its presence releases the aggression of the parent; thus submissive behaviour may indirectly contribute to the survival of the young.

In bovids, evidently each expressive behaviour has basically only one meaning, usually two (dichotomous) effects, but multiple social functions.

A summary review of some of the behaviour patterns discussed and of their distribution in the different species is given as Appendices to this paper in Tables 3-5.

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TABLE 3. THREAT (AND RELATED) DISPLAYS

| Species |  a |  b |  c |  d |  e |  f |  g |  h |  i |  j |  k |  l | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bos primigenius | ++ | – | – | – | (+) | | | | + | – | ? | + | Schloeth 1958 |
| Bibos gaurus | ?? (1) | – | – | – | – | ? | + | ? | | – | + | + | Antonius 1939; Schaller 1967 |
| Bison bison | ++ | – | – | – | | ? | + | | | – | | | McHugh 1958 |
| Boselaphus tragocamelus | – | + | + | exc(2) | ++ | | | | + | – | | ? | Walther 1958 & 1966 |
| Tragelaphus scriptus | – | + | + (3) | – | – | exc | + | | + | | + | ++ | Walther 1964 |
| Tragelaphus spekei | – | ++ | + +(3) | – | – | exc | exc | – | ++ | – | + | + | Walther 1964 |
| Tragelaphus angasi | – | | ++ | – | – | exc | + | ++ | ++ | ? | ++ | ++ | Burckhardt in Walther 1964 |
| Tragelaphus imberbis | – | ++ | + | – | – | exc | + | – | ++ | – | + | + | Walther 1964 |
| Tragelaphus strepsiceros | – | ++ | ++ | – | – | exc | + | | ++ | – | + | ++ | Walther 1958 & 1964 |
| Taurotragus oryx | – | ? | + | – | – | exc | | + | + | | ++ | ++ | Walther 1958 |
| Cephalophus nigrifrons | + | – | + (3) | – | – | | | | + | – | ? | + | Walther u.o. |
| Oreotragus oreotragus | ? | | + | – | – | + | | – | ++ | – | ++ | ++ | Walther u.o. |
| Connochaetes taurinus | ++ | – | – | – | ++ | ++ | + | – | + | | + | ? | Walther 1965, Estes 1969 |
| Alcelaphus buselaphus | ++ | – | – | – | ++ | | ++ | – | ++ | – | + | + | Backhaus 1959; Walther u.o. |
| Damaliscus lunatus | + | – | – | (+) | ++ | | ++ | | ++ | | | + | Walther u.o.; Joubert u.o. |
| Damaliscus dorcas | | – | – | – | ++ | | ++ | ? | ++ | | + | | Walther 1969 & u.o. |
| Oryx gazella | ++ | – | – | – | + | | ++ | | | (+) | + | ++ | Walther 1958 |
| Hippotragus niger | + | – | – | – | + | | | + | ++ | + | + | ++ | Huth 1970; Walther u.o. |
| Hippotragus equinus | ? | – | – | – | + | | + | | | ++ | | ++ | Joubert u.o. |
| Kobus ellipsiprymnus | – | ++ | + | – | – | + | | | ++ | + | + | ++ | Walther u.o. |
| Onotragus megaceros | – | ++ (3) | | exc | – | | | + | ++ | – | + | ++ | Walther u.o. |
| Aepyceros melampus | – | | + | (+) (4) | – | ? | ++ | + | + | – | + | ++ | Schenkel 1966; Walther u.o. |
| Gazella gazella | ? | – | – | – | – | | | | ++ | ++ | + | exc | Walther u.o. |
| Gazella dorcas | + | – | – | – | – | exc | + (5) | exc | ++ | ++ | exc | exc | Walther 1966 & u.o. |
| Gazella thomsoni | exc | – | – | – | – | – | + (5) | exc | ++ | ++ | exc | exc | Walther 1958 & 1968 |
| Gazella subgutturosa | + | | – | – | – | | + (5) | exc | ++ | + | + | | Walther u.o. |
| Gazella soemmeringi | + | – | – | – | – | + | | | + | | + | ++ | Walther 1964 |
| Gazella granti | exc | exc | – | (+)(4) | – | ? | + (5) | ++ | ++ | (+) | + | + (5) | Walther 1965 & 1968 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Litocranius walleri | ? | + | – | – | – | + | | – | ? | – | + | ++ | Walther 1961 |
| Antilope cervicapra | | – | ? | – | – | + | + | ++ | ++ | – | + | + | Walther 1959 |
| Ovis ammon | + | – | – | ++ | – | ++ | | – | ++ | ? | – | ? | Walther 1960 |
| Ovis canadensis | | – | – | ++ | – | + | + | – | ++ | – | – | – | Geist 1968 |
| Ammotragus lervia | – | – | – | exc | – | | | – | ++ | – | – | – | Haas 1959; Walter u.o. |
| Capra ibex | – | – | – | ++ | – | + | | + | ++ | – | + (6) | – | Walther 1960 |
| Capra falconeri | – | – | – | ++ | – | + | + | | ++ | – | – | – | Walther 1960 |
| Oreamnos americanus | + | – | – | + (7) | – | – | + | + | ++ | – | + | – | Geist 1965 |
| Rupicapra rupicapra | – | – | – | exc | – | | + | + | ++ | – | + | + | Walther 1960; Kramer 1969 |

TABLE 3 EXPLANATORY NOTES

Behaviour patterns:

a. Pawing the ground (without urination or defecation) in hostile encounters
b. Nose (vertically) upward posture (in females)
c. Symbolic snapping (in females)
d. Rising on hindlegs in hostile encounters
e. Dropping down onto 'knees'
f. Head-shaking (like humans in negation)
g. Symbolic butting and/or head-nodding (like humans in affirmation)
h. Downward sweep of head and horns
i. Medial presentation of horns
j. High presentation of horns
k. Low presentation of horns
1. Head-low posture

It should be kept in mind that this table gives excusively threat displays but not fighting behaviour.

Remarks:

(1) infrequent sweeps of a forefoot
(2) exclusively observed in females
(3) sometimes also found in males
(4) only used by males against females
(5) more frequent in females than in males
(6) swing-out movement before rising on hindlegs
(7) head-plunge: not found in adult males

Signs and abbreviations:

+ = clearly observed or described
++ = especially pronounced and/or frequent
(+) = performance somewhat diminished or aberrant
? ? = clearly observed or described but debatable whether or not it belongs to the behaviour under discussion
? = possibly present but not clearly observed or described
exc = exceptionally observed in exceptional situations
— = never observed or reported; very probably does not occur
no sign = never observed or reported; however, material insufficient for a negative statement
u.o. = unpublished observation

*References*

Always referred to that author who— to the best of my knowledge— gave the first clear description of the particular behaviour in the species concerned. A second author is only quoted if he significantly added to the information published by the first-named author.

TABU 4. DOMINANCE DISPLAYS IN HOSTILE ENCOUNTERS

| | Broadside displays | | | | | Frontal displays | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | a | b | c | d | e | f | g | h | i | Reference |
| Bos primlgenlus | ++(1) | ? | – | – | – | (+)(2) | ? | – | | Schloeth 1958 & 1961 |
| Blbos gaurus | ? | ++(1) | – | – | – | | ? | | | Antonius 1939; Schaller 1967 |
| Bison blson | ? | ? | | – | – | ? (2) | ? | | | MeHugh 1958 |
| Boselaphus tragocamelus | | ? | ++ | ? | | | | | ++ | Antonius 1939; Walther 1958 |
| Tragelaphus scriptus | – | | ++ | – | – | | | | ? | Walther 1964 |
| Tragelaphus spekei | – | | ? | | – | | | | + | Walther 1964 |
| Tragelaphus angast | + | ? | – | ? | + | | | ? | | Burckhardt In Walther 1964 |
| Tragelaphus imberbis | – | – | – | ++ | ++ | + | + | + | – | Walther 1964 |
| Tragelaphus strepsiceros | ? | + +(1) | – | ++ | ++ | + | + | ? | – | Walther 1964 |
| Taurotragus oryx | ? | – | – | ? | ++ | (+)(2) | | – | exc | Walther 1958 |
| Connochaetes taurinus | ? | ??(3) | – | – | +(4) | ++ | ? | – | – | Estes 1969 |
| Alcelaphus buselaphus | | ??(3) | – | ? | + | + | + | | | Backhaus 1959; Walther u.o. |
| Damaliscus lunatus | ? | ??(3) | ? | ++ | + | ++ | + | + | | Walther u.o. |
| Oryx gazella | ??(5) | ?(4) | – | ? | + +(4) | (+)(2) | + | | – | Walther 1958 & 1965 |
| Hippotragus niger | ? | | – | – | + (4) | | | – | – | Huth 1970 |
| Hippotragus equinus | + +(6) | | – | – | +(4) | | ? | – | – | Joubert u.o. |
| Kobus ellipsiprymnus | +(4) | | – | ? | +(4) | | + | ? | ? | Walther u.o. |
| Adenota kob | – | | – | | | ++ | + | ++ | – | Buechner & Schloeth 1965; Leothold 1986 |
| Onotragus megaceros | – | | – | | ? | + (7) | +(7) | +(7) | | Walther u.o. |
| Aepyceros melampus | | | | – | + | ++ | + | | ++ | Schenkel 1966 |
| Gazella gazella | + (4) | – | – | – | +(8) | | | – | – | Walther u.o.; Grau u.o. |
| Gazella dorcas | +(6) | – | – | – | – | exc(2) | ? | ? | exc | Walther u.o. |
| Gazella thomsonl | – | ??(3) | exc | – | – | exc(2) | – | – | – | Walther 1964 & 1968 |
| Gazella granti | + +(4) | – | – | + +(9) | + +(9) | exc(2) | + | + | – | Walther 1965 & 1968 |
| Litocranius walleri | – | – | – | ? | + | + | ++ | ++ | – | Walther 1961 |
| Antilope cervlcapra | | – | – | ++ | ++ | + | + | + | – | Schneider 1931; Walther 1959 |
| Ovis ainmon | ? | – | – | + | + (4) | + | + +(10) | + | + +(10) | Walther 1960 |
| Ovis canadensis | – | – | – | + | + | + | + (10) | + | + +(11) | Geist 1966 |
| Capra ibex | ? | – | – | – | | | – | – | exc | Walther 1960 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Capra falconeri | ++(4) | – | – | – | – | ??(12) | | – | – | Walther 1960 |
| Oreamnos americanus | | ++ | | – | – | | – | – | | Geist 1965 |
| Rupicapra rupicapra | | ++ | – | ? | ++ | | + | ? | ? | Walther 1960; Krämer 1969 |

TABLE 4. EXPLANATORY NOTES

*Behaviour patterns:*

a. Arched-neck posture
b. Head-low posture
c. and i. Head-and-neck-stretched-forwarf pesture
d. and h. Lifted-head posture
e. and g. Erected posture
f. Head-turn (approximately 90°)

*Remarks:*

(1) hindfeet under body
(2) not erected but in 'normal' posture
(3) agonistic grazing (in both opponents)
(4) often combined with angled horns
(5) very similar to erected posture
(6) posture of the head as in high presentation of horns
(7) only observed in adolescent males
(8) often with strongly pronounced sideward inclination of the head
(9) usually combined with head-flagging
(10) sometimes combined with the kick with the foreleg
(11) often combined with twist of the head
(12) throwing the head towards the shoulder

As in the other tables, the sketches give the postures very roughly; finer species-specific differences and variations are not presented. In short-necked species (cattle, wildebeest, etc.), the erected posture and the lifted-head posture are only approximately equivalent to the corresponding behaviour patterns in longed-necked species.

Signs and references as in Table 3.

TABLE 5. MALE COURTSHIP DISPLAYS

| | Broadside displays$^{(1)}$ | | | | Postures in following the ♀$^{(2)}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| |  |  |  |  |  |  |  |  |  |  |
| Species | a | b | c | d | e | f | g | h | i | j |
| Bos primigenlus | – | | (+)$^{(4)}$ | +$^{(5)}$ | – | | (+)$^{(6)}$ | ? | – | – |
| Poephagus mutus | – | + +$^{(7)}$ | (+)$^{(4)}$ | +$^{(5)}$ | – | | (+)$^{(6)}$ | | – | – |
| Bison bison | ?$^{(8)}$ | ? | (+)$^{(4)}$ | | – | | (+)$^{(6)}$ | | – | |
| Boselaphus tragocamelus | | ?$^{(8)}$ | – | – | | | | + +$^{(9)}$ | – | |
| Tragelaphug scriptus | | + +$^{(10)}$ | – | – | ? | +$^{(11)}$ | | + + | – | ?? |
| Tragelaphus spekei | | +$^{(10)}$ | – | – | ? | ? | | + + | – | ? |
| Tragelaphus angasl | (+)$^{(12)}$ | +$^{(10)}$ | +$^{(8)}$ | | | | | + + | – | |
| Tragelaphus imberbis | – | + +$^{(10)}$ | + +$^{(8)}$ | + +$^{(8)}$ | exc | +$^{(11)}$ | exc | + + | – | – |
| Tragelaphus strepsiceros | exc$^{(8)}$ | + +$^{(10)}$ | + +$^{(8)}$ | + +$^{(8)}$ | + | + | + | + + | – | – |
| Taurotragus oryx | – | + +$^{(10)}$ | – | – | ? | ? | – | + + | – | – |
| Cephalophus nigrifrons | – | – | – | – | | ? | – | + | – | |
| Raphiceros campestris | – | – | – | – | | + | – | + | – | |
| Rhynchotragus kirki | – | – | – | – | | ? | | + + | – | |
| Connochaetes taurinus | | + +$^{(13)}$ | – | ?$^{(14)}$ | | | | +$^{(15)}$ | | |
| Alcelaphus buselaphus | – | + +$^{(13)}$ | – | – | | | | +$^{(15)}$ | | – |
| Damaliscus lunatus | – | +$^{(16)}$ | + +$^{(16)}$ | – | ? | | +$^{(15)}$ | +$^{(15)}$ | +$^{(11)}$ | – |
| Damaliscus dorcas | – | +$^{(14)}$ | – | | ? | + | | + + | +$^{(11)}$ | – |
| Oryz gazella | – | – | ?$^{(14)}$ | (+)$^{(14)}$ | – | +$^{(11)}$ | | – | – | – |
| Hlppotragus niger | – | – | ?$^{(14)}$ | +$^{(14)}$ | | + | – | – | – | – |
| Hippotragus equinus | – | | – | | | + + | | | – | – |
| Kobus ellipsiprymnus | – | | | | | ? | | + | – | – |
| Adenota kob | – | | ?$^{(14)}$ | ?$^{(14)}$ | | + | + + | | – | – |
| Hydrotragus leche | – | | | | | | | + + | – | – |
| Onotragus megaceros | – | | | +$^{(14)}$ | + | + | | + + | – | ? |
| Redunca arundinum | – | | | | | ? | | + | – | – |
| Aepyceros melampus | – | exc$^{(8)}$ | – | – | | ? | | + + | – | – |
| Gazella gazella | – | ?$^{(10)}$ | – | – | | | + + | ? | +$^{(17)}$ | – |
| Gazella dorcas | | +$^{(10)}$ | – | – | | +$^{(11)}$ | ? | + + | – | – |
| Gaxella thomsoni | – | +$^{(8)}$ | – | – | – | exc | + + | + + | – | – |
| Gazella subgutturosa | – | +$^{(8)}$ | – | – | | + + | + | + + | – | – |
| Gazella soemmeringi | – | +$^{(10)}$ | – | +$^{(7)}$ | + | + + | + | + | – | – |
| Gazella granti | – | – | exc$^{(14)}$ | exc$^{(14)}$ | – | + | + + | exc | – | – |
| Litocranius walleri | – | – | – | – | + | + + | + + | – | – | – |
| Antilope cervicapra | – | – | +$^{(10)}$ | | – | +$^{(15)}$ | + +$^{(15)}$ | – | – | – |
| Ovis ammon | – | +$^{(19)}$ | – | – | – | | – | + +$^{(20)}$ | – | – |
| Ovis canadensis | – | + | – | – | + | + | – | + +$^{(20)}$ | – | – |
| Ammotragus lervia | – | | – | | | | – | + + | – | – |
| Capra ibex | – | exc$^{(19)}$ | – | – | – | | – | + + | – | – |
| Capra falconeri | – | + +$^{(19)}$ | – | – | – | + | – | + +$^{(20)}$ | – | – |
| Oreamnos americanus | – | – | – | – | – | – | – | + + | – | – |
| Rupicapra rupicapra | | – | – | – | – | + + | + | + | – | |

*(See next page for Explanatory Notes*

| Laufschlag | | | Mounting postures[3] | | | | | |
|---|---|---|---|---|---|---|---|---|
| k | 1 | m | n | o | p | q | r | Reference |
| – | – | – | ++ | | | | | Schloeth 1961;Sambraus 1968 |
| – | – | – | ++ | – | – | – | – | Walther u.o. |
| – | – | – | + | | – | – | – | McHugh 1958 |
| – | – | – | + | ? | | – | – | Walther 19S8 & u.o. |
| – | – | – | ++ | – | – | – | – | Walther 1964 |
| – | – | – | ++ | – | – | – | – | Walther 1958 |
| – | – | – | ? | | | – | – | Burckhardt in Walther 1964 |
| – | – | – | + | – | | – | – | Walther 1958 |
| – | – | – | ++ | – | – | – | – | Walther 1958 1 1964 |
| – | – | – | ++ | – | – | – | – | Walther 1958 |
| | ++ | – | – | ? | ++ | | – | Walther u.o. |
| | ++ | | – | – | | (+) | ? | Walther u.o. |
| | ? | | – | – | | (+) | ? | Ziegler-Slmon 1957; Simonetta 1966 |
| – | – | – | | ? | | – | – | Estes 1969 |
| – | – | – | – | ++ | – | – | – | Backhaus 1958; Walther u.o. |
| | +[11] | – | – | ++ | – | – | – | Walther 1966 & 1968 |
| | | | – | ? | | – | – | Walther u.o. |
| – | ++ | | – | – | – | ++ | – | Walther 1958 |
| – | ++ | – | – | – | – | ++ | – | Huth 1970 |
| – | ++ | | – | – | – | ++ | – | Backhaus 1959; Joubert u.o. |
| + | + | – | – | – | ? | + | – | Riley-Worthington 1965; Walther u.o. |
| + | ++ | | – | – | ? | + | – | Buechner 4 Schloeth 1965 |
| | ?? | | – | – | – | + | – | Lent 1969 |
| exc | ++ | – | – | – | – | ++ | – | Walther 1964 & u.o. |
| – | – | – | – | – | | + | – | Jungius 1970 |
| – | – | – | – | – | | ++ | – | Schenkel 1966; Walther u.o. |
| ? | + | – | – | – | – | | ++ | Grau u.o.; Walther u.o. |
| + | ++ | – | – | – | – | exc | ++ | Walther 1968 |
| – | ++ | ++ | – | – | – | exc | ++ | Walther 1958 & 1964 |
| – | + | | – | – | – | exc | ++ | Walther 1968 |
| – | ?? | – | – | – | – | – | ++ | Walther 1964 |
| – | – | (+)[18] | – | – | – | exc | ++ | Walther 1965 |
| – | ++ | ++ | – | – | – | exc | ++ | Backhaus 1958; Walther 1958 |
| – | – | (+)[18] | – | – | – | | ++ | Backhaus 1958, Walther 1959 |
| ++[20] | ++ | – | – | – | – | ++ | – | Walther 1960 |
| ++ | ++ | | – | – | – | ++ | – | Geist 1968 |
| – | – | – | – | – | – | ++ | – | Haas 1959; Walther u.o. |
| ++ | + | – | – | – | – | ++ | – | Hainard 1953; Walther 1960 |
| ++[20] | + | – | – | – | – | ++ | – | Walther 1960 |
| ++ | ++ | – | – | ++ | – | – | – | Geist 1965 |
| ??[21] | – | – | – | – | ++ | – | – | Walther 1960; Krämer 1969 |

TABLE 5. EXPLANATORY NOTES

*Behaviour patterns:*

a. and j. Head-low posture
b. and h. Head-and-neck-stretched-forward posture
c. and g. Lifted-head posture
d. and f. Erected posture
e. Head-turn (approximately 90°)
i. Arched-neck posture
k. Kick with the foreleg combined with head-and-neck-stretched-forward posture
l. Kick with the foreleg in normal or slightly erected posture
m. Kick with the foreleg combined with lifted-head posture
n. Mounting with chest, chin and sometimes also throat on the female's back
o. Mounting with chest and nose (vertically) on the female's back
p. Mounting with chest on the female's back; head and neck leaning forward but not touching the female's body
q. Mounting with chest on the female's back; neck erected
r. Mounting in standing or walking behind the female; chest does not touch the female's back.

Neither flehmen nor mere sniffing or licking the female's vulva are included in these postures.

*Remarks:*

(1) including postures in lateral position (parallel or reverse-parallel) to the female
(2) also in approaching the female frontally or from the flank
(3) Mounting postures are not, of course, expressive behaviour but they are of special interest for the interpretation of certain courtship and superiority displays.
(4) in reverse-parallel position; raising the head before mounting
(5) in reverse-parallel position; only slightly different from the 'normal' posture
(6) raising the head
(7) in parallel or in reverse-parallel position
(8) in front of the female
(9) with tail raised vertically
(10) parallel; during lateral escort
(11) before mounting
(12) similar to low presentation of horns; in front of the female
(13) with ear-drop; in reverse-parallel position
(14) in reverse-parallel position
(15) with ear-drop
(16) with ear-drop; in front of the female
(17) pushing the female's rear with the horns
(18) stiff-legged, big step with one foreleg
(19) parallel; during lateral escort; often with twist of the head
(20) often with twist of the head
(21) stiff-legged pawing the ground in herding females

Signs and references as in Table 3.

Paper No. 3

# Social Functions of Various Scent Glands in Certain Ungulates and the Problems Encountered in Experimental Studies of Scent Communication

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## ABSTRACT

Several aspects of scent communication in black-tailed deer are described. The various factors influencing responses to whole and fractionated social odors are discussed. The examples are taken from black-tailed deer and pronghorn.

## INTRODUCTION

Since time immemorial, hunters have been familiar with the peculiar odors emanating from the scent glands of large game animals. But up to this time we have remained ignorant of the functions these odors fulfill in the life of each species. Even in areas where interest in the biology and conservation of large ugulates is intense, their uses of scent communication have never been investigated.

The European Red deer (*Cervus elaphus*), for instance, has a large circumcaudal gland that extends over most of the tail. The strong odor and taste of the gland caused Aristotle to say that this deer had its gall bladder in its tail. There are six additional scent glands in the Red deer (Schaffer, 1940; Burckhardt, 1958), and we do not know the function of any of them.

The situation is similar with reference to the New World deer. Here the deer of the genus *Odocoileus* possess at least three distinct, well-developed scent glands: the tarsal, metatarsal and interdigital glands. Reported observations regarding their activation did nothing to clarify their functions. Recently, however, in a long-term study of olfactory communication in the blacktailed deer, we investigated the two main questions:

1. What information do certain scents carry in various social situations?
2. What is the nature of the scent gland product?

To solve the first problem, we had to observe different social groups of animals and manipulate their social structures. The second, more demanding, problem required the development of new bio-essay techniques for each odor investigated, and utilization of microchemical techniques which sometimes may be very involved.

Although our work yields more details every month, the presently identified functions of social odors in blacktailed deer can be summarized as follows. A large part of this account is a condensation of the results given in Müller-Schwarze, 1971. All reported behavior was observed both in captive deer and in wild blacktailed deer at all times of the year.

### Odors that affect indirect encounters between individuals

Blacktailed deer leave scent marks in their environment that may serve as signals for other conspecifics. These marks are created by rubbing the forehead on wood, by deposits of urine and feces, and by the action of the interdigital scent gland. These scents are used especially during the rutting season.

### Forehead rubbing

Males and sometimes females rub their forehead against twig tips, tree stems, low bushes or high roots. A deer will approach a twig, sniff it and rub its forehead vertically with a turning component. This can be repeated so that rubbing and sniffing alternate several times. There are shared and exclusive rubbing sites; the number of shared sites increases during the rutting season. Other males or females often sniff such marked twigs. Newcomers to a pen containing marked twigs often back off from such a site. Low ranking males sniff the marked twigs most often. The frequency of rubbing increases from spring to the fall rutting season. The females sniff twigs more often in fall than in spring. This may be interpreted as behavior that ensures encounters of the two sexes during the rutting season. Observations of deer in captivity have allowed a better separation of sniffing in feeding behavior and sniffing connected with marking behavior.

### Urine and feces

All droppings left by deer may be potentially informative to other individuals. We often see deer sniff fecal pellets or urine on the ground with no further behavioral consequence. But during the rut, urine left by females is particularly attractive to a male. The male invariably stops there, sniffs and licks the urine, and shows the Flehmen repeatedly in response to each urine patch he encounters.

### Interdigital glands

The interdigital glands are very well developed in blacktailed deer (Quay and Müller-Schwarze, 1970). In contrast to that finding, however, we do not observe regular responses to interdigital scent. Occasionally a deer is seen to sniff the deep footprints of an escaping conspecific, but no further response is noted.

During the rut males sniff with their nose on the ground, a behavior that might be induced by interdigital scent of footprints of females or males.

### Odors used in direct encounters between individuals

Two animals separated by considerable distance may exchange a number of signals. Two such signals are olfactory: the metatarsal scent and the odor of urine sprayed about during rub-urinating.

The animal discharges metatarsal scent in alarming situations such as when approached by a dog, being chased, cornered or caught by people, or entering an unfamiliar area. Therefore this odor falls into the category of alarm pheromones. It originates in the metatarsal glands on the outside of each hindfoot. We have observed deer responding to metatarsal scent which had been discharged by other individuals.

Rub-urinating occurs as part of the threatening behavior when two mature males meet during the rutting season. One of them will rub his hocks together while urinating on them. Simultaneously a strong odor can be noticed in the area. Fawns also rub-urinate. Hand-raised fawns rub-urinate particularly often during the night and after sudden separation from the caretaker. When a fawn that lives with its mother rub-urinates the mother and other deer are attracted to the fawn. After rub-urination the tarsal hair tufts are soaked with urine. It is licked off afterwards, except in males in the rut where the material accumulates on the entire hindfoot.

### Odors used in close contact

When two deer are close enough to touch one another, they will sniff at several preferred areas of the body. There is a naso-nasal contact and a sniffing of the tarsal organs and the anogenital area.

Naso-nasal contacts occur between deer that know each other. The naso-nasal contact may culminate in a mutual licking of head and neck areas.

Blacktailed deer in close proximity will sniff each other and their tarsal organs regularly at a rate of about once per individual per hour. During hours of darkness this frequency increases to 5-6 per hour. The frequency also increases, and often more drastically, when a strange deer joins the group. Then the sniffing becomes part of the sequence of agonistic behavior. By sniffing the stranger and also the familiar deer, an individual may constantly compare the individual odors.

Mothers sniff and lick the anogenital area of their fawns. Sniffing of the anogenital area is also performed by both sexes during courtship. In maternal behavior this will lead to the drinking of urine and the eating of feces of the fawn. This results in **a** circle; the licking mother stimulates the fawn to suck more.

It is not necessary that an overt behavior is exhibited in response to an odor stimulus. An animal may only sniff various objects at one time and remember their information content for use in an encounter at a later time, in much the same fashion as we read shop signs in passing and remember them for future action.

Finally it should be emphasized that the same sound or smell may release different responses in different addressees. Two examples illustrate this point: In blacktailed deer a post-parturient doe bleats repeatedly. A single bleat will cause her own fawn to approach her, but another adult female to turn away. In pronghorn, males may approach conspecifics with a sudden lateral turn of the head and discharge subauricular scent at the same time. A male will withdraw upon this approach, while to a female it is a courtship gesture.

## Scent gland structure

Without knowing the behavior of a species, predictions on the use of pheromones can be made on the basis of an inspection of the scent glands. In the black-tailed deer we find three well developed scent glands: the metatarsal, tarsal and interdigital glands. One extreme, the matatarsal gland consists of extremely developed sudoriferous glands. This would indicate that an airborne odor is produced there. Furthermore, there is little or no variation of the gland size of activity with age, sex or season. This would mean that a non-reproductive, social scent is secreted there. The other extreme, the antorbital gland, shows barely any glandular tissue, so that its behavioral significance would be minimal (Quay and Müller-Schwarze, 1970).

## Experiments with whole and fractionated scents

The correlations between a given social situation and specific odors can only be clarified by experiments. Introduction of a stranger into an established group, reunion of formerly acquainted animals, releasing a group of animals into an unfamiliar area, or artificial presentation of odors from different individuals to test animals are some of the methods that are used to determine social effects of pheromones.

The nature of the olfactory stimulus can be characterized by dividing the often very complex mixtures into their components. This requires extraction and distillation procedures and microchemical techniques such as gas liquid chromatography (GLC).

Before a specific fraction can be presented as a stimulus to the experimental animals, the amount of each substance present in the scent sample has to be exactly determined. As we are dealing with amounts in the microgram and nanogram ranges, the peak size which a given compound produces on a recorder chart is accepted as a measurement.

When testing animals with scent fractions, one has to consider biological and chemical facts. The basic behavioral factors are: seasonal and diurnal readiness to respond, context of ongoing behavior, early experience, multisensory control of behavior, personal relationships between group members, distances over which the specific scents work. The releasing stimulus for marking in the natural environment has to be known. Other biological parameters such as habituation, conditioning, background odor, detection threshold and odor structure, may influence the response to the odor(s).

Chemical properties influencing the results are the concentration of the odorants, the volatility of the substances, the stability of the component substances in the high temperatures of the gas chromatograph, the choice of organic solvent, and the substratum on which the odoriferous components are applied.

The following examples of experimental considerations are mostly taken from the blacktailed deer with which we have most experience. Some points are illustrated by our recent experiments with pronghorn antelope (*Antilocapra americana*).

## Seasonal and diurnal variation of readiness to respond

Needless to say, some social odors will be particularly effective during the mating season, while others, like the alarm pheromones, will show little seasonal variation in either their rate of scent secretion or the intensity of the response(s). For animals that are active day and night such as the blacktailed deer and the pronghorn, the time of day with maximum readiness to respond has to be found. Among deer, mid-day is a rest period with little locomotion taking place. Therefore mid-day would be a poor time for any odor test requiring an animal to move from one place to another. On the other hand, mid-day is a time of frequent mutual licking, and therefore favorable to scent experiments calling for close range sniffing and licking responses between individuals. During the hours of darkness young deer sniff the tarsal organs of group members more often. It is therefore of advantage to schedule experiments with tarsal scent close to the night hours.

### Spatial considerations

Certain olfactory responses are more likely in one environment than in another. One such behavior is sniffing twigs that may carry scent from forehead rubbing by males. This is typical for deer entering a new area. Before a deer engages in social contacts, he explores the area and sniffs many twigs, even though other individuals may approach and try to sniff or attack him. Experiments with odors applied on trees are therefore best performed in an area that is unfamiliar to the deer.

The spatial dimensions of the deer's environment are important, as is the placement of the odor if it is applied to the body of a test animal. Deer react to the presence of experimental tarsal scent immediately by sniffing the air and turning to the tarsal organ of one individual for further sniffing and licking. If the tarsal odor is applied to the forehead or side of an individual, the other deer will still investigate the tarsal organs, and not find the actual location.

### Temporal context

While working with tarsal scent we discovered that the general activity pattern affects the deer's willingness to respond to the experimental odor. After resting, the deer get up, stretch, urinate, drink some water, and eat. Only after the first bout of eating are they ready to sniff or lick one another. A sample of the tarsal scent fraction to be tested can then be effectively applied to one of the animals, and others will then approach and lick.

### Early experience

The conditions under which a mammal grows up will mold the olfactory responses. Some of our hand-raised blacktailed deer were extremely attached to people and did not show the typical responses to the tarsal and metatarsal odors. Yet they bred normally and exhibited the typical epigamic agonistic behavior. The most typical and consistent responses were found in deer which had been with their mother for several days or weeks, had been raised in a group, or both. Early specific olfactory experience may effect social responses (Müller-Schwarze, 1971).

### Multisensory control of behavior

The alarm response of blacktailed deer is triggered by auditory, visual and chemical signals. When one individual notices a source of danger, such as a dog, it assumes the alert posture with head held high and all sensory organs focussed on the source of disturbance. At the same time it discharges metatarsal scent. If the disturbance continues the animal may stamp a forefoot on the ground and/or utter a hissing sound, then break into a stiff trot, and stop again to focus its attention on the potential source of danger. Metatarsal scent may be discharged again during each of these phases. This multisensory control has consequences for experimentation concerned with only one sensory modality. Will a complete or a consistent response be released by metatarsal scent alone ?

### Personal relationships between group members

Mammals evidence individual variations for a given odor (Schultze-Westrum, 1965; Hesterman and Mykytowycz, 1968). Responses of experimental animals can therefore differ depending on whether an odor was taken from a stranger or from a familiar individual, and with the specific donor among a number of known individuals. This can be illustrated by the marking behavior of the male pronghorn. In a group composed of one two-year-old and two one-year-old males, the two males ranking first and second, each showed his strongest sniffing, licking, rubbing and thrashing responses to the subauricular odor of the male ranking immediately below them. Also a two-year-old male responded strongly to the subauricular odor of a strange adult male, and much less to his own odor and to an untreated marking post.

### Distances over which scents are effective

It is difficult to determine the distances over which deer or other ungulates detect a scent. Primarily a function of molecules moving in air, the ultimate distance depends on a number of environmental variables. From observations we know that airborne odors such as the metatarsal scent, transmit messages between deer of the same group when distances between individuals do not exceed 20-30 meters for long periods of time. Odors carried on the body or deposited on twigs or the ground are examined by deer at close range with the muzzle often touching the substratum. We have often observed that a buck will not notice the urine of a doe on the ground as close as three meters away, if he failed to see, smell or hear the doe urinate. Blacktailed deer and other species, such as the chital *Axis axis* (Schaller, 1967), even investigate predator odors at close range. In experiments, optimal responses are obtained when odors are presented at close range. Females sometimes detect the male tarsal scent from 5 m, but always at 2 m.

### The releasing stimulus situation for marking

Scents may be deposited on objects in stereotyped acts of marking in response to basically three situations. An animal may find an object that is unmarked, marked by itself, or marked by another individual. As indicated by experiments with a male Thomson's gazelle *Gazella thomsoni* (Hummel, 1968) and pronghorn antelope (Müller-Schwarze, unpublished), their own scent on an object releases as strong a response as an unmarked object, while the scent of strange individuals triggers a stronger response. The response of the male pronghorn consists of sniffing, licking, marking in turn or thrashing the object. The reactions of a female pronghorn were the reverse. She licked and rubbed with her forehead untreated posts and those with subauricular scent of a strange male equally often, but gave a stronger response to the subauricular odor of the male she had lived with since three days of age.

### Habituation

We have identified different habituation rates for different scents. When presented with tarsal scent nine times within six hours, a female deer rapidly responded less and less. When the tarsal scent was presented only three times in six hours, her response did not decrease. The normal frequency of sniffing each other's tarsal organs in a group of deer is about once per individual in an hour of activity time.

An alarm pheromone would be expected to cause less habituation with repeated stimulation. This was the case with the metatarsal scent where several tests could be run within an hour without any noticeable habituation.

### Conditioning

Ungulates are available for experiments only in small numbers, and each individual has to be used many times for odor testing. During the recurring experience it may learn to respond to other clues associated with the experiment. For instance, if the odor is dissolved in an organic solvent with a smell of its own, this substance may start to release a response by itself.

### Background odor

The odor(s) surrounding an experimental sample may influence the response. When, for instance, tarsal scent of adult males was applied on the hindleg of a male, females in the group were attracted and sniffed and licked it. The response was weaker or absent when the same tarsal scent sample was sprayed on the hindleg of a female in the same group.

### Detection threshold

In pilot experiments, the threshold concentration of a given odor must be determined. The actual discrimination experiments with fractionated scents can then be carried out with a concentration well above threshold. The upper limit may be set by changing responses of the animals or, more often, by the scarcity of the scent material.

### Odor structure

Up to now we have found three different types of odor composition: (1) in complex odors several behavior-releasing components may act only as a whole (odor gestalt); (2) several components may act alone, but reinforce each other; (3) a single substance may be responsible for a particular response.

### Conclusion

We have studied the structure of pheromones and their place in ungulate behavior to decipher the information they provide for a given individual in a certain behavioral context. In any such attempt, we face a dilemma: we know that a chain of behavioral events involving two or more individuals is controlled by a wide variety of stimuli, including all sensory modalities. Yet, in the interest of a 'controlled' experiment, we isolate a specific olfactory part of the complex. Thus we can at best obtain only partial responses, however consistent they may be from test to test. The reactions are perfectly suited to reach our goals of finding the active principles in a scent, and to determine certain stimulus-response relationships. But are the responses still the same as would occur in the original context? Is the professional sniffer who specializes in discriminating fine nuances of coffee flavor representative of the average customer who may choose his coffee in different ways, maybe just on the basis of the color of the label on the can? Would the preference for, or avoidance of, a certain chemical substance in a controlled experiment, duplicate itself during a complex chain of events with multisensory control? In domestic sheep, for instance, rams may cease temporarily to rely on olfactory stimuli when mounting an artificial vagina, so that it subsequently does not distinguish between estrous and non-estrous ewes. Over a period of time, however, the ram's ability to discriminate olfactorily is restored (Lindsay, 1965).

Not only the conditions of the experiment, but also the captivity of the animal may alter olfactory and other responses. Does forehead rubbing in captive deer, and 'jaw patch' marking in captive pronghorn, differ in intensity or frequency from the wild form? To check for possible differences and to appreciate the significance of the various responses in a natural population it is essential to go back into the wild and to observe free ranging animals.

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**Paper No. 4**

# Scent Marking in Captive Maxwell's Duikers

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## ABSTRACT

Scent marking with the maxillary gland by *Cephalophus maxwellii* was studied at the Bronx Zoo. The relationship between social status and the frequency of marking was of particular interest. Nine duikers, in three groups each consisting of one male and three females, were observed for 21 months. Unfamiliar duikers were added to each group in order to test the effect this would have on the frequency of marking by the group members.

Males initiated 82% of the bouts of reciprocal grooming. Males groomed females in 61% of the grooming exchanges; females groomed females in 8%; and females groomed males in 30%. One female in each group (type A female) groomed the male more frequently than the other (type B female) did.

Male one, which could defeat either of the other males, marked the edges of a large outside enclosure thoroughly, when put in it, and marked more frequently in this enclosure than did the other males.

In the inside cages, males marked on objects an average of 5. 6 times/10 min., type A females 2.8 times/10 min., and type B females .08 times/10 min. After an unfamiliar male had been present, males increased the frequency of their marking to an average of 11. 5 times/10 min.; the females did not mark more frequently. After an unfamiliar female had been present, type A females increased the frequency of their marking to an average of 11.1 times/10 min.; type B females and males did not mark more frequently.

Males and type A females pressed their glands together (marked mutually) an average of 1 time/10 min. Mutual marking between males and type B females and between two females was much less frequent. The frequency of mutual marking between all group members increased after an unfamiliar duiker of either sex had been present. Mutual marking also occurred between two males as an introduction to fighting.

It was concluded that duikers which mark frequently on objects do have a high social status and that they do mark even more frequently after they encounter an unfamiliar duiker of the same sex.

## INTRODUCTION

The importance of chemical communication in mammals is well recognized. Nevertheless, our knowledge of this subject is still meager. A good way to enlarge our knowledge is to study ruminants because most species have one or more conspicuous scent glands (see Müller-Schwarze, Paper 3 this volume).

In order to gain a better understanding of chemical communication it is essential that we learn more about scent marking, as it is one of the major forms of chemical communication. Only a few quantitative studies have been done on markings: that of Schultze-Westrum (1965) on sugar gliders; of Mykytowycz (1969) on rabbits; of Thiessen *et al.* (1968) on gerbils; of Epple (1970) on marmosets; and of Johnston (1970) on hamsters. These studies have been reviewed by Rails (1971). The need for quantitative studies remains great.

I have studied scent marking in captive Maxwell's duikers, *Cephalophus maxwellii* (H. Smith). A preliminary report on the study was published previously (Rails, 1969). Maxwell's duikers are small antelopes native to the forests of West Africa. Their social behavior is little known as it has not been studied in the field. It is known, however, that they do not form herds and live either solitarily or in pairs. They are probably territorial. The available information on most aspects of the biology of *C. maxwellii* has been summarized (Rails, 1972).

Marking in Maxwell's duiker has not previously been studied systematically; a limited amount of data on marking is contained in Aeschlimann's general study of the behavior of a captive group. Captive duikers are well suited for a quantitative study of marking for several reasons. Marking appears to be an important form of chemical communication in duikers if we can judge by the frequency with which it occurs. Captive animals are easy to observe. (The behavior of Maxwell's duiker would be very difficult to observe in the field.) In addition, in this species there is no danger of confusing marking with other behavior patterns and no difficulty in deciding whether or not marking occurred.

Of particular interest was the relationship between the frequency of marking in individual animals and, first, the social status of the individual and, secondly, the presence or absence of strange duikers in the individual's social group. It is known that, in many species, individuals of high social status mark more frequently than subordinates do. I attempted to determine whether duikers behaved in a similar way. Epple (1970) found that marmosets mark more frequently after encounters with strange members of their own sex than they do after encounters with strange members of the opposite sex. She predicted (personal communication) that I would discover that duikers behaved similarly if I tested the effect of introducing strange duikers into established social groups.

## METHODS AND MATERIALS

The duikers were observed at the New York Zoological Park (Bronx Zoo) two or three mornings a week for 21 months beginning in September 1968. During most of this period there were nine individuals (Table 1). The duikers were kept in three groups, each of which consisted of one male and two females. The composition of the groups is shown in Table 1.

TABLE 1. MAXWELL'S DUIKERS AT THE BRONX ZOO

| Individual | | | |
|---|---|---|---|
| Male one | I | wild trapped | most vigorous male |
| Male two | II | wild trapped | |
| Male three | III | wild trapped | appears older than other males |
| Female one | I | wild trapped | |
| Female two | II | wild trapped | |
| Female three | III | born in zoo | hand reared |
| Female white | I | born in zoo<br>Dec. 31, 1967 | female one's daughter |
| Female red | II | born in zoo<br>Feb. 22, 1969 | female two's daughter |
| Female green | III | born in zoo<br>Jan. 18, 1969<br>died July 1969 | female three's daughter<br>died from eating a piece of wire |

Each group of duikers was kept during the winter in an indoor cage 3 to 4 meters square. The building where the duikers were caged was closed to zoo visitors. A group of duikers was sometimes let out into a large enclosure on summer days. The outside enclosure ('The African Plains') was approximately 46 by 108 meters in size.

It had a savanna-like appearance as most of it was covered by short grass interspersed with large trees. The edges of the enclosure had dense shrubbery consisting mainly of 'Tree-of-Heaven' saplings (*Ailanthus altissima*). The enclosure was also occupied by a herd of nyala *Tragelaphus angasi.* The duikers were fed chopped fruits and vegetables, kale or cabbage, monkey chow, and hay.

When observing the duikers in the indoor cages I stood outside the cage; when observing them in the outside enclosure I walked around inside the enclosure. Unless otherwise stated, my data are derived from observations on the duikers in the indoor cages. All observations of marking and grooming were made between 9 and 11:30 a.m. because the duikers were most active then. In order to test the effect of strangers, an animal was added to an established social group. Since all the duikers at the zoo have met one another at some time, the additional animal was not really a stranger. I have termed it an 'unfamiliar duiker'. The unfamiliar duiker was removed after about 10 minutes. If serious fighting occurred, it was removed even before 10 minutes had elapsed. The marking activity of the group members was recorded for one hour immediately after the unfamiliar duiker had been removed. Each unfamiliar duiker was added to each group three times—with each test on a different day. Group females were removed, left overnight, and reintroduced the next day.

A nonparametric test, the Kruskal-Wallis one-way analysis of variance (Siegel, 1956), was used in appropriate cases. The parametric *t* test was used for the remainder of the data because the small size of the samples (n = 3 in most cases) made it impossible to apply its nonparametric analogues. The *t* test requires the assumption that the population has a normal distribution. I have no way of knowing whether or not my data are samples from populations with normal distributions. However, I am inclined to believe that the *t* test gives valid results. According to Tate and Clelland (1957): 'There is a vast amount of empirical evidence that parametric methods give satisfactory results despite markedly non-normal populations.'

## RESULTS

### Grooming

So that the reader will understand my data on scent marking, I will first describe grooming among duikers. A duiker allogrooms by licking and nibbling the fur of another duiker's head, chest, and shoulders (Fig. 1). It grooms the area around the horns especially often and for long periods. The two duikers usually stand facing each other. The duiker being groomed is practically motionless, with its head, and sometimes its shoulders, lowered.

A duiker usually begins a bout of grooming by walking up to another duiker and licking it. Males were the initial groomers in 82% of the 600 bouts recorded (p = .005)

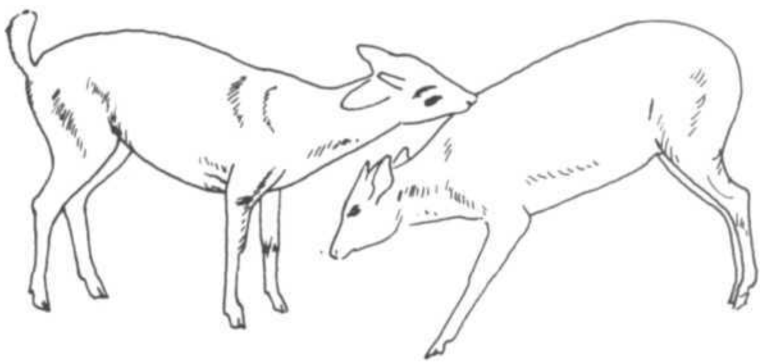

Fig. 1. Grooming: female ('white') left, male ('one') right.

(Table 2). After duiker Y is groomed by duiker X, Y sometimes, but not always, grooms X in return. Such reciprocal grooming (Sparks, 1967) may be repeated a number of times. I call this series of grooming exchanges a bout.

There was a total of 1954 exchanges in the 600 bouts (Table 3). Exchanges in which males groomed females comprised 61% of the total, more than would be expected if the duikers groomed each other on a random basis (p = . 05). Each male groomed one female in his group more than the other, but the difference was not statistically significant. Exchanges in which females groomed other females comprised only 8% of the total, less than would be expected if the choice of a grooming partner were random (p = . 02). Exchanges in which females groomed males comprised 30% of the total, which is close to what would be expected if grooming were random. In each group, there was one female which groomed the male much more than the other female did (p = . 05). I call this female the type A female (females one, two, and three) and the less frequently groomed one, the type B female (females white, red, and green).

TABLE 2. INITIATION OF GROOMING BOUTS

| | Number of bouts initiated | |
|---|---|---|
| Group | Male | Female |
| I | 164 | 36 |
| II | 149 | 51 |
| III | 181 | 18 |

Each group was observed until 200 bouts were recorded.

TABLE 3. NUMBER OF INSTANCES OF GROOMING

| Group | Groomer | Groomed | | | Total |
|---|---|---|---|---|---|
| | | Male one | Female one | Female white | |
| I | Male one | – | 242 | 168 | 410 |
| | Female white | 124 | – | 31 | 155 |
| | Female one | 7 | 15 | – | 22 |
| | | Male two | Female two | Female red | |
| II | Male two | – | 271 | 180 | 451 |
| | Female two | 198 | – | | 224 |
| | Female red | 45 | 11 | – | 56 |
| | | Male three | Female three | Female green | |
| III | Male three | – | 197 | 140 | 337 |
| | Female three | 132 | – | 31 | |
| | Female green | 89 | 47 | – | 136 |

### Scent marking

Duikers of the subfamily Cephalophinae mark with the large gland below and in front of each eye. The structure of this gland differs from that of the preorbital glands of all other ruminants. Weber (1888) suggested that the glands of duikers be called maxillary glands and Schaffer (1940) adopted this term. The gross morphology of the maxillary glands in *C. maxwellii* was described by Pocock (1910). The swelling below each eye is surmounted by a naked, concave arc of skin roughly 2. 5 cm. in length studded with a row of pores from which the secretion of the gland emerges. Histological studies reveal that both sebaceous and apocrine glands are present (Weber, 1888; Schaffer, 1940).

The color of the gland's secretion ranges from colorless to bluish. Weber stated that all males have a colorless secretion and all females a bluish one. All the males at the Bronx Zoo do have a colorless secretion. However not all the females have a bluish secretion: some have a colorless secretion. The color of the secretion of an individual female sometimes changes: the color of the secretion of female three was usually bluish but became colorless while she was pregnant and changed to bluish again after her calf was born. Furthermore, the color of the secretion of her female calf, female green, was originally bluish and later became colorless. (The secretion of the calves of other females was colorless and remained so.)

Duikers mark by pressing either of the maxillary glands against objects. This behavior was first described by Rahm (1960) and is illustrated in papers by Aeschlimann (1963) and Rails (1971).

### Marking on objects in the outside enclosure

When a male duiker was let into the outside enclosure after being kept inside for several days, the first thing he usually did was to mark. He marked mostly on the trunks of the saplings that grew around the edges of the enclosure. He walked from sapling to sapling and usually covered the entire perimeter one or more times before he began to feed or rest.

The marking at these times was the most vigorous I observed. After pressing his gland against a sapling with considerable force, the male often thrashed the sapling with his horns and pawed the ground around it. Marking was done especially frequently at these times. One male once marked 31 times in ten mintues, the highest frequency I ever observed. The initial period of vigorous and frequent marking often lasted for about an hour.

There were considerable differences in the manner in which the three males marked after being let out. Male one, who could defeat either of the other two males in a fight, marked the edges of the enclosure most thoroughly. His marking was the most vigorous and was usually kept up longer than that of the other males. Male one also marked at a higher frequency than the other males. After 10 days of being kept inside, for example, male one marked an average of 21, male two 8.4, and male three 2. 5 times per ten minutes during the first hour outside.

### Marking on objects in the inside cages

In the inside cages, the duikers marked on objects such as the food and water containers, cage bars, and door edges. The frequency with which the individual marked is shown in Table 4.

When only the members of the group had been present, the male in each group marked more than either of the females, and the type A female (the one who groomed the male) marked more than the type B female did (p = .011).

Female three was the type A female in Group HI and her daughter, female green, five months old, was the type B female when I began to collect the data shown in Table 4. When she was six months old, female green became the type A female of Group III and female three became the type B female. This change is the reason why I have shown marking frequencies for each of these females twice in Table 3, once under type A and once under type B.

### Marking after encounters with unfamiliar duikers

A male duiker marked more frequently after another male had temporarily been present in the group, but showed no increase after an extra female had been present (p = .01) (Table 4). The type A females marked more frequently after an extra female had been present but did not do so after an extra male had been present

TABLE 4. SCENT MARKING ON OBJECTS IN THE ENVIRONMENT

| Group membership | With own group only | After encounter with: Non-group male | Non-group female A | Non-group female B | Group female A | Group female B |
|---|---|---|---|---|---|---|
| | | *Males* | | | | |
| I | 6.6 | 15.2 | 6.1 | 5.1 | 7.2 | 6.2 |
| II | 5.8 | 10.7 | 6.2 | 6.0 | 5.3 | 6.0 |
| III | 4.4 | 8.6 | 4.1 | 4.9 | 5.1 | 4.7 |
| | | *Type A females* | | | | |
| I | 3.5 | 3.7 | 18.6 | 14.1 | – | 3.4 |
| II | 3.4 | 3.1 | 12.2 | 10.4 | – | 2.6 |
| III | 1.5 | 0 | 1.7 | – | – | – |
| III | 2.7 | 4.1 | 11.9 | 17.6 | – | 4.3 |
| | | *Type B females* | | | | |
| I | 0.06 | 0 | 0.09 | 0.05 | 0.1 | – |
| II | 0 | 0.1 | 0 | 0.04 | 0.2 | – |
| III (♀3) | 0.2 | 0 | 0.1 | 0 | 0.03 | – |
| III (♀G) | 0.04 | 0 | 0.03 | – | – | – |

Each figure gives the mean number of marks with the maxillary gland for 180 ten-minute periods of observation.

(p = .025). The type A female in Group III, female three, was an exception. Soon after the time of the experiments, however, she became a type B female. A type B female did not mark more frequently after either an extra male or an extra female had been present. The removal and reintroduction of either the type A or B female of a group did not affect the frequency with which the other female marked.

### Mutual marking

Duikers mark on the glands of other duikers **as** well as on objects in the environment. Two duikers, facing each other, press together the maxillary glands, first on one side of their faces and then on the other (Fig. 2). This mutual marking between a female and a male or between two females was first described by Aeschlimann (1963).

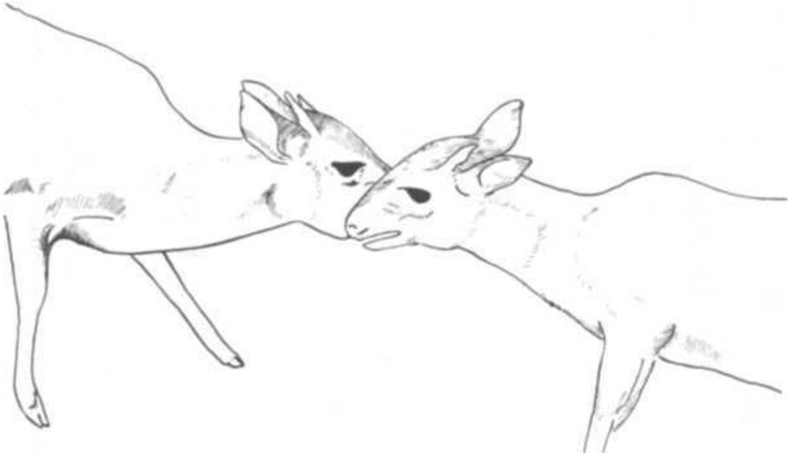

Fig. 2. Mutual scent marking between male three, left, and female green, right.

When only the members of the group had been present, most of the mutual marking was between the male and the type A female (p = . 05) (Table 5). Mutual marking between the male and the type B female and between the two females was much less frequent. The frequency of mutual marking between all group members increased after either an extra male or female had been present (p = .025).

Although it has not previously been noted, mutual marking also occurs between two males. On several occasions I observed that two males, which had been allowed into an outside corral, approximately 30 meters in diameter, at the same time, became aware of each other's presence, hurried toward each other, marked each other's glands with great vigor, and clashed against each other forehead to forehead. The males, having momentarly paused in their fighting, always marked each other again before resuming. Two males mark each other much more forcefully than a male and a female or two females do. It seemed that each male was trying to force the other's head to the ground. A more detailed description of fighting, based on motion pictures, is in preparation.

## DISCUSSION

The duikers I studied marked very frequently in terms of the frequencies with which other species mark. For example, the male duikers marked an average of 5.6 times per 10 minutes but dominant male marmosets mark an average of only 10 times per hour (Epple, 1970) and dominant male rabbits an average of 7 times per hour (Mykytowycz, 1965). The frequency with which the male duikers marked may strike one as incredibly high. It is, however, not too different from that reported by Aeschlimann for a captive male of the same species at the same time of day: 3. 8 times per 10 minutes (a total of 79 times in the period from 8:30 a.m. to noon). I

TABLE 5. MUTUAL SCENT MARKING

| Group | With own group only | After encounter with: Non-group male | Non-group female |
|---|---|---|---|
| | | *Male-type A female* | |
| I | .9 | 6.6 | 5.7 |
| II | 1.0 | 4.3 | 7.2 |
| III | 1.2 | 6.1 | 4.2 |
| | | *Male-type B female* | |
| I | .2 | 4.2 | *2.9* |
| II | 0 | 3.1 | 3.5 |
| III(♀3) | .3 | 5.8 | 6.1 |
| | | *Female-female* | |
| I | .09 | 3.1 | 2.7 |
| II | .02 | 1.9 | 2.4 |
| III(♀3) | .06 | 2.6 | 3.3 |

Each figure gives the mean number of marks for 180 ten-minute periods of observation. If the two duikers pressed the glands on one side of their faces only, it was counted as one mark. If they pressed together the glands first on one side of their faces and then on the other side, it was counted as two marks.

would have obtained a lower frequency of marking had I extended my observations throughout the day because there were periods during which the duikers rarely marked: they lay down to rest and ruminate about noon and spent much of their time eating after they were fed about 2 p.m. It is conceivable that duikers in the wild do not mark as frequently as those in captivity. I felt that the duikers at the zoo sometimes marked because they had little else to do.

The duikers occasionally marked on the horns and back of other duikers instead of objects. They did so when in the same cage with a group of the much larger bay duiker *C. dorsalis.* The bay duikers were immobile for long periods during the day because, being nocturnal, they were asleep or resting. Female zebra duikers *C. zebra,* at the Frankfurt Zoo, have been observed to mark on the head, legs and back of other duikers (Frädrich, 1964). Frädrich thought that they marked calves in this way because they perceived them as new objects in the cage.

Exposure to an unfamiliar duiker of either sex was a stimulus which caused an increase in the frequency of mutual marking within a group. However, a high frequency of mutual marking was also caused by other unusual and mildly frightening stimuli such as prolonged noises and people with whom the duikers were unfamiliar. In contrast, exposure to an unfamiliar duiker of the same sex was the only stimulus I found which produced a large increase in the frequency of marking on objects in the indoor cages. In fact, most other unusual stimuli caused a decrease in the frequency of marking on objects. The duikers did not mark more frequently when new objects were put into their cages. Their behavior was different in this respect from that of the zebra duikers at the Frankfurt Zoo which were stimulated to mark by new objects. The reason the Maxwell's duikers did not do so was that they were very frightened of new objects and avoided them for hours or even days.

I think the differences between the behavior of the type A and the type B females were not due to the immaturity of the latter although, at the beginning of the study, each was younger than the type A female in her group (Table 1). First, female green became a type A female when she was only six months old, replacing female three who was over five years old. Secondly, I saw all the type B females behave, at least in part, as type A females under some conditions: they marked objects frequently when their group was placed in the large outside enclosure; they did a lot of mutual marking with the male of another group when two groups were temporarily put in the same cage. Thirdly, females two and three, who were undoubtedly mature, behaved as type B females when they were in a cage together with male one and female one. (I saw this behavior during preliminary observations on the duikers prior to the beginning of the present study.) Under these conditions, only female one behaved as a type A female, although females two and three did so when they were members of the groups observed in this study.

I don't know what did cause the differences in behavior between the type A and the type B females. I think it may have been the fact that the type B females could not provide themselves with 'unattached' males. Perhaps duikers normally live in pairs as dik-diks do (Hendrichs and Hendrichs, 1971). If this is true, the type B females would be artifacts due to the excess of females at the zoo.

It can be concluded that duikers which mark frequently on objects do have a high social status and that they do mark even more frequently after they encounter an unfamiliar duiker of the same sex. Male one, which marked more than twice as frequently as male two, and eight times as frequently as male three, in the large outdoor enclosure, could defeat either of them in a fight. He also marked at a higher frequency than the others did in the small, indoor cages although the differences were not statistically significant. The type A females, which marked more frequently than the type B females, had a higher social status in that they had a closer relationship with the male–they spent more time grooming him and marked mutually with him more often. Both males and type A females marked even more frequently after an unfamiliar duiker of the same sex had been present.

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**Paper No. 5**

# A Comparison of the Social Behaviour of the Equidae

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## ABSTRACT

In the Equidae two types of social organization have evolved. The plains zebra (*Equus quagga*), mountain zebra (*E. zebra*), horse (*E. przewalskii*) and possibly also the Asiatic wild ass (*E. hemionus*) live in coherent family groups, consisting of one stallion, one to several mares and their young. Surplus stallions are found in stallion groups. The young leave their original families in a set pattern. No territories are established in these species.

In the Grévy zebra (*E. grevyi*) and the wild ass (*E. africanus*) the stallions keep large territories which they, however, only defend under certain conditions, i.e. when an oestrous mare is near the boundary.

Apart from the mare-foal relationships there are no personal bonds between any two or more individuals.

Most of the equine populations live in areas with marked seasons.

In the non-territorial species the reproductive groups migrate as units. In the territorial species the sexes segregate for part of the year, a feature which will certainly influence the reproductive rate, especially in areas with irregular rainfall.

## INTRODUCTION

There are six species of modern equids: the plains (or Burchell's) zebra (*Equus quagga*) with five subspecies: *boehmi* (Boehm's or Grant's zebra), *chapmani* (Chapman's zebra), *antiquorum* (Damara zebra), *burchelli* (Burchell's zebra) and *quagga* (Quagga); the mountain zebra (*E. zebra*) with two subspecies: *zebra* (Cape Mountain zebra) and *hartmannae* (Hartmann's zebra); Grévy's zebra (*E. grevyi*); the wild horse (*E. przewalskii*); the ass (*E. africanus*) with three subspecies: *atlanticus* (Atlas-), *africanus* (Nubian-) and *somalicus* (Somali wild ass); and the Asiatic wild ass (*E. hemionus*) with four subspecies: *hemionus* (Kulan), *kiang* (Kiang), *onager* (Onager) and *hemippus* (Syrian wild ass).

The domestic horse (*E. przewalskii* f. *caballus*) and the donkey (*E. africanus* f. *asinus*) are the domesticated forms of the wild horse and of the wild ass, respectively.

The quagga, the true Burchell zebra, the Atlas wild ass and most probably also the wild horse have been exterminated in the wild, and only of the latter is there a breeding stock, consisting of about 200 individuals, in zoological gardens.

A comparison of the behaviour is at the present moment possible for only five of the six species as there is practically nothing known about the Asiatic wild ass. Also, the recordings on the wild horse are very fragmentary and cannot be used as a basis for a good comparison. However, a population of feral horses has recently been studied intensively in southern England (Tyler, 1969), although the population is not natural with respect to its sex ratio.

The equids are all very much alike. There are a few qualitative differences like the stripe patterns in the zebras, a dew lap which is a feature of the mountain zebra, the presence or absence of infundibula in the lower incisors and the presence or absence of the so-called chestnuts which are epidermal growths on the inner sides of the legs.

All equids can be interbred in captivity, demonstrating their close relationship. It could therefore be expected that their behaviour is similar as well. In fact, a number of behaviour patterns are practically identical in all the equine species. In their social organization there are, however, considerable differences.

## A. SOCIAL ORGANIZATION

The plains zebra and the mountain zebra live in coherent family groups consisting of one stallion with one to several mares and their young, and in stallion groups. These social units are non-territorial and move freely in rather large home ranges which they share with conspecifics and whose sizes depend on the ecological conditions of the area. In Ngorongoro Crater the smallest home ranges of plains zebra measured 80 sq. km, the largest about 200 sq. km; those of the mountain zebra in South Africa were much smaller (3-5 sq. km). In both species the family groups were found to be permanent units as far as the adult members are concerned. Mares normally stay for their lifetimes in the same group, even when they are very old or sick. Old and sick stallions may be replaced by younger and healthier ones; they then join stallion groups (Fig. 1). The stallion groups are more variable in their composition, but some individuals may stay together for many years as well.

In the plains zebra the mechanics of this social set-up could be studied in detail (Klingel, 1967). In the mountain zebra the same results were found even though it was not possible to observe the actual processes leading to them (Klingel, 1968, 1969a). The social organization of the horse is basically the same as well (Tyler, 1969).

Mating only takes place between a family stallion and his mares and there is no competition amongst stallions for adult mares. Adolescent mares, however, during oestrus, attract stallions in the vicinity of their groups. These stallions, family stallions and bachelors, surround the group and try to separate the mare from her group members. The family stallion defends by attacking individual stallions, but eventually the young mare will be separated from her group by the large number of suitors. Usually the young mare does not stay with the stallion who abducted her as the fight over her continues until the end of her oestrus period. With the next oestrus it all starts over again until the mare reaches the age of 2 to 2½ years when she becomes a permanent member of a group.

The different attitude of stallions towards adolescent and adult mares is caused by the conspicuous oestrus posture of the younger mares, whereas in adult mares oestrus is optically inconspicuous and this is a prerequisite for the stability of the groups. It is also a behavioural adaptation. The mares come into oestrus a few days after foaling and, as only the family stallion will attend to her, there is a minimum of disturbance and chasing and the young foal is quite safe.

Abducting a young mare is one way of stallions starting a family or, when they are already in control of one, of increasing the number of their mares. The other possibility is for a stallion to replace an old or sick family stallion or to take on a group whose stallion has died. Even in these cases the group formation stays intact and the new stallion takes on the group as a whole. When a family stallion is not in full control of his group, this is obviously noticed by bachelors and one of them will stay in permanent contact with that group, slowly, without a fight, taking over and pushing the original stallion out.

When there is a family without a stallion, the first mature stallion to come by will stick around and will immediately be respected by other stallions, days or even weeks before the mares have accepted and acknowledged him. If such a stallion already has a family of his own the two groups will be quite separate at first, but after some time they amalgamate and the mares will form a new dominance order.

The young stallion stays with his family much longer than the young mare, namely up to the age of 4 years. He leaves at an earlier age when his mother has a new foal and when there are no play mates, stallions of similar age, in the family. There is no evidence of family stallions chasing their adolescent sons away; in contrast, they search for them when they get lost. The colts eventually join stallion groups, and from the age of 5 to 6 years they start to compete with other stallions for adolescent mares.

Fig. 1. Plains zebra families and stallion groups in the Serengeti.

Fig. 2. A Grévy's zebra stallion (right) with a mixed herd of conspecifics in his territory in northern Kenya.

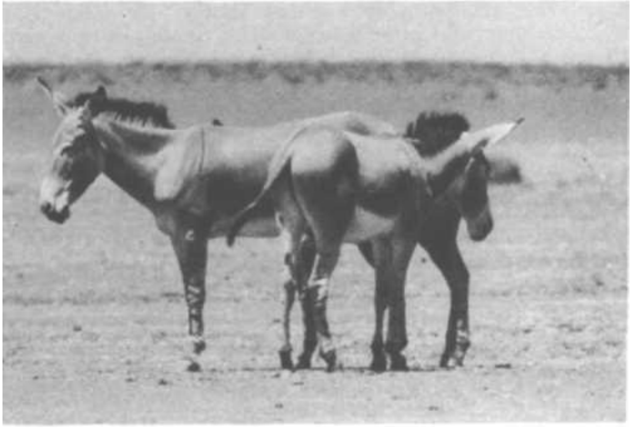

Fig. 3. Wild ass mare (left) with yearling and two-year-old male foals in the Danakil, Ethiopia.

The social organization of the other two African equids, the Grévy's zebra and the wild ass, is completely different from the above. In these species there are no permanent bonds between any two or more adult animals. These are found solitary or in a variety of different associations: stallion groups, mare groups, groups of mares and foals, and mixed herds. All these groups are variable and their composition may change even within hours. The only bonds existing are those between a mare and her foal or foals. Of the solitary stallions, some are territorial.

Of the two species, I have been able to study Grévy's zebra in detail (Klingel, 1969b, 1972). My observations on the wild ass are still fragmentary due to the shyness of the animals and to the fact that the time available for this work was very limited. The observations strongly suggest, however, that the social organization of the wild ass is identical to that of Grévy's zebra. Observations on burrows support my results (Moehlman, 1971).

The territoriality of these species is of particular interest. There is firstly the extraordinary size of the territories. The territories of Grévy's zebra stallions in my working area near Wamba in northern Kenya measured from 2. 7 to 10. 5 sq. km with an average of 5. 75 sq. km. Those of the wild ass near Tendaho in the Danakil region of Ethiopia seem to be even larger. The territories of those two species are to my knowledge the largest male territories ever recorded in a herbivore.

The second important feature is the tolerance of the territorial stallion towards conspecifics including other males which means that he does not prevent them from entering his territory. Within the territory those males respect the territorial stallion and do not interfere when he is engaged in mating activities. If they happen to get near a mare in oestrus the territorial stallion chases them away. I have never observed him to be challenged (Fig. 2).

With few exceptions the territorial boundaries are defended only when there is an oestrous mare near the boundary. Then territorial neighbours will fight with each other; simultaneously each of them will try to make the mare walk towards the centre of his territory. As soon as one of them succeeds, the fighting ceases and the successful stallion follows his mare; the other one waits at the boundary.

Some of the boundary points were found by recording the places where fights between territorial neighbours took place. In order to find more of them we made oestrous mares walk towards the boundaries by driving them with a vehicle. Since territorial stallions move with their mares, and as the neighbours are usually alerted by the precopulatory activity of a pair, we could induce the stallions to fight anywhere along the boundary and thus find its alignment.

The territories are marked mainly static-optically, that is by the sheer presence of the owner. In addition he signals his presence acoustically. Dung piles are found mainly along the territorial boundaries; these are used probably for years by the territorial stallions and also serve to mark the territory, not to warn potential intruders, however, but for the orientation of the territorial animal itself.

The function of the territorial system in these species became clear when I observed an oestrous mare in an area without territories. For two hours she was courted by up to 9 stallions at a time. These stallions were practically continuously fighting each other and therefore none of them succeeded in copulating with the mare. The group eventually moved into a territory where the territorial stallion took over. The other stallions moved away while he copulated with the mare.

The territories of Grévy's zebra and of the wild ass are accordingly mating territories. Due to the territorial system only one particular male, which is the territorial stallion, will court a mare at any one time since all the other males are behaving as subordinate to him.

There is no explanation for the immense size of the territories which do not seem to have any other function. The tolerance, however, of the territorial stallion towards other stallions can be considered to be a consequence of the size of the territories: it is unimaginable how a stallion could possibly fend off intruders from his boundaries when they are, on an average, over 10 km long.

The stallions leave their territories for short periods of time in order to walk to their drinking places. At least the Grévy's zebra stallions keep their territories throughout the year and probably for many years, even during the dry seasons when the mares and foals and the non-territorial stallions leave the area because of the shortage of food and water. In the extremely dry months of August and September 1968, some of the territorial stallions in my study area left their territories for a few weeks, but they returned to them before the start of the rains and before the arrival of the rest of the population. During the dry season of 1971, practically all the territorial males in my study area had left; however, some returned with the onset of the rains and went back to their territories which they had occupied as early as 1967.

This type of social organization, characterized by the instability of the groups and by the existence of non-exclusive male territories, is not altogether restricted to the equids. Owen-Smith (1971) has recently discovered an interesting parallel in the white rhinoceros where the territorial bulls are tolerant to subsidiary bulls. In the white rhinoceros, however, the subsidiary males live permanently in one particular territory, whereas in Grévy's zebra and in the wild ass they are not restricted at all.

## B. SOCIAL BEHAVIOUR

As I have mentioned above, some behaviour patterns are identical or similar in the various equine species. This is true for the fighting, social grooming, mother-child relationship and largely for the greeting and mating behaviour. Other patterns, however, are quite different and they can be correlated with the social organization.

### Fighting

Five phases of fighting can be distinguished: running (which means chasing and fleeing), circling, neck-wrestling, biting and kicking. The fighting behaviour is hardly ritualized, but very rarely leads to serious injuries, the teeth and hooves of the equids being rather ineffective, considering the sturdiness of the animals.

### Mother-Child Relationship

In the mother-child relationship of the equids there seems to be one general feature, irrespective of the type of social organization. We have observed it in the plains zebra and Grévy's zebra, and have also been able to confirm Tyler's observations in the horse (Klingel, 1969c; Klingel and Klingel, 1966).

During the first days after birth, a mare of these species, and probably of the other ones as well, will not tolerate any other animals in the vicinity of her foal but chases them away by threatening, kicking and biting them, or prevents their contact with the foal by moving between the two. In the plains zebra and in the horse, she even attacks the stallion, who is in other circumstances the dominant animal.

Young foals display the following response as soon as they stand up shortly after being born. They follow their mothers and also any other large objects like cars, people or conspecifics. Only after several days do they get to know their mothers and are no longer attracted by strange objects. The foals therefore have no innate recognition of their conspecifics' image. They obviously have a sensitive phase of imprinting during the first days after birth when they learn to know their mother. I am fully aware of the fact that I have only circumstantial evidence, but I do not see an alternative explanation.

The behaviour of the mares is correlated with the learning behaviour of the foal. When the foal is a few days old, the mare's aggressiveness towards other animals ceases and she allows her conspecifics to contact her foal.

One special feature of mother-child relationship could be found in Grévy's zebra. Whereas normally the mare stays with her foal as in the other equine species, she does abandon it in one ecological situation. This happens during the dry season when water is available only far away from the grazing grounds. In contrast to several other ungulate species the young do not have an appropriate behaviour, e.g. hiding. They stand upright where their mothers left them and they are thus very conspicuous. Also they are not guarded by a nurse, even though there is occasionally an adult nearby. It is obvious that these foals are particularly vulnerable to predation.

## Greeting

The greeting behaviour consists in all species of naso-nasal and naso-genital contacts. The latter, as well as the facial expressions, are different in the different species; and in the plains zebra there is a final jump which has no parallel in other species.

## Mating

In the mating behaviour there are some slight differences in the precopulatory activity and in the posture of the mare (Klingel, 1969c; Klingel and Klingel, 1968).

## Marking

The marking behaviour consists in all equine species of the animals defecating and/or urinating onto the faeces and/or urine of their conspecifics. This pattern is displayed mainly by stallions and foals, but to some extent also by mares. The Grévy's zebra and wild ass stallions have, in addition, the habit of defecating preferentially onto their own faeces. Thus they build up the enormous dung piles which cover several square meters and are up to 40 cm high. Only in these two species does the marking behaviour serve an obvious purpose, as I have pointed out previously.

An earlier explanation of the marking behaviour in the plains zebra was given by Trumler (1958). He claimed that a stallion, by marking the droppings of a mare altered their smell, and thus hid from other stallions the fact that the mare was in oestrus. My observations show clearly that this is not the case. A stallion does not mark all the faeces and urine of an oestrous mare, and even when other stallions come across such unmarked droppings they do not approach the mare but respect the presence of the family stallion.

The marking behaviour of the non-territorial equids has, as far as I have observed, no obvious function.

## Dominance and Leadership

In the non-territorial species, the plains zebra and the mountain zebra, I discovered an order of dominance among the members of the families, the stallion being the alpha-animal. He also occasionally leads the group during migration. Normally, however, the highest ranking mare leads and the other mares follow her in the order of their dominance. If a mare walks in front of a higher ranking one, she will be attacked and threatened by that animal until she takes her proper place. The young of a given mare follow her in the order of their youth, the youngest first. In the presence of its mother a foal has a rank just below that of its mother. The stallion usually brings up the rear or moves parallel to the group.

In bachelor groups there is an order of dominance among the subadult members, whereas all the adult stallions seem to be of equally high rank. The leader in these groups is always an adult stallion.

No dominance hierarchy could be found in the territorial species, the Grévy's zebra and the wild ass. In these, a territorial stallion is, of course, dominant over all his conspecifics as long as he is in his territory. The adult members of the various associations all seem to be of equally low rank, and also there is no order of leadership. Any one member, male or female, of such a group may start walking and thereby induce the others to follow. When the others do not react this animal may continue on its way or return to the group. During the migrations the leading animal may be replaced, even after distances of only 20 to 30 m, and no antagonism has been observed to occur in such instances.

## Search for Lost Group Members

This feature of group behaviour is also restricted to the non-territorial species. It has so far been observed in the plains zebra only.

When one animal has lost contact with the rest of the group, for instance while sleeping, it searches for the others and is being looked for by them. All family members search for each other with the exception of mares who do not search for other mares or for colts older than two years.

In two instances I observed a stallion grabbing with his teeth a sedated mare by a fold of skin on her neck and leading her back to the rest of the family. It is difficult to make a final judgment about this behaviour which has never been observed under natural circumstances and which can therefore hardly be considered to be innate or learned. This would only leave the explanation of its being the result of a primitive form of insight.

In Grévy's zebra and in the wild ass it is, of course, only the mare and her foal who search for each other (Fig. 3).

### Guards

Two further behaviour patterns demonstrate, again, how strongly plains zebra family groups act as units. Whereas in all the equine and some other ungulate species a female will wake her young when she is disturbed, in the plains zebra even other members of a group will do so frequently, as when the mother is too frightened to go close to the foal or when she is not aware of the danger. When resting, by day or by night, there is always at least one adult or subadult member of a family standing and alert while the others are sleeping in a recumbent position.

In the mountain zebra, I have, in several instances, observed stallions guarding their families at water holes.

## C. ECOLOGICAL ASPECTS

The African equids, with the exception of a few small populations, live in areas where their food and water supplies change drastically during the year. This forces them to migrate either regularly, where there is periodical rainfall, or irregularly where the rainfalls are episodical.

It is obvious that the non-territorial species have an advantage over the territorial ones, as they are not restricted in their movements and as the population as a whole can make use of good grazing anywhere within reach. During the entire year the population can potentially reproduce, as males and females are permanently together.

In the territorial species, at least in Grévy's zebra, this is basically different. Territories are established only in the grazing areas occupied during the rainy season. In the dry seasons the mares and the non-territorial stallions migrate whereas the territorial stallions remain behind. The migratory stallions will not establish territories in the areas occupied during the dry season, and therefore they are quite unlikely to mate with the mares. This means that the reproductive adults of the population are segregated during a large part of the year and that reproduction is thus limited to the rainy seasons. In regions with regular seasons this is no great disadvantage to the species. Since all equids have a gestation period of about one year, the foals will all be born during a rainy season. However, both Grévy's zebra and the wild ass live to a large extent in areas with irregular rainfalls, and in these areas their sexual segregation during the dry periods will certainly reduce their reproductive rate.

## D. STATUS AND CONSERVATION

The major threat to the free-living equids is, in general, the continuous and increasing competition for food and water with domestic stock. Every year additional areas are claimed by the pastoralists, areas which consequently are degraded and eventually will become useless to both wild animals and domestic stock unless conservation measures are enforced.

In addition, all the equids are subject to poaching which has, in the past, led to local extermination. It is still an important factor.

As I have mentioned previously, the wild horse has probably been exterminated in the wild. It should, however, be possible to release into a suitable area a breeding group of wild horses from zoological gardens and thus reestablish the species in its natural habitat. This would also prevent the eventual domestication which is inevitable in a population bred continuously in captivity.

Of the wild asses, the Somali wild ass number 2000 to 3000 individuals in the Danakil areas of Ethiopia (Klingel, 1970) and about 250 in northern Somalia near Las Anod (Hunt, 1970). Very little is known of the Nubian wild ass which occurs in the Nubian Desert of the Sudan and in northern Erithrea. The wild asses are, over their whole range, fully protected by law.

The Ethiopian Wildlife Conservation Organization is considering the establishment of a game preserve in the Danakil. In Ethiopia and Somalia wild ass meat, fat and internal organs are regarded as medicines and a considerable number of animals are shot because of this superstition.

Of the Asiatic wild ass there are several populations in game reserves in the USSR and in Iran; others, like the reserve in the Little Rann of Kutch in India, are reasonably safe from poaching as they are not interfered with by the local population. The status of the species as a whole is unknown.

The number of Grévy's zebra number is of the order of 10, 000 head in Kenya, but only a small portion of them inhabit the area of Lake Rudolf National Park. Their status in Ethiopia and Somalia is unknown, but some herds are known to exist in the Omo valley and in the southern Danakil.

The most common equid, the plains zebra, ranges from the southern Sudan and southern Ethiopia to South- and South-west Africa and can be estimated to number several hundred thousand head.

It is well protected in a number of game reserves and National Parks, e.g. the Mara, Serengeti, Ngorongoro, Wankie, Gorongosa, Kruger and Etosha.

The Cape Mountain zebra numbers about 120 individuals, mostly in the Mountain Zebra National Park in the Cape Province, South Africa.

Hartmann's zebra, of South-west Africa and Angola, ranges in the order of 10, 000 head, and some populations are effectively protected in game reserves.

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Paper No. 6

# A Comparison of Behaviour in the Suidae

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## ABSTRACT

The aim of this paper is primarily to draw attention to a group of even-toed ungulates which for various reasons has not yet been carefully studied. Compared with other hoofed animals, only a small number of forms is included in this group. Although these ungulates are generally considered to be 'primitive' and 'uniform' in regard to their behaviour, this review, which deals mainly with *Sus scrofa* and *Phacochoerus aethiopicus,* shows how many interesting aspects could be revealed by a closer ethological, sociological and ecological study. Appropriate research especially regarding agonistic behaviour and mother-child relationships seems to offer much promise.

## INTRODUCTION

Wild pigs are widely distributed over Europe, Africa and Asia. Although most of the eight recent species are relatively numerous and play a rather important ecological role, only a few of them have so far been carefully studied in the wild. The following observations therefore refer mainly to the European Wild Boar (*Sus scrofa*), including its domestic or feral descendants (Hohr, 1960; Porzig, 1966), and the African Warthog (*Phacochoerus aethiopicus*) (Geigy, 1955; Frädrich, 1965) (Fig. 1). Some behaviour aspects of the African Giant Forest Hog (*Hylochoerus meinertzhageni*) (Ewer, 1958; 1960) and the African Bushpig (*Polamochoerus porcus*) are known from observations both in the wild and in zoological gardens. Practically unknown are their relatives in Asia, the Bearded Pig (*Sus barbatus*), the Javan Pig (*Sus verrucosus*), the rare Babyrusa (*Babyrousa babyrussa*), and the recently rediscovered Pigmy Hog (*Sus salvanius*). The lack of intensive field studies is mainly due to the fact that wild pigs are hunted nearly everywhere because they are regarded as a pest to crops and are highly estimated for their meat. Consequently, nearly all of them have adopted more or less nocturnal habits. Their intelligence, shyness and vigilance combined with an actue sense of smell and hearing make them more difficult to study in the wild than other ungulates. Because of veterinary importation restrictions, African and Asiatic species are seldom exhibited in American and European zoo collections, so even the possibility of studying them in captivity is very limited.

## HOME RANGE AND ACTIVITY

Compared with other ungulates, most members of the Suidae are not specialized in regard to food. This lack of specialization has enabled them to occupy nearly all regions as long as there is at least a minimum of suitable vegetation. *Sus scrofa* for instance has an extremely extended distribution reaching from the Mediterranean Sea to the temperate regions of Europe, and from the cold areas of Northeast Asia to the tropics. Moreover, it was successfully introduced in parts of North and South America and Australia. Wild boars are to be found from sea level to mountainous regions, they inhabit all types of forest, swamps and even densely populated cultivated land. *Polamochoerus, Sus verrucosus* and *Sus barbatus* show a similar adaption, although to a lesser degree.

In regard to their home range or territory it can only be assumed that there are two different types of the Suidae. The first, represented by *Hylochoerus* and *Phacochoerus,* is to a high degree sedentary. Whereas the former is a forest-dwelling species, the latter prefers open grassland, but both inhabit relatively small areas which they seldom leave. The second type shows a trend towards more or less sedentary habits

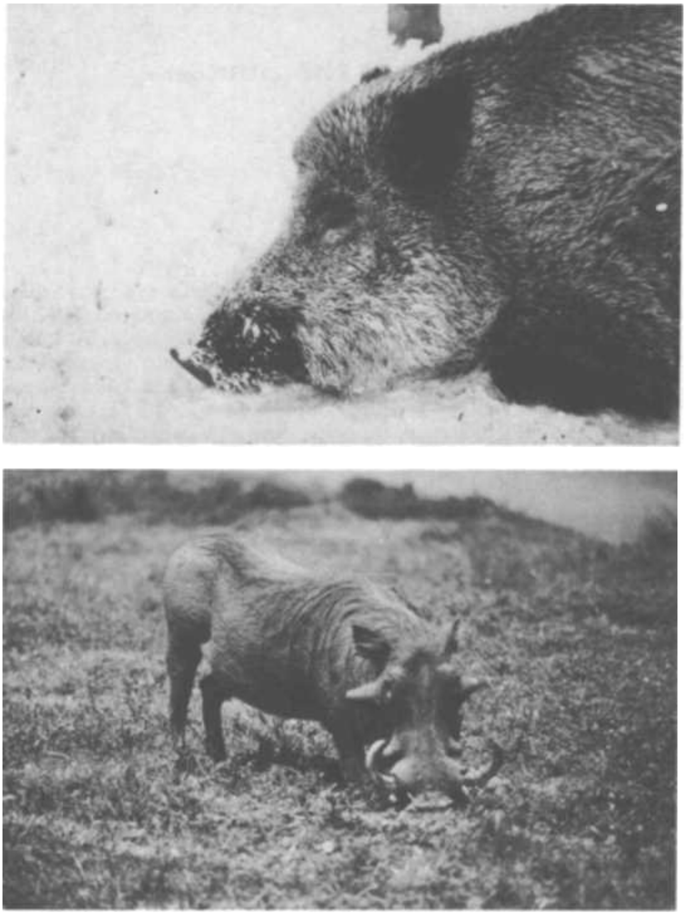

Fig. 1. Top: head of an adult European wild boar
Below: adult male Warthog in typical grazing stance

but depending on ecological conditions, it may roam about in search of better feeding places. Usually movement is irregular (*Polamochoerus*), but cases of periodical movements have been reported. These may occur when certain regions used for feeding become flooded in a certain season or when snowfall in the mountains forces the animals to go down into the plains and valleys (*Sus scrofa*). A part of the population of *Sus barbatus* migrates periodically in very large groups over considerable distances. The reasons for this type of migration which seems to be unique in the Suidae are still unknown.

In an area inhabited by wild pigs, the following fixed points are always to be found:

(a) Resting places. In order to protect themselves during the long period of deep sleep, pigs use or establish shelters. They may root moulds which are often upholstered with vegetal material, they construct temporary sleeping nests of considerable size (especially in the colder season), or they use burrows dug by other mammals. Resting places are normally occupied by more than one individual because pigs, more than other Artiodactyla except the hippos, belong to the 'contact type.'

(b) In hot weather pigs seek shade and water. In order to lower body temperature and as a protective measure against insects, they use wallows. Those places are regularly visited and are obviously of great importance. Drinking places usually lie nearby.

(c) Because of their short neck and clumsy shape, body care behaviour is not as highly developed as in other ungulates. Pigs scratch the anterior part of their body with hind feet. The other parts have to be treated by rubbing. Most wild pigs will rub their body wherever they can, but they show a clear preference for certain rubbing spots (trees, rocks, anthills), especially after wallowing.

(d) Feeding places.

(e) Defecation spots have been reported from *Phacochoerus,* but in this species they do not seem to be of great importance, though probably they are of importance in the case of *Hylochoerus.*

The different fixed points within the home range are connected to each other by a network of paths which are regularly used. In most cases, there is no evidence that a certain area is defended (except for the nest) or that any kind of marking is used in parts of an area in order to keep others away. The only species which has so far been found to be territorial is the Warthog (d'Huart, 1971). As the latter is a highly specialized grass eater, it lives preferably in open grassland. In this biotope, it is much more exposed to predators than are forest-dwelling species. The burrows made by the Aardvark (*Orcyteropus afer*) are used not only for sleeping during the night, but also as places of refuge in case of danger. It appears therefore that *Phacochoerus* is more sedentary than other species and that territorial behaviour has been developed. Details in this matter have still to be checked.

As man nearly always and everywhere exercises an influence on wild pig populations it is doubtful whether they can be regarded as diurnal or nocturnal. In relatively undisturbed areas, there seems to be a trend towards diurnal activity (Gundlach, 1967) in *Sus scrofa* but this may change in accordance with the seasons. The only strictly diurnal species, at least in most parts of its range, is *Phacochoerus.* It spends the night in burrows and shows a more or less exact 12:12 hours rhythm, which varies only with the geographical latitude. Whereas ruminants and equids do not seem to have extended sleeping phases, these are very obvious in all non-ruminating Artiodactyla. A prolonged phase of deep sleep is usually followed by a long phase of activity. The latter may be interrupted by short resting periods. The duration of sleep or inactivity depends on the age of the individual animal and is — among other factors — controlled mainly by air temperature. Feeding is the main activity and requires many hours. Only a relatively short time is spent in wallowing or other activities.

## SOCIAL ORGANIZATION

Although the social organization of Artiodactyla has received increasing attention during recent years, our knowledge of the Suidae in this field is still extremely limited. In wild and feral *Sus scrofa,* the basic social unit is the female and her litter (mother family). When after approximately three months the young are weaned, two or more females usually associate and form a larger unit (family group). This organization remains more or less stable until the beginning of the rutting season when the boars join the females. At this time, the young males leave the group voluntarily (Snethlage, 1957) or are chased away by the males (Nasimovic, 1966). What happens to the young females at this time is still unknown. Some authors state that they, too, are chased (Gundlach, 1968), others believe that they remain with their mothers. The number of females a boar may have at this time depends on his ability to fight for them. Usually he gets 1-3 but sometimes even 5-8. After copulation the boars leave the females; the young again follow their mother, but have to leave her as soon as parturition approaches. So the annual cycle in temperate regions is as follows: parturition in springtime — mother family and family groups in summer and autumn — temporary formation of pairs or mating units at the end of autumn or in wintertime — separation of the pregnant females at the end of winter (Gundlach, 1968). Quite often, the young (especially females) of the previous year stay with their mother and the new litter until they have reached sexual maturity. Although the first oestrus is reported to occur at the age of 8-10 months, they are normally first copulated at 18-20 months. Boars seem to remain solitary except during the rutting season. The older they are the more obvious is their trend towards separation. They reach sexual maturity at

8-10 months but, due to the competition with other males, usually they cannot mate until they are 4-5 years old.

Members of the genus *Sus* living in temperate regions always have a more or less fixed breeding season, which is probably not the case in species living in the tropics. So far, their social organization has not been studied.

Warthogs have a restricted farrowing season in most parts of Africa but, in some regions, breeding throughout the year is reported. As *Phacochoerus* avoids the dense forest and sometimes inhabits even semi-arid regions, reproduction is geared to the year-round distribution of rainfall. Usually the young are born in a season when the burrows are dry and perennial grasses are beginning to grow, so that the nursing females are guaranteed optimal food, and the young find protection in the growing vegetation. The sex ratio in this species is approximately 50 males to 50 females; females mature when they are about one year old, males reach sexual maturity one year later (Child, Roth, Kerr, 1968). As opposed to *Sus scrofa*, adult males of *Phacochoerus* stay with the females for a much longer time. They leave them after copulation (the gestation period in this species lasts about 170 days) and join them again when the young (on average 3 per litter) are a few weeks old. There is a clear tendency to monogamy although cases of bigamy are also reported (d'Huart, 1971). Males follow their mother for about two years, females leave her when they are about 18 months old but may occasionally stay with her for longer. Males which are older than 8 years tend to live solitarily whereas old females never live alone. In preferred feeding places large groups of warthogs can sometimes be observed but there is no evidence of any organization above the level of family groups. Even in large aggregations, each social unit shows a certain group distance and maintains its coherence. Animals belonging to the same group normally spend the night in the same burrow. Family groups are reported for *Hylochoerus*. They usually consist of a male, a female and 2-4 young.

## INTRASPECIFIC RELATIONS

Intraspecific communication in the Suidae is based mainly on acoustic signals. Hearing is well developed and they are capable of a variety of different calls. This compensates for their rather poor visual faculty. The sounds of the Suidae consist of grunts, squeals, snarls and snorts. Sometimes sounds are produced by the teeth (*Sus scrofa, Phacochoerus, Babyrousa*). Except for the domestic pig, no sound repertoire of any species has so far been studied in detail; however, a great number of vocalizations can always be distinguished. They comprise contact calls, warning sounds, expressions of pain and of well-being and, finally, mating calls. Usually females and young are more often to be heard than males. Olfactory controls within the group are frequent. The regions preferably sniffed at are the nose of another animal or its genitals. Greeting consists of naso-nasal contacts and is often combined with slight pushing. Grooming is often performed between animals which know each other well. In *Phacochoerus* it can be done with the teeth but mainly consists of rubbing certain body regions with the nose, especially those parts which the animal cannot reach with its hind feet. Mutual licking is rare. Except for hippos and to a much lesser degree tapirs, there is no ungulate group in which close body contact in periods of inactivity is as frequently to be seen as in pigs. The intensity of this contact depends on the degree of friendly relations between certain animals and is reinforced by low air temperature. It apparently signifies comfort, protection and temperature regulation.

## AGONISTIC BEHAVIOUR

Due to their omnivorous habits, competition for food is much more common in pigs than in other Artiodactyla. In the wild, Sus scrofa and Phacochoerus seldom show agonistic behaviour but in captivity it can regularly be seen at feeding time. The more preferred a certain food, the more frequent and violent the interactions, so rank order can easily be studied in this situation. There is often a hasty collection of a large amount of food which is carried to a 'safe' place. This behaviour is reminiscent of carnivores, especially canids. As soon as the food is deposited it is quickly swallowed and, while eating, the animal turns its rear towards its competitors. If one of them approaches, short warning grunts are sometimes sufficient to keep him away. If a rival is not respected, the defending animal may threaten the other by a short and sudden upward movement of the head without touching him. If even this is in vain, the rival is pushed with the shoulder region or more or less vigorously with the snout. In this case, he can be slightly lifted or even thrown or knocked over. An animal repulsed in this way usually lowers its head and walks backward. During food defence, biting often occurs in *Sus scrofa* but not in *Phacochoerus.* Adult boars are so dominating that they do not have to defend their food.

In some species of Suidae, a remarkable trend towards cephalization of display organs can be observed (Portman; Geist, 1966;Theius, 1970). *Sus scrofa* represents a type with a relatively undifferentiated head, and it shows no obvious sexual dimorphism, except for the larger size of the male. In adult males of all the other species, the head at least is clearly pronounced and set off against the body. This contrast is caused by various structures. *Sus barbatus* has hair tufts on the snout or on the cheeks, some subspecies of *Polamochoerus* have a black, mask-like face contrasting with the bright red body. Wart-like skin outgrowths are to be found in *Sus verrucosus, Polamochoerus, Hylochoerus,* and *Phacochoerus.* The development of the upper tusks is correlated with these structures. In *Sus scrofa, Sus barbatus* and *Potamochoerus* they are hardly visible, in *Sus verrucosus* much more obvious, in *Hylochoerus* and *Phacochoerus* they reach their maximal size, and in the male *Babyrousa* their strangest form. Considering the head shape as well as form and length of the tusks it can be anticipated that they are closely connected with display and fighting behaviour .

The main weapons of the Suidae are not the well developed upper tusks but their lower counterparts: these are much smaller but sharper and therefore a more useful instrument. As they are normally more or less covered by the upper tusks they become efficient only when the animal opens its mouth. Two different forms of interspecific combat posture can be distinguished in the Suidae: the lateral engagement of species with long and narrow faces, lacking any skin outgrowths and having only short tusks; and the frontal engagement of species which have a broad head, thick skull, long tusks and face structures. The first type of fighting is to be found in *Sus scrofa* and most probably will also be found in *Sus barbatus.* An intermediate fighting method was described for *Polamochoerus*; the males of this species have skin protuberances on their face but the tusks are rather small. Frontal fighting occurs in *Phacochoerus,* and most likely it will also be found in *Babyrousa.* Although both types are damaging fights there is enough evidence to suggest that the lateral or broadside engagement is the more ancient and primitive one whereas the frontal fight represents an advanced method.

## Lateral fighting

In young species of wild *Sus scrofa,* the following behaviour can be observed (Gundlach, 1968). Two animals strut shoulder to shoulder or at a certain distance from each other. In both, the hair along the dorsal line is vertically bristled, the head is lowered and slightly turned towards the opponent. Usually, one of the animals circles the other and finally stands rectangularly in front of him, displaying his side. After that, both opponents stand nose to nose. They then face each other with shoulders in apposition and apply side pressure. This position may be maintained for several minutes. Later, each one tries to put his snout under the other's hip joint in order to overturn him. In this type of fight, neither of the opponents is bitten or damaged: it serves merely as a trial of strength. The beginning of a serious lateral fight in domestic pigs is very similar but quickly changes. In a serious encounter, both males utter deep-throated, barking grunts. They grind their teeth, snap their jaws and produce large amounts of saliva. As the tension mounts, each boar thrusts his head and neck repeatedly to the side and upwards. With open mouth and bared teeth, they slash each other's head-and-shoulder region and inflict deep vertical lacerations (Hafez, 1062). Fighting boars always await the opportunity to cease shoulder contact and to bite a front leg, the neck or ears of the opponent. In *Sus scrofa* and probably also in other species, a defensive mechanism reduces the efficiency of the sharp lower tusks.

Animals which are known to employ the lateral engagement have a thick, heavy skin. In the European Wild Boar, males fight mainly during the rutting season. In this period, which lasts for several months, the males develop a heavy connective tissue shield on the anterior lateral sides of their body. This body region is often impregnated with tree gum, and so acquires a further protective layer (Snethlage, 1957). When blows on the lateral sides are exchanged, the shield must be considered as very advantageous. When the rutting and fighting season is over, the old males continue to live solitarily and the shield is reduced. Females fight in the same way, but their lower tusks are only poorly developed, so the inflicted wounds are never as deep and long as in damaged males.

### Frontal fighting

This has been described by several authors, mainly for the Warthog (Fig. 2). The latter's preliminary strutting, circling and display are very reminiscent of the similar behaviour of *Sus scrofa.* A displaying boar walks stiff-legged and jerkily, with mane erect, body held tense and slightly arched, and lowered head turned towards the opponent. Later, they push each other head to head more or less violently. The contact area may be frontal, but is mainly confined to the anterior surfaces of the tusks and the snout. Each attack comprises attempts to get behind the defensive tusks, interspersed with trials of strength in which each animal tries to push the other backward. The first impression is that of a sportive encounter such as is usual in young animals. In the fight of adult males and females, however, the observer will soon see that this impression is incorrect. Warthogs do not have a defence mechanism like the shield in *Sus scrofa*, and the only way to protect the vulnerable side is to remain as long as possible in close head-to head contact. Each blow is followed by an attempt to catch it by a counter blow and thus to make it inefficient. After fighting in this manner for some time, the defeated animal gradually sinks lower, 'kneels' down in order to get a safer position, squeals loudly and holds the head lowered. If the dominating animal breaks off the fight, the loser will suddenly turn and run off at full speed. The dominating boar may pursue the other for a short distance but then gives up. As far as we know, serious mutilations of warthogs in the wild are seldom to be seen. This sort of intraspecific combat therefore seems to be much more 'progressive' than the lateral type found in *Sus scrofa* and other species. Geist, (1955), clearly showed that bovids and suids followed similar evolutionary roads in fighting. Laterally fighting pigs and Mountain Goats on the one hand, wild cattle and frontally fighting suids on the other, are similar in their modes of combat, hornlike organs and defence mechanisms.

## PRE-COPULATORY BEHAVIOUR

Olfactory orientation seems to be very important in the sexual behaviour of the Suidae although the significance of the scent glands is not yet fully known. During the oestrus, the males frequently sniff at the urine of the females and sometimes lick it. In this period female warthogs urinate more often than usual. After having sniffed at a urine spot, the male stands over it and marks the place by urinating on it. Similar behaviour has been found in some Equidae. The smell of the urine probably indicates whether or not the female is ready for mating. In *Sus scrofa* and *Phacochoerus*, mating is always preceded by courtship behaviour, in which the male Warthog shows a broadside display basically similar to the threat display but slightly modified. Sometimes, he pursues the female over considerable distances in a quick walk or trot. He utters short, rhythmical grunts, and this noise is reinforced by the clacking of his teeth, which produces a good deal of saliva. The noise is similar to that of a running motor. When the female's walk ceases, the boar intensively nuzzles her vulva and sides, this massage seems to quieten her, and finally he mounts for copulation. Precopulatory behaviour has also been described for domestic *Sus scrofa.* The male follows the female and noses her vulva, body and sides. This activity is accompanied by a special 'mating song' consisting of a series of soft rhythmical grunts. The male repeatedly urinates, chews persistently and produces a large quantity of saliva. Females in oestrus show a typical immobilization reflex when the boar is present. (In 50% of the cases, this reflex can be released by exerting pressure on

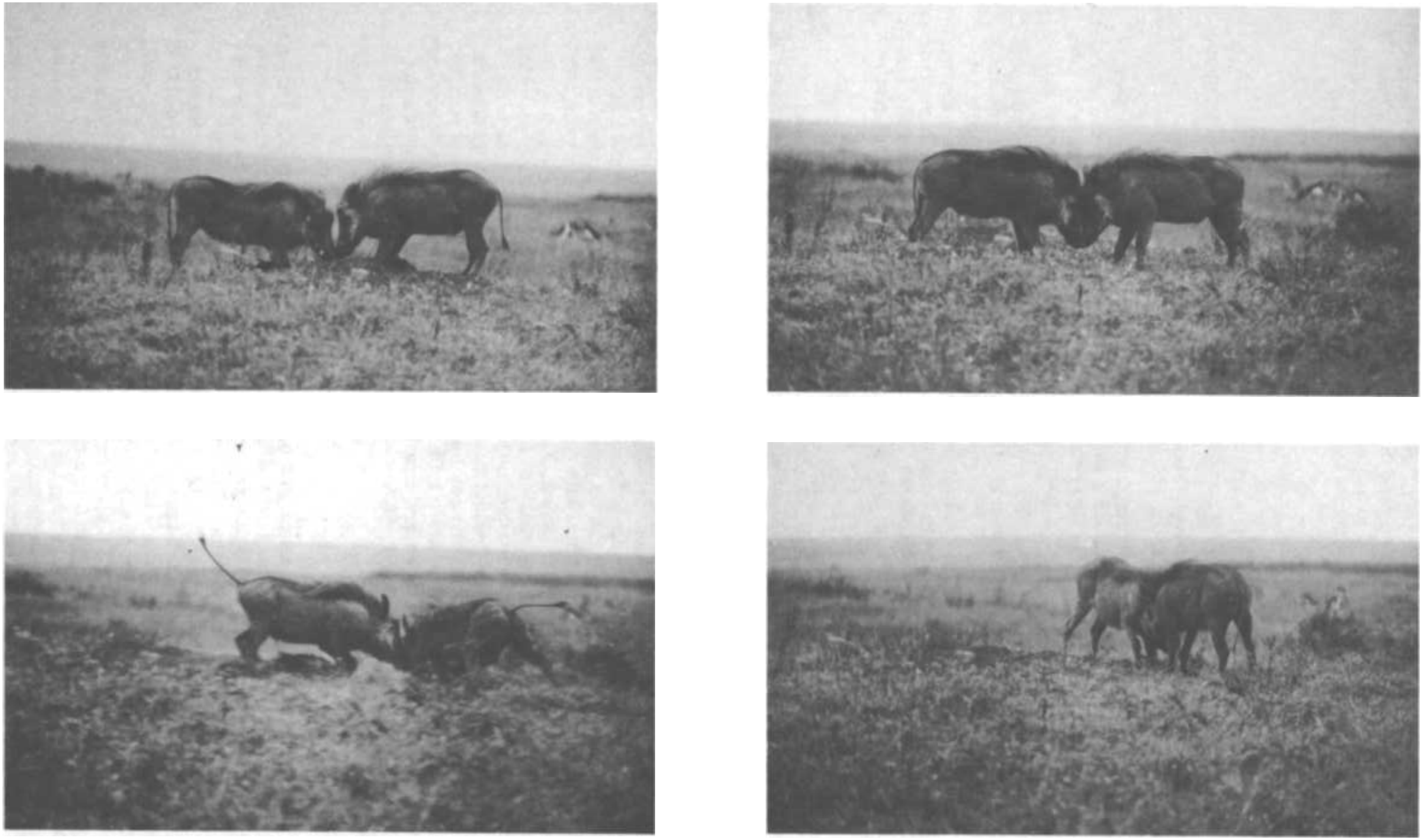

Fig. 2. Frontal fighting of male sub-adult warthogs.

the back of the female while the male is absent.) Acoustic signals produced by the boar reinforce this reaction, and so probably does his scent (Signoret *et al.*, 1961). It seems that in *Phacochoerus* and in *Sus scrofa*, the rhythmical sounds of the male have an important effect on the readiness of the female for mating.

## REPRODUCTION

With regard to reproduction, pigs differ widely from other ungulates in certain points.

(1) Their gestation period is relatively short. It lasts, depending on the species and the age of the individual animal, from 114 to 175 days.

(2) Pigs are the only true multiparous ungulates. Whereas, at best, all the others give birth to twins or triplets (including the Chinese Water Deer, *Hydropotes inermis*, often quoted as an exception), their litters usually consist of three, four, five or even more piglets (in domestic breeds, an average of 10 or more young is not unusual).

(3) Compared with their mother, newborn pigs are very small. In the domestig pig, for instance, the birth weight of a neonate is only 1%, and the whole litter does not surpass 8% of the mother's weight. In some cases (domestic pig, Warthog) the newborn animals are unable to regulate their body temperature during the first days after birth. All these criteria are to be found not only in pigs but also in insectivores, several groups of carnivores and rodents. Like these, probably all representatives of the Suidae family show a more or less developed nest building behaviour just before parturition.

### (a) Nest building

Nesting behaviour is best known in the European Wild Boar and the domestic pig. In the wild, the female first selects a suitable, undisturbed place after having left the young of the previous year. Several phases of nest building can be distinguished. First, with her snout she digs a mould having approximately the length of her body. Then she collects dry grass, leaves and small sticks in a diameter of about 50 m around the mould and may carry this material in her mouth for considerable distances before dropping it in the nest area. After this, she distributes it by rooting and moving in a circle until the mould is equally upholstered. Leaves and grass lying outside the nest are brought in by pawing with forelegs. These actions are repeated several times. When the nest has reached a certain height, the female may collect thicker, up to 2 m long branches. They are covered with hay and grass so that finally only their protruding ends are to be seen. Branches and finer material are brought in by turn. So the nest consists, when it is finished, of several layers and is about 1 m high. When the animal enters the heap, she periodically roots out the center of it so that the nest becomes flatter and flatter and assumes a round or oval form (Gundlach, 1968). The more imminent is parturition, the more seldom are nest building activities to be seen, and finally the females lie down. Many species show a similar behaviour. Only in *Phacochoerus* is nest building activity poorly developed.

### (b) Birth

As it usually takes place in a nest or in a burrow (*Phacochoerus*), there are very few observations of the birth process in the wild. Reports on farrowing domestic sows and some findings in captive wild species indicate, however, that birth in the Suidae differs in several aspects from that of other ungulates. Normally, the young are born while the female is lying on her side. Only in a few cases may they be delivered when she is lying on her belly or standing up. The average duration of farrowing in domestic pigs with numerous litters is 3-4 hours (Hafez, 1963), but due to the small size of the piglets the last phase of expulsion is much faster than in long-legged or long-necked species. Because of their more or less cylindrical and roundish shape, young pigs are born in anterior position as often as in posterior position. The neonates are covered by quickly drying transparent foetal membranes. The umbilical cord is detached by the repeated struggles of the young to reach the teats or by the movements of the female. The mother does nothing to help free the young from the membranes, she very seldom—if ever—licks them and usually does not eat the placenta. This lack of maternal care which is reported also from the closely related Hippopotami and the Tylopods seems to be non-typical for most of the ungulates. It has led Hediger to classify these three families as representative of the 'inactive' type of maternal care. That does not mean, however, that the females do not care at all for their young: they only do so in another way.

### (c) Mother-child relations

Contrary to most other ungulates, young pigs do not follow their mother after birth. As they spend the first days of their life in a nest, they can be regarded as nidicolous although anatomically and physiologically they belong to the nidifugous mammals; to a certain degree, they represent an intermediate stage. During this time young pigs are forced to stay in close contact with their mother and litter mates in order to conserve body heat. The less they are covered by hair, the more essential is this 'huddling together'. The female, therefore, very seldom leaves her young. She has not only to warm them but also to protect them, otherwise the young would fall victim to many predators. Although they belong to the so-called inactive type, the females are not inactive at all. The mother roots the young together in an area away from where she wants to lie down. When she is lying on her side or on her belly, the squeal of a piglet is sufficient to make her stand up or to change her position. So it is guaranteed that none of the small young is squeezed to death by her heavy body. During the first days after parturition, nesting material is brought in by pawing with the forelegs. Nose to nose contact between the mother and her young is frequently to be seen. By olfactory means she apparently learns to recognize them, and this ability increases with the age of the litter. Foster piglets therefore will not usually be accepted when they are older than two days. A disturbed female warns her young by special warning grunts. The young then crouch motionless until the danger is over. The younger the litter, the more ready is the mother to defend them. If a piglet is seized it squeals immediately and without interruption; the intruder is then attacked not only by the victim's own mother but also by other females which have young. These social attacks are reported to be especially dangerous. With the increasing age of the young this readiness for defence fades away.

### (d) Nursing

Within ghe first seconds or minutes after birth, the young try to reach the teats and to get milk. Sometimes, they are still attached to the umbilical cord when they start suckling. The nursing female is lying on her side. This position is typical for the Suidae, Hippopotami and Tapirs, but is not to be found in other ungulate families. Before suckling, the young vigorously nose the surrounding of the teats. In this phase, they are often very excited, and the female utters short, rythmical grunts. Later, the mother's voice becomes softer and finally fades away. When the milk flow begins, the young are extremely calm. As milk is available only for a short time, the young are intent on nursing as fast as possible. When the meal is over, they normally nose the belly again violently, but later this activity stops and the young fall asleep. In wild and domestic specimens of *Sus scrofa* it was observed that each young tries to occupy a special teat. This behaviour can already be seen during the first day. The young defends its 'own' nipple by pushing away its litter mates, by biting or by slashing them with its sharp and rather long canine teeth. Once a special teat is selected, the young normally does not drink from other nipples. The teat in question will be retained during the whole suckling period, regardless of the side on which the mother lies down. It is still unknown by what mechanism this teat or suckling order is established. Neither the milk production nor the smell of the nipple seem to play an important role in this recognition. In small litters, some of the teats are not used for suckling and those atrophy very soon. From studies on captive *Sus scrofa* it is reported that sometimes the young of one female change over to another in order to suckle, and in some cases they are allowed to do so. In the wild, however, the newly arrived are often chased by this female or by her young when they are older. Because of the group distance the young do not normally have any close contact with other young and their mothers during the suckling period. As long as the piglets are young, nursing depends mainly on the mother. When she wants them to suckle, she selects a suitable place, lies down and invites them by grunting. When the young are older, they force their mother to lie down by violently massaging her sides and belly. In response to this nosing, she automatically takes the nursing position like tapirs do when their side is stroked. During the first three weeks, after having suckled, the young of *Sus scrofa* touch the mother's nose with their own and this nasal contact seems to be a very important link between the female and her offspring. After leaving the nest the female makes the young follow her by making short, rhythmical grunts. Outside the nest they remain in close contact with their litter mates. If one gets lost the others squeal and try to find it; the mother then becomes excited, goes to meet them and touches them with her snout. When the young become older, the attachment to the nest gradually declines.

As mentioned before, pigs are an exception among the ungulates, because they spend the first part of their life in a nest, burrow or similar protected place. As previously stated, however, it is going too far to classify them as true nidicolous mammals. The development of behaviour patterns clearly show that this species can easily be compared with that of other, higher developed Artiodactyla. Apart from rolling on the back and wallowing, all behaviour patterns in different function systems are already present within a few days after birth, or mature soon afterwards. Even the basic elements of mating behaviour, nest building and fighting are performed in a fully coordinated fashion by animals which are only a few days old (Gundlach, 1968).

### Play

Like most ungulates, adult pigs in the wild very seldom seem to play. In young ones, however, this is different, especially while they are under the care of their mother. After leaving the nest or burrow, they will play as often as possible. Three types of play can be distinguished: social play, solitary play and play with objects. Social play usually consists of fighting, and for this play-type most individuals select special litter mates having approximately the same size as themselves. In pursuit plays, however, this preference is not observed: one animal suddenly runs away, and all the others follow over a long distance. A young one which is playing without any companions, thrusts its head to the side and repeatedly whirls round itself. Between these whirling movements, it tries to scratch its head, rub itself, makes wallowing movements or may also jump up and down on the spot. Play with objects is especially interesting. As a result of their omnivorous habits, pigs are used to lifting objects from the ground with their snout or to taking them in their mouths. Playful digging is often to be seen, as well as throwing objects high in the air. Unusual objects are often regarded as a sort of trophy. They are taken with the mouth and carried away, while others pursue the finder and try to tear the object away in order to destroy it. All this is reminiscent of the behaviour of Canids in a similar situation.

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Paper No. 7

# Social Behaviour of the Collared Peccary *Dicotylestajacu*(L.)

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## ABSTRACT

Peccaries are social animals which live in herds throughout their lives. Although the number of animals in a herd may vary from 2 to over 50, most herds contain between 5 and 15 animals. With the exception of natural gains and losses within the herd and an occasional animal joining or leaving, the herd is a permanent social organization. No temporary seasonal groups according to sex and age occur, as does happen among many ungulates where male bands and harems are common at certain seasons. The sex and age ratios of individual herds represent a sample of the population as a whole, and are not a result of particular behavioural divisions. The males are sexually active throughout the entire year and females may bear young at any time of year, although the height of parturition is in July and August. There appear to be more females than males at birth, but in adult populations the sex ratio is nearly even.

The home range of the individual herds of peccaries has been found to vary from two-tenths of a square mile to one and a half square miles in area. Scent marking within the home range is common. Except for some overlapping of herds at water-holes at the borders of home ranges, herds avoid the home ranges of other herds.

The most common agressive action among herd members is the 'squabble' where two animals face each other in a 'sparring' position. The most common threats are a rapid, loud chattering of the teeth which makes a series of staccato sounds, and a close-range threat which is made by opening the mouth and showing the teeth. Fighting is seldom seen among members of wild herds.

## INTRODUCTION

Unlike most ungulates, whose group size and composition change during the year, the collared peccary is a herd animal throughout its life (Seton, 1929; Jennings and Harris, 1953; Knipe, 1957; Neal, 1959; Sowls, 1966; and Schweinsburg and Sowls, in press). No temporary male bands or female harems interrupt the yearly cycle of social relationships in this species. The only exception to this rule is the occasional existence of old, infirm animals which are referred to as 'solitarios' in the American southwest and Mexico (Leopold, 1959). These, however, are rare and generally do not live long.

The purpose of this paper is to review the existing knowledge of the social behaviour of this animal and to describe recent work that has been conducted at the Arizona Cooperative Wildlife Research Unit in Arizona. The scientific name used for the collared peccary in this paper follows Woodburne (1968).

## METHODS AND MATERIALS

The Arizona Cooperative Wildlife Research Unit has been studying various phases of the biology of the collared peccary since 1956. These studies have been concentrated on reproduction, population dynamics, feeding habits and foods eaten, home range and movements. Since 1958, a penned herd of from 10 to 40 animals has been kept at the

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[1] A contribution of the Arizona Cooperative Wildlife Research Unit: University of Arizona, Arizona Game and Fish Department, The Wildlife Management Institute, and U.S. Bureau of Sport Fisheries and Wildlife cooperating.

University at Tucson, Arizona. Also, between 1956 and 1968, a total of 186 individual wild peccaries were trapped, tagged and released in the Tucson Mountains as part of the home range and population studies. Many of these animals were recaptured in successive years. Thus, the knowledge of the social behaviour of this species resulted partly as a by-product of a larger, more inclusive study.

Several different techniques were used to study various aspects of social behaviour. The dominance order in small penned herds was determined by withholding food for a period of time before testing, a technique used by Beilharz and Cox (1967) for domestic swine. I either withheld water to create a competitive situation or furnished particularly desirable weeds and fresh vegetables, chopped into fine pieces which could not be carried away. I considered an animal in a herd to be dominant if it displaced another animal when eating or drinking. Inter-actions between herd members were classed into two categories in the same manner as that used by McHugh (1958) for the American buffalo: (1) Passive dominance, when one animal responded toward another without show of force; and (2) Aggression, when force or threat was used to displace another animal or when a subordinate animal was blocked from access to the food. To study contact behaviour during night hours I placed a camera equipped with a strobe unit at the entrance to the shelter of one penned herd and took photographs of the group while the animals were sleeping. To learn more about the function of the scent gland of the peccary I observed the behaviour of animals which had had their scent glands surgically removed. The scent glands from penned twin females were removed when they were 33 days old. The small scars healed quickly and these two animals were kept in captivity and observed for a period of 3½ years following the scent gland removal. Their interactions with other peccaries of different sex and age were observed.

To measure the response of animals to scent from strange animals, I removed scent from animals in one of the pen areas and placed it on posts in a small open paddock 250 feet away. In this way I could introduce scent from animals which were not in close contact with the animals being tested.

All of the figures of the various postures and actions in this paper were sketched from photographic images of live animals.

## HERD SIZE AND COMPOSITION

The herd is the most common social unit in the life of the collared peccary. Its size, variation and make-up are therefore important. Numerous writers have reported on the herd size of the collared peccary. Knipe (1957) reported on 127 herds in Arizona and found that the number of animals in the herds ranged from 1 to 21 and averaged 8. 5 in the years between 1948 and 1954. Knipe also gave estimates of three additional herds which numbered from 40 to 53. His figures represent the largest amount of published information based on accurate counts of undisturbed herds. Seventy percent of the herds Knipe observed were of ten or fewer animals. Only nine percent reported by him had more than 15 animals. Knipe observed only four instances of lone peccaries. In the Tucson Mountains of Arizona, Minnamon (1962) found an average herd size of 7. Bigler (1964) found that 12 herds in the Tortolita Mountains in Arizona averaged 7. 2 animals each. In the years between 1959 and 1971 in Arizona, hunters were interviewed at checking stations operated by the Arizona Cooperative Wildlife Research Unit. The 851 herds from which hunters took animals averaged 7. 9 animals per herd. Of 48 herds which I observed in southern Arizona where the animals were undisturbed I found numbers varied from 1 to 18 and averaged 8.0

The number of animals in the herds varies greatly between different areas and at different times. It is influenced by the amount and effectiveness of rainfall which influences reproduction and survival of peccaries and by the severity of the winter weather, especially at the higher elevations at the northern fringe of the animal's range. Concentrated hunting pressure also causes the number of animals in the herds to vary.

Seasonal fighting during the breeding season which is so spectacular among some ungulates is almost lacking in peccaries. When fighting does occur, both animals attack 'head-on' and opponents bite each other about the head and neck. Jaws may become inter-locked and a 'whirl-around' motion and 'throw-down' occur. A well-defined hierarchy can be observed in penned herds, but it is hard to detect in wild herds. Females are usually dominant over males.

Both sexes have a scent gland on the back from which they are able to squirt liquid musk for several inches at will. With it they mark trees, rocks, and similar objects within the home range of a herd. The scent gland is a skin gland and has been successfully removed surgically. Penned animals without scent glands appeared to live normal lives and showed no detrimental effects caused by gland removal. Friendly peccaries engaged in a reciprocal rubbing action in which two peccaries stood facing in opposite directions with sides touching while each vigorously rubbed the side of its head against the other's hindquarters and scent gland. Reciprocal rubbing is done by both sexes or a combination of sexes.

Females appeared to initiate most courting actions and mating. Actions which are seen during mating time but are not restricted to reproductive behaviour include mutual sniffing of the scent gland, a 'nuzzling' where each animal puts it head on the neck of the other and reciprocal rubbing or mutual grooming. Actions between male and female which are restricted to reproductive behaviour include the male sniffing the vulva of the female, the female sniffing the penis of the male, and the riding of the male by the female.

The young stay very close to the mother and follow the mother when but a few hours old. In captivity the mother defends the young against all intruders and threatens other peccaries which come close. In wild herds, however, the mother flees from intruders with the herd and the young usually 'freeze' to the ground and hide. Strong following tendencies are apparent but there is no clear evidence of leadership within the herds. Physical contact between herd members is common, especially when resting or sleeping.

## INTRODUCTION

There is some evidence that the herds today are not so large as they were in earlier years. Roosevelt (1893) reported that herds in Texas numbered 20 to 30 animals. I have known many hunters in Arizona who tell me that herds in that state are not so large as in former years. Unfortunately these accounts are hard to evaluate and data on early herd size is lacking. From the standpoint of studies of social behaviour I have concluded that herds could vary from 2 animals to over 50. Most of the herds encountered range, however, from about 5 to 15.

The sex of a peccary can be observed only at close range when the external genitals of the adult males can be seen. Hence the only accurate determinations of the sex and age of all the animals in a herd have been furnished by workers who trapped and handled the animals. Only Neal (1959) and Schweinsburg (1971) have recorded the sex of all members of individual wild herds. Neal reported the following: a herd of 6 which was composed of 3 adult males, 1 adult female and 2 immature females; a herd of 15 which was composed of 3 adult males, 6 adult females, 2 immature males, and 4 immature females; and a herd of 7 which was composed of 1 adult male, 4 adult females, 1 immature male, and 1 immature female. Of the 28 animals in three herds reported by Neal, 10 were males and 18 were females. Schweinsburg (1971) reported on two herds for which he had sex and age data on all members. One herd was composed of 8 animals including 3 adult males, 4 adult females, and 1 immature female; while the other was composed of 7 animals including 4 adult males, 2 adult females and 1 juvenile female. Of the 15 animals in two herds reported by Schweinsburg, 7 were males and 8 were females. No evidence of any temporary seasonal grouping according to sex have been reported. Nor have there been reports of strong evidence that animals were driven from the herds or that solitary animals are common.

Sowls (1966) reported larger numbers of females at birth than males (of 60 young of which the sex was known, 62 percent were females, and 38 percent were males). Since these figures were first published, additional records were obtained bringing the total to 147 young. Of this number 88 or 60 percent were females and 59 or 40 percent were males. Between 1957 and 1971, 2, 563 adult peccaries killed by hunters were examined at checking stations; 1, 342 were males, and 1, 221 were females, a 52 : 48 ratio in favor of males. Of 186 adults captured in the Tucson mountains between 1956 and 1968, 82 (44 percent) were males and 104 (56 percent) were females.

## HERD STABILITY

The most common changes in herd size occur because of deaths or births; but occasionally animals move out of a herd or new animals join a herd. Schweinsburg (1971) concluded that changes of two types occur. The first were temporary fluctuations which were the result of animals leaving the herd after fighting or when the herd was scattered by a disturbance. When temporary fluctuations occured the members stayed within the home range of the herd and later regrouped. The second group of changes he termed 'herd alterations' and included permanent changes where herd members left the home range of the herd or when wandering animals joined a herd and remained with it. Schweinsburg studied movements between two herds during a two-year period and reported five instances in which animals shifted from one herd to another. All of these five animals left the home range of one herd and stayed within the home range of the herd which they joined. Schweinsburg found no instances in which animals shuttled between herds.

## MOVEMENT PATTERNS OF THE HERD

A herd of peccaries normally moves slowly over the feeding terrain in a widely-spaced group. The spacing of animals varies with the type of foods being taken. When rainfall is plentiful and small succulent plants are common, herds are loosely scattered; but during the dry season, when such plants as *Agave* sp. or prickly pear, *Opuntia* sp. are taken, then animals are forced to congregate about certain plants. Even in these situations, conflict between herd members is not common, although some squabbling occurs.

The feeding pattern in relation to time of day and temperature has been described by several writers (Enders, 1930; Jennings and Harris, 1953; Elder, 1956; Knipe, 1957; Eddy, 1961; Minnamon, 1962; Bigler, 1964; Ellisor and Harwell, 1969). Most writers agreed that the herds feed mainly in the early morning and late evening hours and that there is considerable nocturnal movement and feeding during the hot summer months. The amount of daylight feeding seems to vary greatly with the temperature; and during the cool winter months, animals feed all day.

## HOME RANGE

The home range of the collared peccary has been described by several writers. By retrapping and field identification of 143 marked animals, Minnamon (1962) concluded that the home range of the collared peccary in the Tucson Mountains of Arizona was less than 1.5 of a square mile. Bigler (1964), who carried out a similar study in the Tortolita Mountains of Arizona, found that the minimum home range varied from 1.0 to 3.1 square miles. A study based on individually marked animals in the Texas brush country (Ellisor and Harwell, 1969) revealed average home ranges of .48 and .85 of a square mile in two study areas. These authors obtained a total of 1, 333 sightings of 66 marked animals by using bells attached to collars to aid in finding the animals in heavy brush. Schweinsburg (1969 and 1971) placed plastic harnesses on individual animals to identify them in the Tucson Mountains of Arizona and used radio transmitters attached to these collars to aid in the rapid location of herds. He concluded that the home ranges of four herds were . 50,. 20,. 30, and. 60 of a square mile in size. Day (1969, 1970) placed radio transmitters on collared peccaries in three herds in Arizona and found the home range to be up to 1. 50 square miles in area. Schweinsburg (1969, 1971) spoke of 'core areas' which were parts of the home range most commonly used, a concept first put forth by Kaufman (1962) and enlarged upon by Jewell (1966).

In the Tucson Mountains where several herds drank from the same waterholes during the dry seasons there was an overlapping of home ranges. Schweinsburg (1971) found boundary overlaps of up to 200 yards where home ranges of individual herds met at waterholes and desirable bedding areas. He did not find more than one herd using a bedding area at one time. A herd's definite and strong affinity for specific areas seems to be true whether other herds are in the area or not. Scent marking within the home range informs other animals that the area is already occupied. Ellisor and Harwell (1969) used the words 'home range' and 'territory' interchangeably and discussed the overlapping of the home ranges of different herds. In describing their Texas study they say (p. 427): 'Territorial behavior made it possible to accurately define home range boundaries by plotting points at which herds repeatedly refused to venture farther from the center of activity'.

## INTRASPECIFIC AGGRESSIVE BEHAVIOUR

Frädrich (1967) has described some aspects of the aggressive behaviour of the collared peccary and compared its behaviour with that of some species of *Suidae*. Schweinsburg (1969) and Schweinsburg and Sowls (in press) have described other aspects. Since these papers have been completed I have continued investigating other phases of the aggressive behaviour of the peccary. Thus the discussion on aggressive behaviour for this species includes both published and unpublished material.

### (a) the squabble

Schweinsburg and Sowls (in press) have described some of the aggressive actions of the collared peccary. The most common aggressive action is what these writers have termed 'the squabble'. In this action (Fig. 1) two animals face each other in a 'sparring' position. Canine teeth are usually brought together in a sharp clatter. The ears of both animals are held flattened against the back of the head. Occasionally animals receive cuts about the face and head during squabbles. The squabbles are commonly seen and heard both in wild herds and among penned herds.

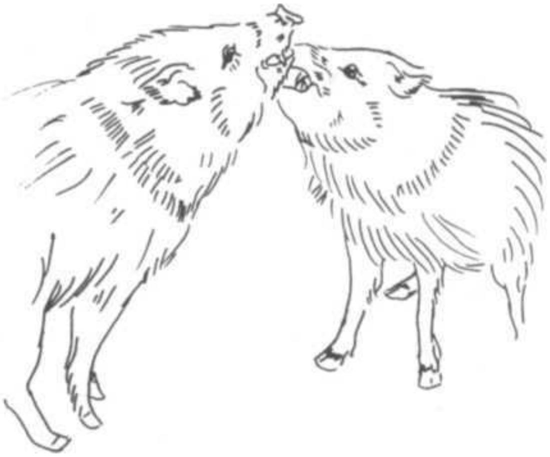

Fig. 1. Head to head 'squabble'

### (b) tooth chattering and threatening

Even before their canine teeth are well-developed, young peccaries bring their jaws together making a threatening staccato sound. As the animals grow older and the canine teeth develop, the sound comes from the forceful bringing together of the smooth faces of the canine teeth. The sounds are made in short groups. Of a series of 19 chatterings made by a female with young, the average number of tooth impacts was 3.1; the number of impacts varied from 2 to 5 in a series. An explosive 'woof often accompanies the tooth chattering. Tooth chattering, while being an intraspecific threat, is also an interspecific threat. A 'close-range' threat which is also either intraspecific or interspecific is the opening of the mouth and the showing of the teeth. This action is usually a defensive action of a subordinate animal.

### (c) fighting

The fighting actions of several species of *Suidae,* which are closely related to the collared peccary, have been described by Frädrich (1965 and 1967). He found two basic fighting positions: (1) a frontal attack which is used by the Warthog, *Phacochoerus aethiopicus* P., the bushpig, *Polamochoerus porcus* L., and the giant forest hog, *Hylochoerus* sp.; and (2) a lateral attack which is used by the wild boar, *Sus Scrofa.* In the first type of fighting the opponents come directly at each other with hair bristled and push each other backward. In the second type of attack the opponents circle each other and press their shoulders together and bite each other about the shoulders, throat, forelegs and ears and try to overturn each other. Frädrich observed that warthogs seldom bite each other in these encounters but that the wild boars and bushpigs do.

Schweinsburg and Sowls (in press) studied penned peccaries which were placed together in neutral enclosures. They described the *whirl-around* motion in which the two became locked together at the jaws and circled around each other. This action is often followed by a *throw down* because both animals become exhausted and fall to the ground and finally release their hold. The retreat of one of the animals usually follows.

Our observations have indicated that the fighting of the collared peccary is primarily frontal, but that in some respects it resembles lateral fighting. The peccaries we observed bit their opponents with their long sharp teeth. When they attacked, they 'charged' head-on but did not push. Most of the biting was directed toward the head, neck and shoulders. As they became tired they tended to bite their oppenent's flanks and hindquarters. The advanced stages of fighting which included the whirl-around and the throw-down were seldom seen unless antagonistic animals which normally did not live together were placed in the same enclosure.

### (d) dominance order in penned herds

No one has been able to observe wild marked individuals consistently enough to determine orders of social dominance in wild herds. Occasional interactions between herd members can be noted, but more often than not the squabbling is hidden from view. Inasmuch as the squabbling often takes place over bedding sites, heavy vegetation and bluffs hide the animals from view.

Among 14 small herds of penned animals which had lived together for several months or more, a dominance hierarchy was evident and could be experimentally determined. Following the methods previously described, the gathering of data on social ranking in small penned herds was undertaken. The results of these tests are given in Table 1. In these trials, sex, age and size were variables which could be measured. One other variable which could not be measured, however, was the tameness or wildness of the individuals and the influence of these factors on behaviour and the validity of the observations. Animals which had been hand-reared were not afraid of man, while those which were not hand-reared remained farthest from the observers and from the food piles. This resulted in a lack of decisive encounters between individuals in some pens. It is for this reason that many vague dominance positions existed in our picture of the dominance hierarchies of these herds.

Ten adult males and 21 adult females were involved in these trials. Usually females dominated males. Only in two of these herds did I observe instances of females definitely being subordinate to males. These two females had been raised as pets but so also had the males which were dominant over them. In one instance a small young male was consistently dominant over a larger and older female. There are, at this time, insufficient data to ascertain the importance of size as an influence on social rank.

### (e) submission

In the encounters just described subordinate animals showed their position by retreat

TABLE 1. RESULTS OF TESTS TO DETERMINE DOMINANCE IN SMALL HERDS OF PENNED ANIMALS

| Herd No. | Composition | No. of Trials | Interactions | | Remarks |
|---|---|---|---|---|---|
| | | | Aggressions | Passive Dominance | |
| 1 | 5 immature ♀♀ | 2 | 5 | 0 | Situation vague. One female definitely dominant over 2 others. |
| 2 | 3 adult ♀♀<br>1 adult ♂♂ | 2 | 5 | 0 | One female dominant over 1 other female. All others eat peacefully at 12' apart and no apparent aggression |
| 3 | 2 adult ♀♀ | 6 | 7 | 2 | Same female always dominant. |
| 4 | 2 adult ♀♀<br>1 adult ♂♂<br>1 juvenile ♀♀ | 7 | 21 | 3 | One female clearly dominant over all other in pen. Male dominant over subordinate adult female. |
| 5 | 1 adult ♀♀<br>1 adult ♂♂<br>1 juvenile ♀♀ | 1 | 2 | 1 | Adult female dominant. Situation between male and juvenile female vague. |
| 6 | 3 adult ♀♀<br>1 adult ♂♂ | 2 | 1 | 4 | One adult female dominant over all others. Position of others not clear. |
| 7 | 2 adult ♀♀<br>1 adult ♂♂ | 3 | 6 | 3 | Definite order with same female always dominant and male subordinate to both females. |

| | | | | | |
|---|---|---|---|---|---|
| 8 | 2 adult ♂♂<br>2 adult ♀♀<br>one has 2 young | 5 | 25 | 1 | Female with young aggressive and dominant. Other female dominant over both males. No aggression between the two males. |
| 9 | Same as Herd #8 except that each female had 2 young | 4 | 2 | | Female with older young remained dominant. |
| 10 | 2 adult ♀♀<br>1 adult ♂♂<br>1 juvenile ♀♀ | 1 | 11 | | One adult female dominant over all others but position of lower three vague |
| 11 | 5 adult ♀♀ | 5 | 24 | | Data gathered at water cup. Order clear on all 5 animals and order remained same each time except second animal moved to vague position on 3rd trial. |
| 12 | 2 adult ♂♂<br>1 adult ♀♀<br>1 juvenile ♂♂ | 6 | 17 | 2 | One adult male dominant over all others. Adult female dominant over second male. |
| 13 | 3 adult ♀♀ | 1 | 3 | | One female clearly dominant over other two. |
| 14 | 1 adult ♀♀<br>1 juvenile ♂♂<br>(age: 14 mos.) | 4 | 19 | 4 | Juvenile male dominant over adult female on all occasions. |

when threatened. This, in most cases, meant backing away from the threatening animal which was dominant. Schweinsburg and Sowls (in press) have described the elevated position of the head among dominant animals during face to face encounters. Total and sudden submission of a subordinate animal may occur when two animals are against each other in a 'nuzzling position' (Fig. 2), when the subordinate animal relaxes and sits on its hind quarters (Fig. 3). In this instance a small adult male was being encountered by a larger and older male which was clearly dominant over him. In this particular encounter fighting was avoided.

Fig. 2. Two adults 'nuzzling'

Fig. 3. Subordinate animal taking submissive position

### (f) aggression among young peccaries

Aggressive actions over food are conspicuous at all ages. The young fought for the mother's milk; and the adults squabbled for food even when it was plentiful. Head to head squabbling was noted even among litter mates less than 48 hours old. I saw a good demonstration of this when two litter mates (both females) engaged in a series of squabbles that lasted about two minutes. The same pair engaged in a similar fight two days later in which each siezed the other by the neck area and began the whirl-around motion which has been described under fighting of adults. The young animals did not seem capable of holding on as mature animals do and hence no throw-down occurred.

The tendency of animals to stand close together and compete for food was most noticeable among young, penned animals. For example, I received a pair of 3-day-old female orphans which quickly learned to drink milk from a shallow dish; however, one grew much faster than its sister, and soon the subordinant animal became stunted and undernourished because it was consistently crowded from the food dish. When I placed several dishes in the pen at the same time, both animals still stayed together and tried to force each other from the same dish. Control of the food pan was maintained by the dominant animal's placing her knees in the food pan. This type of behaviour was particularly noticeable after the age of six weeks.

## THE SCENT GLAND AND SCENT MARKING

The role of scent in marking the territories of mammals has been described for numerous species. Probably the best known type of scent marking is that employed by certain *Canidae* including the male domestic dog which deposits urine on conspicuous objects (Schenkel, 1947; Lorenz, 1945; and Kleiman, 1966). Other mammals which commonly use urine as a scent marker are the hippopotamus *Hippopotamus amphibius* L. (Frädrich, 1967) and the bush baby *Galago* sp. (Eibl-Eibesfeldt, 1967). The methods by which mammals mark their territories vary with the species (Hediger, 1949 and 1950; and Ewer, 1968). Some mammals not only mark locations but also mark other members of their own species, e.g., the male tree porcupine *Eretkizon* sp. which drenches the female with urine (Eibl-Eibesfeldt, 1967; and Ewer, 1968). Some mammals use not only urine to describe their territory, but also feces. Schaller (1967) has discussed the use of feces and urine as territorial markers of the Indian tiger *Panthera tigris.* A wide variety of mammals possess a scent which is used in this manner. Thus, carnivores, such as the European badger *Meles meles,* the mongooses *Herpestes* sp., and some rodents, e.g. the agouti *Dasyprocta* (Eibl-Eibesfeldt, 1967), possess scent glands which are used to make territorial marks.

Among ungulates scent marking of pathways and territorial locations is well developed. Some species mark areas by urination and defecation, either separately or in combination. Among other species there is an elaborate system of scent marking from glands. The use of the preorbital gland has been described by Walther (1968) for several species of African antelope. Similar scent marking of territories has been described by Schaller (1967) for the sambar deer *Cervus unicolor*, chital deer *Axix axis*, barasingha *Cervus duvauceli,* and blackbuck *Antilope cervicapra.*

### (a) the scent gland of the peccary

Among the members of the Superfamily *Souidea,* only the two members of the family *Tayassuidae*, the collared peccary and the white-lipped peccary, possess a scent gland. The scent gland of the collared peccary is located about six inches ahead of the base of the tail along the dorsal midline. The gland appears as a raised area of skin measuring approximately two by three inches across. The nipple-like protuberance, from which the scent is emitted, is located in the center.

The anatomy and histology of the scent gland of the collared peccary has been described by Werner, Dalquest and Roberts (1952) and by Epling (1956). Epling described it as a compound storage gland complex composed of numerous sebaceous and sudoriferous glands that empty their secretions into a common storage area. He points out (page 246): 'The fact that the entire gland complex is surrounded by a capsule that attaches to the voluntary cutaneous trunci muscle gives credence to reports that the secretions may be ejected at will.'

Some early writers called the scent gland of the collared peccary, an extra navel, because of its superficial appearance. Father Ignaz Pfefferkorn (1795:112) described the scent gland in this way: 'In the middle of its back is a navel-shaped hole from which is exuded a heavy odor of musk, which spreads throughout the flesh and makes it distasteful. For this reason, almost all the Spaniards have an aversion to it.' Tyson (1683:378), earlier, however, described it as a scent gland: '... whereas our musk hog has its scent gland seated on the back, and it has been by most hitherto mistaken for a navel.'

Werner, Dalquest and Roberts (1952) believed that the scent gland served to keep members of the herd together. A similar conclusion was reached by Neal (1959).

Frädrich (1965), Hediger (in Grzimek, 1968), Ewer (1968), Sowls (1969) and Schweinsburg and Sowls (in press) have described its use for marking areas within the home range. The rubbing of the scent gland upon objects within its home range and the deposit of scent there by the peccary appears to be the same type of behaviour which is common in many species and was described earlier by Hediger (1949) and more recently by others.

### (b) release of scent

On several occasions I have seen a peccary squirt a stream of liquid scent several inches. Similar instances of the release of scent has been described by Neal (1959), Mohr (1961) and Schweinsburg (1969). It was commonly seen among penned animals when strange animals came near or when animals were moved to strange quarters. When animals were taken from their home pens and moved to other pens they usually explored the area and marked the fences, posts and other objects. Where posts were marked a conspicuous brown coloration usually remained. When an animal rubbed against a fence there were often short streams of musk being emitted. The backing into objects and leaving scent on them (Fig. 4) was often observed, not only among penned animals but among wild animals. Rocks, tree trunks and stumps having dark areas of oily material on them, were common within the home areas of wild herds. Very often the skin around the scent gland was wet with the dripping liquid.

Fig. 4. Adult leaving scent on post

### (c) effects of scent gland removal

The scent gland of the collared peccary is a skin gland and can be easily removed. To determine what effect the removal of the gland would have on the behaviour and health of animals the gland was surgically removed from two animals in 1968. Two female orphan twins were hand raised; and, when they were 33 days old the scent glands were surgically removed. After the age of six weeks these animals regularly rubbed their scent glands on objects when put into enclosures, appeared in every way to have normal coats, mutually rubbed each other and rubbed other animals (see under (e) mutual grooming). One mated and one successfully bore young three times and the other bore young twice in a period of two years. There was no evidence from the behavioural standpoint, that these animals acted or responded differently from animals possessing a scent gland or that other animals responded differently to them.

### (d) reactions to scent of strange animals

Müller-Schwarze (1967 and 1969) and Brownlee *et al.*, (1969) have found that scent from the tarsal gland of the mule deer was important in individual recognition and that males and females reacted differently to scent. Tembrock (1968) suggested that in the collared peccary the composition of the secretion changes, and in that way different information is transferred.

To determine the reactions of animals to scent of another animal, and to see if any differential reaction could be detected because of sex, I brought penned animals into contact with scent from other animals. Samples of scent from one group of animals 250 feet from the experimental area were placed on removable posts set in a line in a neutral area and individual peccaries were then released into the enclosure.

Reactions of four males and three females were observed. Three of the four males showed more bristling when they approached the posts having male scent then they did when approaching the post with female scent on it; however, all rubbed one post as freely as another. One of the three females tested showed much more excitement over the post with the scent from a female, than a post which had scent from a male. No definite conclusions can, at this time, be drawn on how the reactions of an individual peccary are influenced by the sex or some other characteristic of another peccary's scent. It is clear, however, that all peccaries responded in some way to marked areas.

I used additional animals to study investigative behaviour and to obtain the photographs from which Figures 5 and 6 were sketched. Their investigative behaviour included the sniffing of areas where other animals had left scent (Fig. 5); they rubbed their cheeks and jowls on the scented posts (Fig. 6); and they often rubbed their own scent glands vigorously against these scented areas (Fig. 4). They not only reacted to the scent of others, but also reacted similarly to their own scent which had been left on a post previously. An observation of this was made on August 3, 1971, when I placed a fresh, new post in an open pen; the post had been rubbed on the scent gland of an adult female. When she was put into this pen, she immediately sniffed the marked part of the post and rubbed the post vigorously with her scent gland.

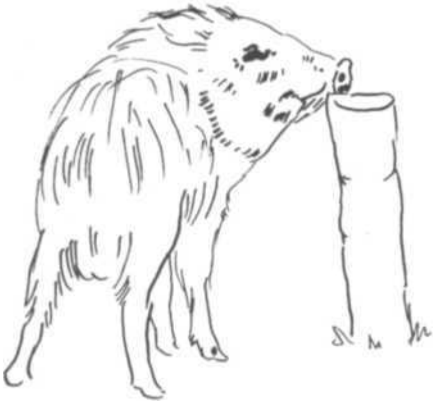

Fig. 5. Adult sniffing scent mark on post

Fig. 6. Adult rubbing cheeks and jowls over scent on post

### (e) mutual grooming

Mutual grooming in peccaries has been described by several writers (Knipe, 1957; Neal, 1959; Frädrich, 1967; and Schweinsburg and Sowls, in press). Frädrich (1967) refers to the mutual grooming in peccaries as a form of greeting and as pleasure-oriented. In this action two peccaries stand in opposite directions with sides touching while each vigorously rubs the side of its head against the other's hindquarters and scent gland (Fig. 7).

Fig. 7. Two adults in reciprocal rubbing action

Mutual grooming is not restricted to animals of either sex or a particular combination of sexes. Sometimes males and females rub each other, sometimes both are males and sometimes both are females. It was most often seen among penned animals when compatible animals were brought together. In the case of males and females that were isolated but which were brought together daily, mutual rubbing nearly always occurred as soon as the animals met. When single males were brought into the same enclosure with several females, the male usually went from one female to another and mutual rubbing occurred. For example, when a lone male was placed in a pen with five adult females, he immediately rubbed reciprocally with one female and successively with three more. The fifth female stayed in the shelter and did not encounter the male.

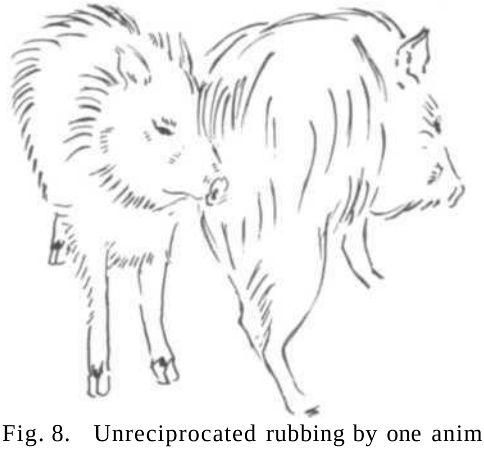

Fig. 8. Unreciprocated rubbing by one animal

Sometimes the rubbing is done by only one animal (Fig. 8). This may happen between friendly animals, but Schweinsburg (1969) has pointed out that there are indications that dominant animals may rub submissive animals and not have the rubbing reciprocated. I observed this behaviour on July 19, 1971, when two adult males, which previously had lived together compatibly, were again put together after being separated for 78 days. One animal rubbed the other animal but the second animal did not reciprocate. In this instance the animal which did the rubbing proved to the the dominant animal when interactions were observed at a later time.

Reciprocal rubbing begins at an early age. Frädrich (1967) says that the mutual grooming behaviour in peccaries appears during the second month of life. Among our penned animals one pair of twins began rubbing each other when 27 days old.

## DEFECATION STATIONS

The use of certain sites for defecation is a well-known phenomenon among certain animals. Hediger (1950) differentiates between diffuse excretion and localized excretion. The collared peccary leaves its feces in localized areas and in this is unlike any other North American ungulate but similar to the New World camels, the alpaca *Lama pacos,* the llama *Lama peruana* and the vicuna *Vicugna vicugna.* Hediger (1950) describes the use of certain places for defecation among captive llamas. Koford (1957) says that these animals of both sexes and all ages use the same dung piles and normally visit the closest piles available. He states further that all three species (vicuna, llama and alpaca) use the same piles.

In captivity, the collared peccary leaves its droppings in one part of the pen. All members of a group in one pen do so. The collared peccary does not always use the same stations in the wild state, however; and scattered droppings will be found along trails and in feeding areas. There are, though, very frequent sites that can certainly be referred to as defecation stations.

Eddy (unpublished manuscript) while studying the food habits of the collared peccary in the Tucson Mountains of southern Arizona, kept careful notes on the scat stations in a 300-acre study area where two herds (one of 12 and one of 17 animals) were observed. In this study area Eddy found 42 scat stations. All of the stations were considered permanent because of an accumulation of considerable fecal material which varied in degree of decomposition. Of the 42 stations, 22 were located on 'saddles' or ridges, 15 were on hillsides, and 5 were along washes. Generally, the stations were under tangles of hackberry *Celtis pallida,* Torr., and palo-verde trees *Cercidium* sp. and in wash bottoms and cave entrances.

## VOCALIZATIONS

No detailed analysis of the vocalizations of the peccary has been completed but several general statements on this subject have been published (Knipe, 1957; and Neal, 1959). Young peccaries emit constant grunting noises that resemble the purr of a cat. As they grow larger, this noise is still almost constantly heard but it is louder, lower-pitched and more articulated. In addition to the purring sounds, very young peccaries emit a variety of squeals, grunts and calls which are heard almost constantly when they are with their mother. When young are left by their mother they cry loudly. Adult animals also make constant sounds and these more closely resemble the grunts of swine, but they are usually rhythmic and regular, and are not made occasionally as in domestic swine. One of these is a very sharp 'bark' not unlike the bark of a dog.

## REPRODUCTIVE BEHAVIOUR

The collared peccary breeds year-round. The chief period of parturition is during the summer rainy seasons, and the main breeding is about five months earlier in late winter (Seton, 1929; Jennings and Harris, 1953; Knipe, 1957; Neal, 1959; Sowls, 1966; and Schweinsburg and Sowls, in press). There are no harems, long-term pair bonds are not formed, and conflict among males in wild herds is not noticeably greater when receptive females are present than at other times (McCullough, 1955; Neal, 1959; Sowls, 1966).

One of the principal aspects of the Arizona Cooperative Wildlife Research Unit's work with peccary has been a study of reproduction. In 1956, when the research unit began work on this animal, even the gestation period was unknown. To determine this, males and females were brought together daily for brief encounters and then kept apart after copulation occurred (Sowls, 1961). Later vasectomized males were used to determine the length and frequency of the oestrous cycle (Sowls, 1966). The bringing together of the males and females on this systematic schedule gave us an opportunity to observe sexual behaviour of the peccary in considerable detail and at various stages of the cycle.

Many female domestic animals, especially cows and hogs (Hafez and Signoret, 1969), exhibit a great restlessness when in heat. It is not uncommon for them to pace ceaselessly in their paddock or cage during this period. In hundreds of observations of female peccaries in heat, hardly any restlessness was observed. A few instances have been exceptional. For example, on December 9, 1958, I noticed that female number 1435 was pacing back and forth in its pen and appeared very restless. A male was already in the pen with her. On May 1, 1959, 143 days later, this female gave birth to two young. At that time we did not realize that the gestation period for the peccary is 142-145 days.

As pointed out earlier, females are usually, but not always, dominant over males. They also initiate most courting actions and mating. When penned males and females were brought together, certain basic behaviours which are typical of most meeting situations were mixed with behavioural patterns which are exclusively associated with

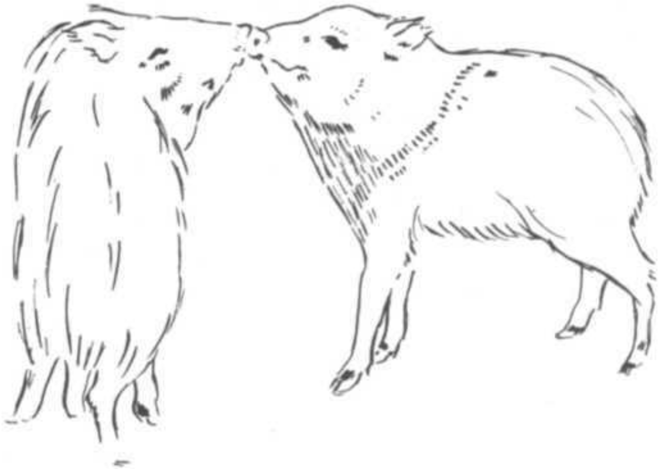

Fig. 9. Nose to nose greeting of two adults

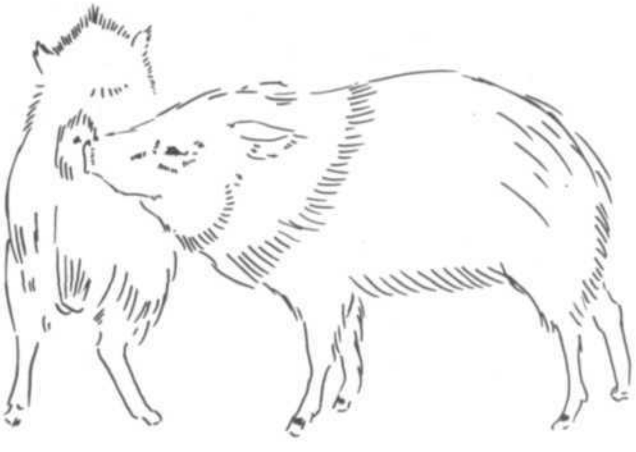

Fig. 10. Adult female sniffing scent gland of adult male

reproduction. The basic behavioural actions common to most meeting situations include a nose to nose greeting which has previously been described by Frädrich (1967), (Fig. 9), a sniffing of the scent gland by either animal (Fig. 10), and 'nuzzling' where each animal leans its head and nose heavily into the shoulder and neck of the other (Fig. 2). Mutual grooming between the male and female accompanies all the above actions when friendly animals are meeting. Actions which are almost entirely associated with reproduction are a sniffing of the vulva by the male (Fig. 11), 'inhibited' biting about the neck and shoulder by both male and female (Fig. 12), and a sniffing of the male's penis as the female puts her head under the male's body (Fig. 13).

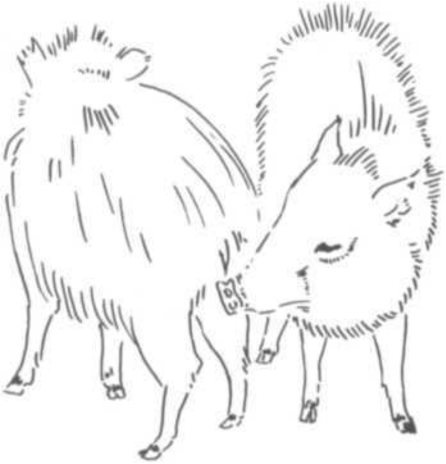

Fig. 11. Adult male sniffing female's vulva

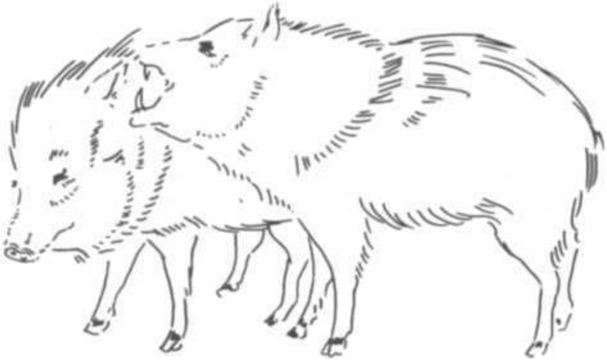

Fig. 12. Inhibited biting about the neck and shoulders

Fig. 13. Female sniffing penis of adult male

Females in heat ride males and occasionally ride other females (Fig. 14). Sometimes copulation (Fig. 15) was almost immediate with no mutual grooming or nuzzling behaviour. The time between initial encounter of the two sexes and coitus which followed was recorded for 277 instances. On 185 or 67 percent of the encounters, coitus occurred less than 5 minutes after meeting. On 26 of these encounters copulation occurred as soon as the animals met. In 89 or 32 percent of the encounters coitus occurred between 5 and 10 minutes after meeting. In only 3 or 1 percent of the encounters was the male with the female more than 10 minutes before copulation took place.

Fig. 14. Female in heat riding male

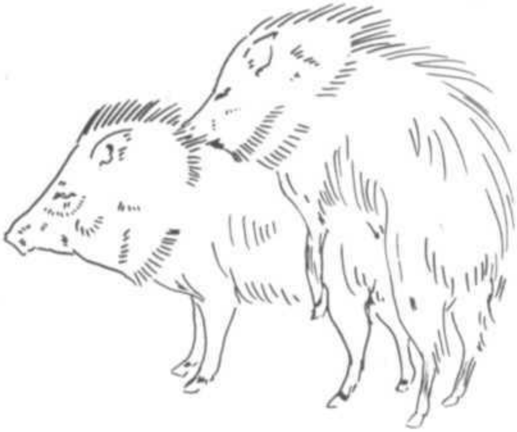

Fig. 15. Copulation

Penned females were found to copulate with several different males in succession. For example, one female copulated with three males in succession as one at a time was put in the pen with her. No information on polyandry in wild herds has been obtained nor has it been observed among penned animals where several males were in the same pen with a female in oestrus. In 45 observed instances the duration of coitus varied from 52 to 210 seconds and averaged 140 seconds. Unreceptive females prevent copulation by holding the very short tail over the vulva. Receptive females raise the tail during courtship and copulation.

## BEHAVIOUR OF MOTHER AND YOUNG

The usual litter size in the collared peccary is two (Knipe, 1957; Neal, 1959; Sowls, 1966). The female has four active mammae and the young are precocial (Sowls, 1966).

When very young, the babies stay either close to or underneath their mother. There is constant communication between them because the young continually emit purring sounds and the mother makes a series of grunts; if other animals approach too closely, she also chatters her teeth in a threatening behaviour.

While nursing her young, the female peccary is usually in a relaxed standing position. The young stand or kneel under her and usually both feed at the same time (Fig. 16).

Fig. 16. Female in normal standing position nursing twins

They nurse often. Sowls, (1966) describes the nursing of two litters of two and a single young among penned peccaries. He found that a litter of two (9 days old) nursed 48 times in 3 hours and spent 24 percent of their time nursing. Another litter of 2 (15 days old) nursed 41 times in 3 hours and spent 16 percent of their time nursing; however, a single young (12 days old) nursed only nine times in 3 hours and spent only 4 percent of its time nursing.

Weaning occurs at about six weeks. It can, however, vary considerably. One captive female had no milk 71 days after parturition, while another female still had a good supply of milk 74 days after parturition. Knipe, (1957) and Neal (1959) described the collared peccary as a poor mother. Schweinsburg, (1969) disagrees with this and gives several instances where mothers defended their young against other adults which came too close.

Among penned animals mothers were found to guard the young closely against other peccaries and other species, including man. Whenever young were born in the pens, we examined them to determine sex and tried to obtain weights and measurements as soon as possible. It was a difficult task because the female invariably charged anyone coming near. A long-handled net was used to scoop up the young while the operator was behind a woven wire fence.

The young usually stayed under their mother (Fig. 17) and were not available for netting until they could be separated from her. After the young were in the net the mother often bit at the net and its handle.

Fig. 17. Young under mother who is in defensive position

The close guarding of young by the mother that I have described among penned animals has not been observed closely in wild herds. The usual thing for a female peccary to do when the herd is disturbed is to run away with the herd and leave the young behind. This behaviour has been described by Knipe (1957) and Neal (1959). The young then normally lie quietly hidden among the rocks and vegetation. I first noted this behaviour on July 8, 1955, when a group of students and I tried to capture a young javelina from a herd. We surrounded a herd in which one female had two young just a few days old. The two young then lay quietly on the ground and remained motionless without making any sounds while the herd and the mother fled. A second young peccary which was a few days old was captured by us on August 3, 1955 by the same method; the reaction of the mother was the same. A number of similar incidents have been described to me by students and cooperators since then.

This usual reaction of very young animals to 'freeze' and hide on the ground has great survival value, but it is not always followed. When herds are disturbed and the mother leaves, the young, on at least some occasions, give forth loud calls in an apparent attempt to attract their mother. One occasion on which I heard the calling of young for a long distance, occurred in 1961. On October 27, I was sitting on a high hill in the Pinal Mountains of Arizona. There was a very strong shifting wind and I could hear the distant sound of what seemed to be a baby javelina. After tracking down the source of the sound, I found two baby peccaries between 1 and 2 days old. The sound had traveled clearly about 600 yards and could serve to attract coyotes *Canis latrans,* bobcats *Lynx rufus* and mountain lions *Felis concolor* that inhabit the same country.

## LEADERSHIP AND FOLLOWING

There is no evidence that herd members become leaders within herds of the collared peccary. Knipe (1957) says of the peccary: 'There is no apparent leadership'. There is, a strong tendency for young peccaries to closely follow their mother from the moment they are born. If a man takes a young peccary away from the mother at a very early age (under 3 days), they follow him around very closely. They will also follow a dog. All of the more than 20 young peccaries which I have hand-reared as pets exhibited a following action. The young tried very hard to stay close to whatever they were following whether it was their mother, or a person, or a dog. I found that one young peccary (timed with a stop-watch and allowed to follow me over a measured course) could run up to 7 miles per hour. When I exceeded this speed, the young animal strayed off and started calling.

Schweinsburg (1969) pointed out that young animals in the wild followed their mothers until they were more than one year old. This same following of the mother to over a year of age can be seen among captive animals. Schweinsburg also described how adult animals followed each other while scattered or in a loose group, and how they filed into line when alarmed or when they were following a narrow trail.

The companionship of individuals has been discussed earlier. Like the young following its mother until it is more than one year old, we have seen young animals attach themselves to another animal of different age or sex.

From the information at hand, it seems likely that leadership as it is known in some animal species such as the red deer (Darling, 1937) and domestic sheep, where there is a strong matriarchal organization, does not exist in the collared peccary. Although no particular animal may be the leader, herd members do follow each other when a single trail is followed or animals begin moving because some stimulus, such as noise, affects all members of the herd at the same time. As Etkin (1963) has pointed out, leadership which exists within a herd is not necessarily associated with the social hierarchy.

## CONTACT BEHAVIOUR

Frädrich (1967) has described the peccary as an animal in which voluntary physical contact is common as in the Suidae and Hippopotomidae. Both among wild herds and among our penned animals, I have noted close physical contact, especially in cold weather. Usually the herd sleeps in small groups in close contact.

Night observations, even among penned animals, are hard to make because the least amount of disturbance startles the animals and causes them to leave their resting positions. To overcome this, I photographed a group, using a remote control, in January of 1971. The night-time low temperature was about 15 degrees F and the animals huddled together in the shelter hut (Fig. 18).

Fig. 18. Sleeping herd of five adults

The most common situation in wild herds is for two or three animals to be sleeping or resting together. Eddy (1959) described the shallow depressions in the ground that were used by small numbers of animals which lay side by side. This same behaviour was often noted among penned animals.

## COMPANIONSHIP

The need of individuals for the presence of others of their own species is strong. This was often seen both in wild herds and among the penned animals. Although there was considerable variation among individuals, penned orphaned twins showed very strong tendencies to stay together. Young animals often followed old males. For example, on June 26, 1958, an adult and a one-quarter grown peccary were observed at a waterhole in the Tucson Mountains. At first this pair appeared to be mother and young. On two later sightings, however, it was found that the adult was an old male. Similar instances of young traveling with adult males were encountered while we were trapping and tagging peccaries. In June, 1965, one adult male was captured four times and each time was accompanied by a one-third grown animal which was with him in the same trap.

## ACKNOWLEDGMENTS

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**Paper No. 8**

# Social Organization of the African Bovidae

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## ABSTRACT

Of 70 African bovids occurring south of the Sahara (69 antelopes and the Cape buffalo), only about 20 have been studied in depth, but this includes half of the 26 genera in 9 of the 11 tribes. This paper surveys the known types of social organization and attempts to relate these to ecological niche. Starting from the premise that the first bovids were small forest dwellers not unlike duikers, bovid evolution is seen primarily as an adaptive radiation into savanna environments affording varied niches and food resources capable of sustaining a high herbivore biomass. All the recent tribes but Bovini were differentiated by the Middle Miocene, long before the spectacular speciation of the late Pliocene and Pleistocene.

Many of the morphological and behavioral adaptations to closed and open habitats are opposite, resulting in a dichotomy between species that inhabit one or the other. An analysis of the 70 species is attempted, from which correlations between morphological traits, habitat preferences and social organization are indicated. Species that live in closed habitats are generally solitary, small, sedentary, cryptically colored browsers with short, simple horns, and hide from danger. Open-country species are mostly gregarious, often distinctively marked grazers of medium to large stature with large and/or complex horns, more mobile, and run away from danger. About 29 bovids are solitary and the other 41 are gregarious. Virtually all of the solitary ones live in closed habitats, against only a dozen gregarious species, few of which are restricted thereto. A provisional arrangement of species at comparable levels of organization is given (Table 5), based on the trend from simple to increasingly complex social behavior evident within most tribes. The most socially advanced—i.e. the most gregarious—tend to achieve the highest population densities and to be ecologically dominant.

All bovids can be characterized as 1) solitary/territorial (Cephalophini,Neotragini, *Redunca);* 2) solitary/non-territorial (bushbuck, Sitatunga); 3) gregarious/territorial (most species); or 4) gregarious/non-territorial (Tragelaphini, Bovini). Seemingly all but about 10 of the African bovids are territorial; the known exceptions all belong to the Bovinae, a subfamily with a possibly long-distinct phylogeny.

Grouping tendencies are shown by many solitary antelopes when attracted into the open onto neutral ground. Such temporary groups were the likely precursors of true herds. Individuals had to band together in order to abandon closed habitat: the herd substitutes for cover, providing concealment for the individual. Besides its many other selective advantages, the herd was thus a passport to the grasslands. Most gregarious species remain sedentary and form only small herds of variable composition, but typically with a female rank hierarchy and leadership. The migratory habits and aggregations of some of the plains species are forecast in a widespread tendency to wet-season dispersal and dry-season concentration.

Three social classes are universal in gregarious bovids: nursery herds (females with or without young); bachelor (all-male) herds and solitary adult males.

About half the African bovids (34 spp.) are gregarious/territorial. The whole range utilized by a population is partitioned into territories, each defended—typically year-round—by an adult male, whose sexual and aggressive behavior affects the distribution and largely effects the separation of the other two classes. The three classes are discussed in turn, using studied species to illustrate different levels of organization and the range of interspecific and intraspecific variation.

Evidence is accumulating that the social *Tragelaphus* species are non-territorial; although fully mature males tend to be solitary, their ranges may overlap. Eland and buffalo form mixed herds, which may include more than one adult male, each sex arranged in a dominance hierarchy. The hypothesis is advanced that bovid (and perhaps many other) male dominance hierarchies are based on a special physiological mechanism—continuing growth of males (only)—whereby differential size as a function of age helps determine rank. This suggests a fundamental difference from territorial societies.

The newborn of all but a few antelopes are concealed for several weeks to months; a rather weak mother/calf bond is rapidly replaced by attraction to the herd or peer group. Precocial young are confined to the Alcelaphini, in which they are correlated with a short calving season, and the buffalo, which seems to be the only African bovid that has evolved a group defense.

## INTRODUCTION

Over one-third (37 percent) of the 187-odd species of hoofed mammals in the world (Anderson and Jones, 1967) are African Bovidae. The 68 (*ibid.*) to 74 (Ansell, 1968) existing African species account for nearly two-thirds (62-63 percent) of all bovids and 44-45 percent of all ruminants (Infraorder Pecora). Only 7 other indigenous wild ruminants occur on the African continent (2 Giraffidae, 1 Cervidae, 1 Tragulidae, and 3 Caprinae). Although the Barbary sheep, *Ammotragus lervia,*, and the ibex, *Capra ibex* and *C. walia* occur to about 13°N, i.e. just south of the Sahara, in the Sudanese Arid Zone and the Ethiopian highlands, respectively (Ansell, 1968), only the African antelopes and the buffalo will be considered here—a total of 70 species (Table 1) [1]

Astonishing diversity of forms is included in this group: at least six subfamilies and 10 tribes (usually treated as subfamilies prior to Simpson, 1945—e.g. Allen, 1939), 26 genera and approximately 63 distinctive kinds of superspecies are lumped (Ansell, 1968; Bigalke, 1968 counts 80 species and ca. 67 superspecies). Eight subfamilies and 11 tribes are recognized in the latest classification (Ansell, 1968). Covering the full ungulate size range, from antelopes weighing less than 10 pounds (4. 5 kg)—pygmy antelope, dikdik, and blue duiker—to giants of more than 1500 pounds (680kg) (eland and buffalo), they occur throughout Africa in every biome, frequently as the dominant faunal elements. In an area with diverse habitats, over a dozen (and up to 17) species may be found within a few square miles (e.g. Serengeti, Kafue, Wankie and Chobe national parks, and Moremi Wildlife Reserve).

Bovids are most often dominant in open country of the savanna and arid-zones, biomes which together occupy over three-quarters of the Ethiopian Faunal Region. Here the most species and highest densities occur. By far the greatest known herbivore biomass of any terrestrial ecosystem has been reached in the African grasslands (Bourliere and Verschuren, 1960; Talbot, 1963; Lamprey, 1964; Field and Laws, 1970). Even without the elephant (*Loxodonta africana*) and the hippo (*Hippopotamus amphibius*), the wild-ungulate biomass of the best African savanna far exceeds that of recent mammals of the Great Plains, the South American savanna, the tundra and the Eurasian steppe (Bourliere, 1961). By contrast, the tropical rain forest, though enormously productive vegetatively, supports a remarkably low vertebrate biomass at ground level. *Brachystegia-Julbernardia-lsoberlinia* woodland, Africa's largest, most uniform vegetational type, which dominates much of the savanna biome, is also relatively faunally impoverished (Darling, 1960; Brown, 1965; Estes, 1972).

So far only about 20 of the African bovids have been the subjects of major field studies (entailing more than a year of observations). Generalizations about bovid social organization might therefore be considered premature. However, the well-known species belong to 9 of the 11 tribes and make up half of the genera; shorter field studies have been made of 7 others in two genera (see Table 1). In sum, representatives of all the major genera have been studied in the wild, except for the forest duikers (*Cephalophus*), of which, nevertheless, one apparently representative super-

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[1] Ansell's amended 1968 classification is followed, except as noted in Table 1. Gentry (1968a) is followed for gazelles.

TABLE 1. LIVING SPECIES AND SUPERSPECIES OF AFRICAN BOVIDS
(excluding Caprinae) based on Ansell, 1968 (as amended) and Gentry, 1968a, and species studied in the field

| Subfamily | Tribe | Genus and Species | | Common Name |
|---|---|---|---|---|
| Cephalophinae | Cephalophini | Cephalophus | (monticola | Blue duiker |
| | | | maxwelli | Maxwell's duiker |
| | | | natalensis (inc. adersi) | Red duiker |
| | | | callipygus | Peter's duiker |
| | | | nigrifrons | Black-fronted duiker |
| | | | zebra | Zebra duiker |
| | | | niger | Black duiker |
| | | | dorsalis (inc. ogilby) | Bay duiker |
| | | | leucogaster | White-bellied duiker |
| | | | rufilatus | Red-flanked duiker |
| | | | jentinki | Jentink's duiker |
| | | | spadix | Abbot's duiker |
| | | | sylvicultor | Yellow-backed duiker |
| | | Sylvicapra | [1]grimmia | Bush or Grey duiker |
| Antilopinae | Neorragini | Neotragus | pygmaeus | Royal antelope |
| | | | batesi | Pygmy antelope |
| | | | moschatus | Suni |
| | | Madoqua | swaynei | Swayne's dikdik |
| | | | saltiana (inc. phillipsi) | Salt's or Phillip's dikdik |
| | | | guentheri | Günther's dikdik |
| | | | [1]kirkii | Kirk's dikdik |
| | | Oreotragus | oreotragus | Klipspringer |
| | | Raphicerus | campestris | Steinbuck |
| | | | sharpei (inc. melanotis) | Grysbuck |
| | | Ourebia | [2]ourebi | Oribi |
| | | Dorcotragus | megalotis | Beira antelope |
| | Antilopini | Gazella | leptoceros | Rhim or Loder's gazelle |
| | | | dorcas | Dorcas gazelle |
| | | | cuvieri | Edmi or Atlas gazelle |
| | | | spekei | Speke's gazelle |
| | | | rufifrons | Red-fronted gazelle |
| | | | [1]thomsoni | Thomson's gazelle |
| | | | soemmeringi | Soemmering's gazelle |
| | | | [1]granti | Grant's gazelle |
| | | | dama | Dama gazelle or Addra |
| | | Antidorcas | [2]marsupialis | Springbok |
| | | Litocranius | [1]walleri | Gerenuk |
| | Ammodorcadini | Ammodorcas | clarkei | Dibatag or Clark's gazelle |

| | | | | |
|---|---|---|---|---|
| Aepycerotinae | Aepycerotini | Aepyceros | [1]melampus | Impala |
| Peleinae | Peleini | Pelea | capreolus | Vaal Rhebuck |
| Reduncinae | Reduncini | Redunca | redunca | Bohor reedbuck |
| | | | [1]arundinum | Common reedbuck |
| | | | fulvorufula | Mountain reedbuck |
| | | Kobus | [1]ellipsiprymnus | Waterbuck |
| | | | [2] (vardoni | Puku |
| | | | [1] (kob | Kob |
| | | | [2] (leche | Lechwe |
| | | | (megaceros | Nile lechwe |
| Hippotraginae | Hippotraglnl | Hippotragus | equinus | Roan |
| | | | niger | Sable |
| | | Oryx | dammah | Scimitar oryx |
| | | | gazella | Oryx and gemsbok |
| | | Addax | nasomaculatus | Addax |
| Alcelaphinae | Alcelaphini | Alcelaphus | [2]lichtensteini | Lichtenstein's hartebeest |
| | | | [1]buselaphus | all other hartebeests |
| | | Damaliscus | hunteri | Hirola or Hunter's hartebeest |
| | | | [1]lunatus | Topi/tsessebe/tiang/korrigum |
| | | | [1]dorcas | Blesbok/bontebok |
| | | Connochaetes | [1]taurinus | Wildebeest or gnu |
| | | | [1]gnou | Black wildebeest or White-tailed gnu |
| Bovinae | Tragelaphini | Tragelaphus | [1]scriptus | Bushbuck |
| | | | [1]spekei | Sitatunga |
| | | | [2]angasi | Nyala |
| | | | buxtoni | Mountain nyala |
| | | | [1]imberbis | Lesser kudu |
| | | | [2]strepsiceros | Greater kudu |
| | | Boocercus | eurycerus | Bongo |
| | | Taurotragus | (oryx | Eland |
| | | | (derbianus | Derby or 'Giant' eland |
| | Bovini | [1]Syncerus caffer | | African buffalo |

bracketed species = superspecies

[1] field study of more than one year

[2] field study of less than one year

species of this comparatively homogenous group has been closely observed in captivity (see below). Observations of captives and information on group size and composition in the wild of other African antelopes not only supplement our knowledge but also appear to justify generalizing from well-known to less well-known but closely related species. Close similarities between members of the same genus and tribe have already been established by some of the major studies. In fact there are very few African bovids for which not even the grouping and distribution patterns are known. It is therefore the author's contention that the basic patterns of bovid social organization are already clear. While a great many important and interesting details remain to be uncovered, the time would seem to be ripe for attempting a synthesis and for advancing hypotheses about the major trends in the evolution of bovid societies. If little more than the bare bones can be presented at this stage, a skeleton can still provide a useful framework, to be fleshed out, modified and perhaps transformed as more information becomes available. The underlying aim is to stimulate interest in the comparative study of African bovids.

In this paper the concept is developed that the extraordinary speciation of African bovids represents primarily an outward radiation from forest, where ruminants originated (Romer 1959; Thenius, 1968; Colbert, 1969) into the grasslands and sub-deserts. Supporting evidence is the fact that forest antelopes remain the least changed from the ancestral type (Thenius, 1968; Eisenberg, 1966), while the most evolved inhabit the savanna and arid zones. Moreover, ancestral traits are apparent in the ontogeny of savanna species, notably in the natal coloration and instinct to hide displayed by most newborn antelopes. Of the many adaptations that led to the successful exploitation of the grasslands, attention will focus on how social behavior is adapted to ecological niche.

Assuming the earliest bovids were in fact forest dwellers, the first and possibly the biggest step toward their adaptive radiation was emergence from cover into the open. It called for a whole series of adaptive changes, many the exact opposite of adaptations to forest life. The differences between those that did and those that did not take this step amount to a basic dichotomy between living African bovids.

## DIFFERENCES BETWEEN FOREST AND PLAINS SPECIES

*Eotragus*, the earliest known bovid, was a small antelope with low-crowned (brachydont) cheek teeth, wide-set, short, straight horns in males only, and pronounced lachrymal fossae, in both sexes, which presumably contained sizeable preorbital glands (Pilgrim, 1939; Thenius, 1969). It was apparently a forest-dwelling browser. The most

TABLE 2. COMPARISON OF A SOLITARY FOREST SPECIES WITH A GREGARIOUS 'PLAINS' SPECIES

| | Forest Species | 'Plains' Species |
|---|---|---|
| Genus | *Cephalophus* | *Oryx* |
| Biome | Lowland and Montane Forest | Sundanese, Somali and South-West Arid |
| Size | small to medium (10-140 lbs) females slightly larger than males | large (300-450 lbs) males considerably larger than females |
| Horns | both sexes, short (2-10 in.), spikelike, often hidden by head crest | both sexes, long (up to 4 ft.), straight or curved (*O. dammah*), very conspicuous |
| Dentition | molars narrow, brachydont; incisor row proportionally narrow | molars broad, hypsodont, with accessory (bovine-like) basal pillars; incisor row wide |
| Conformation | hindquarters more powerful and elevated than forequarters, back rounded, legs comparati- | hind- and forequarters equally developed, back level, legs comparatively long; hoofs with |

TABLE 2 Contd.

| | Forest Species | 'Plains' Species |
|---|---|---|
| | vely short; hoofs with large interdigital cleft and wide splay (Pocock, 1910) | reduced inter-digital cleft and little splay (*ibid.*) |
| Gaits | walk; diagonal stride<br>trot: rarely observed<br>run: dodging, interspersed with flat leaps, head and neck low | parallel stride<br>long, ground-gaining<br>a fast, horselike gallop, head up or at shoulder level |
| Preorbital glands | present and well-developed in both sexes | vestigial or absent |
| Digestive organs | stomachs, particularly rumen and omasum, proportionally small (Hofmann, 1968) | stomachs large, especially the rumen, omasum and abomasum (*ibid.*) |
| Feeding habits | browsers, selective feeders on leaves, fruits, flowers, sometimes animal food (birds, fish, ants, etc.—Dekeyser, 1955; Aeschlimann, 1963) | mixed, 'rough' feeders, mainly grazers |
| Water metabolism | more or less water-dependent | water-independent |
| Color and markings | dark brown to reddish brown, a few tan to pale grey—cryptic; markings of slight to moderate contrast, generally non-revealing, if not disruptive | tan to grey-white—cryptic; black and white markings in moderate to great contrast, revealing |
| Color dimorphism | little or none, young tend to be darker | little or none between sexes, but markings barely indicated in newborn, which are browner |
| Social System | *asocial, monogamous, sedentary, territorial; distributed as pairs, with immature offspring, and solitary (unpaired) males; permanently attached to small home ranges which probably correspond with the territories | †gregarious, polygynous, migratory and nomadic, modified territorial; distributed as mixed herds and solitary males, in large to huge home ranges |
| Breeding | *year-round; females of small species may breed in first, males in second year | seasonal; females breed in second year or later, males probably in fourth year or later |
| Offspring | concealed | concealed |
| Reaction to danger | take cover and hide | flight in open |
| Main activity period | crepuscular or nocturnal (at least where heavily hunted) | diurnal, early morning and late-afternoon activity peaks |

* based mainly on observations of captive *C. monticola* and *maxwelli* (Rails, 1971, and this volume; Aeschlimann, 1963), and gleaned from various published reports about other species (e.g. Dorst and Dandelot, 1970; Maberly, 1962; Stevenson-Hamilton, 1947; Frädrich, 1964)

† based mainly on author's unpublished observations

similar—and perhaps the most primitive—recent bovid is the Indian Four-horned antelope (*Tetracerus quadricornis*), a member of the Boselaphini. Next to *Tetracerus,* forest duikers most nearly resemble *Eotragus;* in fact, both genera retain many skull characters 'which indicate they are survivals of a primitive form' (Pilgrim, 1939:21). Their way of life, and that of most other small to medium-sized antelopes of forest and bush, may be equally close to the ancestral pattern.

To illustrate the dichotomy between primitive antelopes of closed habitats and advanced forms which for convenience may be collectively termed plains species, some characteristics of forest duikers have been compared side by side with those of the oryx, a highly specialized hippotragine antelope (Table 2).

The duiker's build, short, slanted horns, and gaits are adapted to movement through and under dense vegetation, often on soft ground (hence the splayed hoofs). It is a typical *Schlüpfer* type as defined by Hediger (in Bigalke, 1968) and as suggested by the Afrikaans common name (duiker = diving). Its low-crowned molars, narrow incisor row and limited stomach capacity are suited to selective browsing on tender, nourishing vegetation. Rainfall in the forest biome is sufficiently high and reliable to permit occupancy of a small home range/territory while remaining water-dependent, and possible year-round breeding. The presence of undergrowth, intimate knowledge of the home range, nocturnal activity, small size, cryptic coloration and disruptive markings all favor the duikers' habit of hiding from danger. Territorial behavior, observed in both sexes of several species (detailed below) serves the usual function of reserving exclusive rights to an area of suitable habitat for which the demand normally exceeds the supply.

The oryx's build and gaits are adapted to travelling long distances across arid plains, often on hard surfaces (hence the compact hoofs). Healthy adults are too big and well-armed, too fleet and enduring to be taken readily by any predator except the lion. Although the newborn are concealed, oryx avoid heavy cover. The wide, high-crowned cheek teeth with accessory pillars, broad incisor row and capacious stomachs are adapted to harvesting, grinding and digesting quantities of coarse, silicaceous grasses and browse. Water-independence, coupled with migratory and nomadic habits, enable the oryx to exploit vast arid lands at seasons when they are out of range for less desert-adapted species. The formation of mixed herds (adult males together with females and young) is well-adapted to nomadism in a biome where overall population density is perforce very low. The territorial system has also been modified to meet these special conditions (see below). The distinctive long horns and conspicuous markings, which accentuate the head and body contours (Walther, 1966), probably function as species-specific recognition characters (discussed below)[1].

## AN ANALYSIS OF TRAITS

In an effort (1) to determine to what extent the above dichotomy holds for other antelopes of open and closed habitats, (2) to test for possible correlations between habitat, morphology, food habits and social organization, and (3) to elucidate evolutionary trends within the different- tribes, an analysis of the 70 African bovids was undertaken (Table 3). Because behavioral and ecological information about many species (especially Cephalophini, Neotragini, Antilopini and Tragelaphini) is still quite limited, the analysis is necessarily coarse-grained. Also, when comparing morphological characters and social organization, subjective judgements and compromises are unavoidable, particularly when considering polytypic species with pronounced geographical differences (e.g. bushbuck, hartebeest, topi/tsessebe and

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[1] Blaine's (1922) idea that the oryx's markings are concealing through a disruptive effect is belied by the fact that the markings remain faint in calves during the concealment stage.

lechwe; as a rule, the best endowed race was chosen to represent the species—see p. 324). The results (Tables 3 and 4, and Fig. 1) nevertheless tend to bear out the dichotomy and to show some interesting correlations.

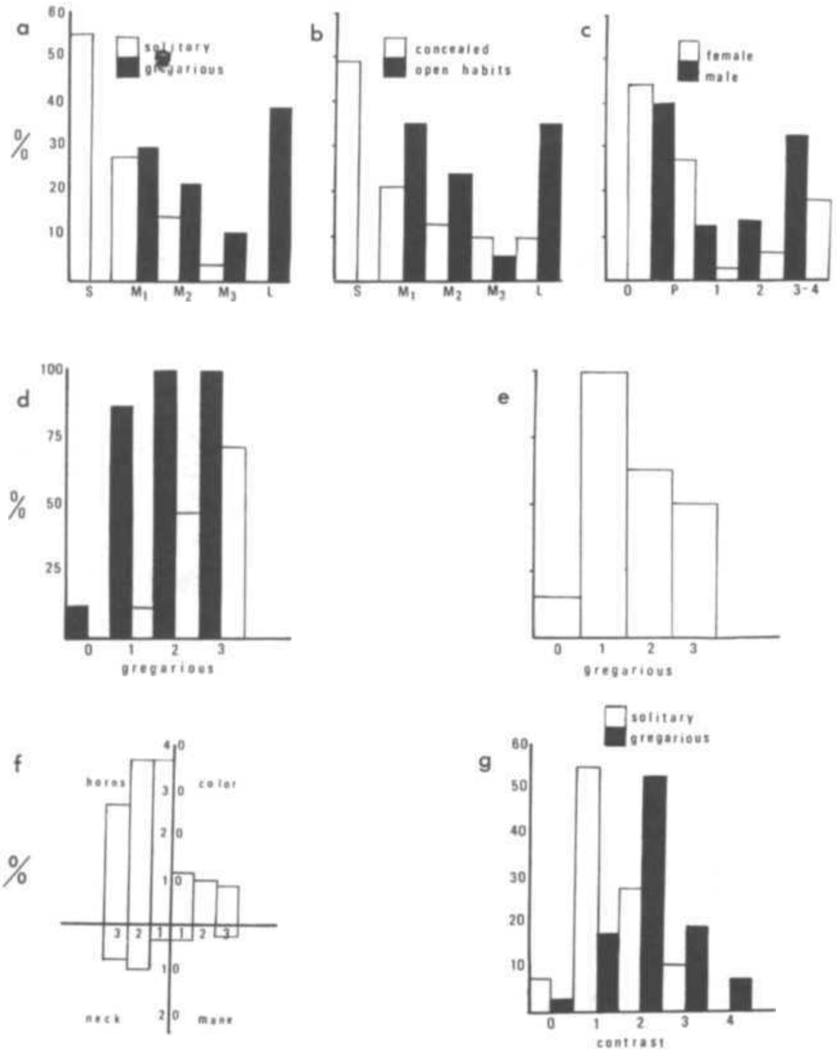

Fig. 1. *Morphological traits:* Symbols as in Tab. 3. a) size of solitary and gregarious species, b) size distribution of species from closed and open habitats. c) comparative horn development. d) %with developed horns (2-4) by class e) pronounced sexual dimorphism by class. f) type and degree (1 = slight, 3 = pronounced) of sexual dimorphism among clearly dimorphic species (n = 50). g) markings contrast with coloration (0 = minimal — 4 = maximal)

TABLE 3. TRIBAL ANALYSIS

*Size:* S = small: < 35 lbs (16 kg); $M_1$ = 35-100 lbs (16-45 kg); $M_2$ = 100-180 lbs (45-82 kg); $M_3$ = 180-300 lbs (82-136 kg); Large => 300 lbs (136 kg).

*Horns:* o = absent; P = short spikes (e.g. duikers); 1 = slightly advanced (dibatag-Thomson's gazelle); 2 = moderately advanced (roan-bushbuck); 3 = advanced (Grant's gazelle-eland); 4 = most advanced (sable-kudu)

*Gregarious scale:* 0 = solitary; 1 = rudimentary, 2 = intermediate, 3 = advanced, 4 = most advanced organization.

| | | Cephalophini | Neotragini | Antilopini | Ammodorcadini | Aepycerotini | Peleini | Reduncini | Hippotragini | Alcelaphini | Tragelaphini | Bovini | Totals | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total | General | 2 | 6 | 3 | 1 | 1 | 1 | 2 | 3 | 3 | 3 | 1 | 26 26 | 100 |
| | species | 14 | 12 | 11 | 1 | 1 | 1 | 8 | 5 | 7 | 9 | 1 | 70 | 100 |
| Size: | Small | 7 | 9 | | | | | | | | | | 16 | 23 |
| | Medium 1 | 4 | 3 | 7 | 1 | | 1 | 2 | | | 1 | | 19 | 27 |
| | " 2 | 3 | | 4 | | 1 | | 5 | | 1 | | | 14 | 20 |
| | " 3 | | | | | | | | 1 | 1 | 3 | | 5 | 7 |
| | Large | | | | | | | 1 | 4 | 5 | 5 | 1 | 16 | 23 |
| Color: | Dark | 5 | 1 | | | | | (3)* | (1)* | 4 | (4)* | 1 | 11 | 16 |
| | Medium | 7 | 11 | 3 | 1 | 1 | 1 | 8 | 3 | 3 | 8 | | 46 | 66 |
| | Light | 2 | | 8 | | | | | 2 | | 1 | | 13 | 18 |
| | Concealing | 14 | 12 | 10 | 1 | 1 | 1 | 8 | 5 | 3 | 9 | | 64 | 91 |
| | Revealing | | | 1 | | | | (3)* | | 4 | | 1 | 6 | 9 |
| Markings | 0 | 2 | | | | | | | | | | 1 | 3 | 4 |
| Contrast | 1 | 5 | 9 | 1 | | | 1 | 4 | | 2 | 1 | | 23 | 33 |
| Rating: | 2 | 5 | 3 | 5 | 1 | 1 | | 4 | 2 | 3 | 6 | | 30 | 43 |
| | 3 | 2 | | 5 | | | | (3)* | 3 | 2 | 2 | | 14 | 20 |
| | Disruptive | 1 | | | | | | | | | 7 | | 8 | 11 |
| Species | Advertising | 1 | | 7 | 1 | 1 | | (3) | 5 | 3 | | | 21 | 30 |
| Horn | ♂ ♀ | | | | | | | | | | | | | |
| Development: | Primitive | 14 13 | 12 | 0 6 | | | | 1 | | | | | 28 19 | 40 48 |
| | Advanced 1 | | | 6 2 | 1 | | | 2 | | | | | 9 2 | 13 5 |
| | " 2 | | | 4 2 | | | | 1 | 2 1 | 2 2 | 1 | | 10 5 | 14 13 |
| | " 3 | | | 1 | | 1 | | 4 | 1 3 | 4 4 | 7 3 | | 18 10 | 26 26 |
| | " 4 | | | | | | | | 2 1 | 1 1 | 1 | 1 1 | 5 3 | 7 8 |
| Dimorphism: | | | | | | | | | | | | | | |
| Sexual | Nil-slight | 14 | 12 | 2 | | | | | 4 | 7 | 1 | 1 | 41 | 59 |
| | Pronounced | | | 9 | 1 | 1 | 1 | 8 | 1 | | 8 | | 29 | 41 |
| Newborn | Nil-slight | 14? | 12 | 4? | 1 | 1 | 1 | 8 | | 3 | 7? | | 51? | 73 |
| | Pronounced | | | 7? | | | | | 5 | 4 | 2 | 1 | 19 | 27 |
| Food: | | | | | | | | | | | | | | |
| Mainly | Browse | 14 | 11 | 9 | 1 | | | | | | 9 | | 44 | |
| Mainly | Grass | | 1 | 2 | | 1 | 1 | 8 | 5 | 7 | | 1 | 26 | 37 |
| Water-dependent | | 13? | 3? | 2? | | 1± | 1 | 8 | 2 | 3± | 5? | 1 | 39 | 56 |
| | Independent | 1 | 9 | 9 | 1 | | | | 3 | 4± | 4 | | 31 | 44 |
| Habitat: | Closed | 14 | 10 | 1± | | 1± | | 2 | 1± | | 7 | 1± | 37 | 53 |
| | Open | | 2 | 10 | 1 | | 1 | 6 | 4 | 7 | 2 | | 33 | 47 |
| Habits: | Concealing | 14 | 11? | 1 | | | | 2 | | | 7 | 1± | 36 | 51 |
| | Non-concealing | | 1 | 10 | 1 | 1 | 1 | 6 | 5 | 7 | 2 | | 34 | 49 |
| | Solitary | 14 | 11 | | | | | 2 | | | 2 | | 29 | 42 |
| | Gregarious 1 | | 1 | 1 | 1 | | 1 | 1 | | | 5 | | 10 | 14 |
| | " 2 | | | 6 | | 1 | | 2 | 2 | 2 | | | 13 | 19 |
| | " 3 | | | 4 | | | | 1 | 1 | 2 | | | 8 | 11 |
| | " 4 | | | | | | | 2 | 2 | 3 | 2 | 1 | 10 | 14 |

* adult males

TABLE 4. TESTS OF CORRELATION BETWEEN SOCIAL SYSTEM AND SELECTED TRAITS

| | Solitary | Gregarious | $X^2$ Value |
|---|---|---|---|
| *Habitat* | | | |
| closed | 27 | 10 | |
| open | 2 | 31 | 29.5** |
| *Diet* | | | |
| Primarily browse | 35[a] | 9 | |
| " grass | 5[a] | 21 | 21.7** |
| *Adult response to danger* | | | |
| Lie out and/or run for cover | 28 | 12 | |
| Avoid cover and run in open | 1 | 29 | 28.7** |
| *Body size* | | | |
| Small to medium (10-1001b) | 24 | 12 | |
| Medium to large (> 100-1600 lb) | 5 | 29 | 16.5** |
| *Male horns* | | | |
| Primitive[b] | 27 | 10 | |
| Advanced | 2 | 31 | 29.5** |
| *Sexual dimorphism* | | | |
| Minimal | 25 | 16 | |
| Pronounced | 4 | 25 | 13.7** |

[a] including the 10 species at a rudimentary level of social organization listed in Table 5.

[b] from short spikes to simple sigmoid curve of medium length as in Thomson's gazelle

**P<.010

Twenty-nine species (41 percent) are solitary (asocial), i.e. adults are typically distributed singly or in pairs (discussion p. 179). All but the klipspringer and possibly the beira, which find security in craggy hills, live in concealment: 16 in lowland or montane forest, one on the edge of the forest-savanna mosaic (red-flanked duiker), 7 in mesic woodland to arid bush, one in swamps (Sitatunga) and 3 in high grassland. Of the 41 gregarious species, only 12 frequent forest, closed woodland or thicket, and no more than 3 (lesser kudu, bongo and nyala) are closely restricted to closed habitats. Five of the 12 are ecotone or 'edge' species (impala, Waterbuck, sable, roan and Lichtenstein's hartebeest). Three are found in a remarkably broad range of habitats—the two elands and the buffalo—and one, the gerenuk, is limited to arid thornbush habitat (see p. 184). However, over a dozen social bovids more or less habitually run for cover when alarmed (including those just named, except elands, also mountain reedbuck, mountain nyala, greater kudu, lechwe, sable, roan and perhaps others), although few if any adopt the recumbent concealment posture seen in solitary species and in most newborn antelopes. Yet in exceptional circumstances even adult plains antelopes may lie flat and thus escape detection (e.g. Thomson's gazelle, and oryx—Walther, 1969; Stewart, 1963). The species most prone to concealment are those at an elementary level of social development (Table 5).

Tests of interaction of habitat preference, response to danger, diet, body size, horn development of the male and sexual dimorphism—with solitary and gregarious habits—

TABLE 5. LEVELS OF SOCIAL ORGANIZATION
A provisional grouping of species at approximately the same level. Arrangements within cells are meant to be in ascending order, but the rankings of *Cephalophus*, **Neotragini**, *Gazella* and social *Tragelaphus* spp. are tentative, while intertribal matchings should be interpreted as only approximate. Question marks indicate cases of particular uncertainty.

| | | | | |
|---|---|---|---|---|
| 4 MOST ADVANCED (Large, dense aggregations or highly integrated, mixed herds) | | | | K. leche<br>K. megaceros |
| 3 ADVANCED (Migratory—except kob; high densities—except addax and/ or large aggregations) | | | G, thomsoni<br>Antidorcas?<br>G. dama<br>G. granti | K. kob |
| 2 INTERMEDIATE (Medium-sized herds; clumped distribution, low density; sedentary—except gazelles) | | | G. soemmeringi<br>G. rufifrons ?<br>G. leptoceros ?<br>G. cuvieri ?<br>G. spekei ?<br>Gazella dorcas | K. vardoni<br>Kobus ellipsiprymmus |
| 1 RUDIMENTARY (Small, loose herds; low density; sedentary) | | | 1 Litocranius | R. fulvorufula |
| GREGARIOUS | | 1 Dorcotragus ? | | |
| ASOCIAL<br>TEMPORARY GROUPS<br>SOLITARY | 1 Sylvicapra<br>3 Big duikers<br>1 C. nigrifrons ?<br>5 Bay duiker type<br>2 Red duiker type<br>2 Blue duikers<br>Cephalophus | 1 Ourebia<br>1 Oreotragus<br>2 Raphicerus<br>4 Madoqua<br>3 Neotragus | | 2 Redunca |
| | Cephalophini | Neotragini | Antilopini | Reduncini |

all yielded significant Chi-square values (Table 4). Figure 1 shows the relative development of morphological characters at different levels of social organization (corresponding to the levels in Table 5).

*Diet:* By my reckoning there are 35 solitary to 9 gregarious browsers and mixed feeders (more browse than grass), and 20 gregarious to 6 solitary grazers and mixed feeders (more grass than browse). The relationship between feeding behavior and social organization has been discussed by Jarman (*in lit.*). In simplest terms, browsing calls for selective feeding on widely dispersed plants: thus browsers tend to have a more dispersed social organization than grazers, among which non-selective ('coarse') grazers can feed side by side in large numbers on suitable pastures.

*Body Size:* Fig. 1a shows that many gregarious antelopes (n = 41) are large ( > 300 lbs (136 kg) = 39 percent), that there are no small ( < 35 lbs 16 kg) gregarious nor large, strictly solitary bovids, while only one solitary antelope (the Sitatunga) weighs more than 180 lbs (82 kg). A size comparison between species of concealed and open habits (Fig. 1b), while presenting much the same pattern, reflects the fact that several large bovids live in cover (three of the Tragelaphini and the buffalo).

Eisenberg (1966) has argued that small size, solitary habits ( = dispersed social system) and concealment behavior are interrelated elements in an anti-predator strategy. An increase in size leads to greater conspicuousness and reduces the advantage of a dispersed system. Perhaps the dense vegetation frequented by bushbuck, Sitatunga and reedbuck is by way of compensation for their comparatively large size.

*Horns:* As shown in Fig. 1d, males of moderately to highly gregarious species all have advanced (large and/or complex) horns. The percentage of females with well-developed horns also increases with gregariousness. But 31 species are hornless (44 percent), half of the other 39 have short spikes like duikers and small gazelles (subgenus *Gazella),* and only 14 (20 percent) have highly evolved horns; all but three of these

| | | | | |
|---|---|---|---|---|
| O. gazella<br>Oryx dammah | C. gnou<br>Connochaetes taurinus<br>D. dorcas | T. oryx<br>Taurotragus derbianus ? | Syncerus | |
| Addax | D. lunatus<br>A, buselaphus | | | |
| H. niger<br>H. equinus | Damaliscus hunteri<br>Alcelaphus lichtensteini | | | Aepyceros |
| | | T. strepsiceros<br>T. imberbis<br>T. buxtoni ?<br>1Boocercus?<br>T. angasi | | Pelea ?<br>Ammodorcas |
| | | T. spekei<br>Tragelaphus scriptus | | |
| Hippotragini | Alcelaphini | Tragelaphini | Bovini | Monotypic Tribes |

belong to the Alcelaphini and Hippotragini, in which the horns of both sexes are similar (Fig. 1c). The male's horns are invariably bigger, except in oryx and eland, where the female's horns, albeit thinner, are often longer.

*Sexual Dimorphism:* In both duikers and neotragines, the two tribes of small antelopes, the female is usually slightly larger than the male (Ansell, 1968; Shortridge, 1934; Malbrant and Maclatchy, 1949). In all the other tribes, the male is larger than the female. As this includes such solitary species as the bushbuck, Sitatunga and reedbucks, there is no apparent correlation of size dimorphism with solitary habits, nor with habitat. But members of the Cephalophini and Neotragini seem to be the only ones (except reedbuck) which live in heterosexual pairs.

Figure le shows that sexual dimorphism is most prevalent among slightly gregarious antelopes. Among advanced antelopes sexual dimorphism is minimal in alcelaphine and hippotragine species, which account for 8 of the 18 most-gregarious bovids (Table 5). Of the 50 species with perceptible sexual dimorphism, differential development of the horns is much the commonest source (Fig. 1f), followed by color: 15 (30 percent) are dimorphic in this respect, 8 moderately to strongly, through adult males becoming darker than females and young (notably *Tragelaphus* and *Kobus* spp., and the sable). A thick neck is a conspicuous male attribute in at least 9 species (Grant's gazelle, gerenuk, kob, reedbucks, sable, elands and buffalo), while beard and/or manes are more developed in the males of a few antelopes (greater kudu, eland, nyala and lechwe). Thicker necks and longer hair usually only supplement the other kinds of dimorphism, but in eland and buffalo powerful necks (including the eland's dewlap), in conjunction with tremendous bulk, are probably more important than horn development in distinguishing adult bulls (discussion p. 195).

*Contrasting Markings:* Contrast was judged purely in relation to general coloration, regardless of possible disruptive or advertising functions. Sexual dimorphism and subspecific differences complicate the evaluation process, as already noted. It was decided that the maximum contrast should be taken as the measure of a species' potential in this direction, even though most conspecifics might be less distinctly patterned. On this basis most of the intermediate to highly gregarious species are seen (Fig. 1g) to have markings in moderate to strong contrast (2-4 on the scale) with their overall coloration, while solitary species generally have relatively uncontrasting markings. Thus, many forest duikers have extensive black markings on back, muzzle and legs, but the prevailing chestnut to dark-brown coloration makes dark markings inconspicuous. Exceptions are the zebra and yellow-backed duikers. Neotragines and reedbucks, along with most savanna species of open habitats, have extensive white markings, which again are of minimal contrast against a tan or medium-brown background (tail 'flags' and rump patches of many species excluded); indeed countershading, from darker dorsal to white ventral outline, is a well-known principle of camouflage (Cott, 1940). However, white markings are conspicuous in dark animals, as exemplified in the above-mentioned sexually dimorphic antelopes. There are very few savanna species in which both sexes are dark: several alcelaphines (wildebeest, blesbok and topi) and the buffalo. The majority—at least of females and juveniles-range from tan or grey to medium brown, shades presumably not far removed from those of the ancestral savanna dwellers, as seen in virtually all neonates. Nevertheless, some species have achieved strong contrast by means of dark markings bordering areas of white, most notably the facial markings of Hippotragini and Antilopini, the side stripes of oryx and gazelles (also the beira, reportedly the most nearly sociable of the Neotragini), and white rump patches set off by vertical black lines (pygal stripes) in a few gazelles (Estes, 1967a). Dark patches on the upper limbs are found in several tribes, of greater or lesser contrast depending on the coloration of adjacent areas: extensive blotches in Alcelaphini, oryx, and the Kafue lechwe, (*K. l. kafuensis*), garters in Tragelaphini, and lines down the fronts of the legs in Reduncini. As Moynihan(1960) noted in social birds, highly gregarious species can 'afford' to be more conspicuous than less gregarious forms because of the greater security afforded by numbers. In this respect, solid dark coloration as in the black wildebeest and savanna buffalo (the less-social forest race, S. *c. nannus* is red-brown), and reverse countershading (from darker below to lighter above), as in the topi and blue wildebeest, are at least as conspicuous as the bold markings of oryx and gazelles. Darkness, reverse countershading, shininess and conspicuous markings are all combined in the blesbok/bontebok, perhaps the gaudiest of all antelopes (the glossy black and white bull sable may be equally conspicuous in the open, but is surprisingly hard to see in woodland, where lone bulls spend most of their time—the typical setting should be considered when evaluating concealing or revealing markings and coloration).

But beyond merely being conspicuous, species-typical coloration/marking patterns, horn shapes and/or body configuration usually add up to a unique appearance, suggesting that selection for species-specific recognition has had much to do with the evolution of these structures. In Moynihan's (*op. cit.*) words, 'It will be generally advantageous for *any* species to be as conspicuous as possible, insofar as conspicuousness will make it easier for individuals to locate and recognize one another.' This would explain the striking appearance of many antelopes that do not hide from predators, and the fact that the most gregarious species tend to be the most conspicuous.

The absence of pronounced sexual dimorphism in the most advanced bovids may also be viewed in this light. In the case of highly conspicuous antelopes, the emphasis seems clearly to be on distinguishing the species rather than the sexes. Grouping without regard to sex is particularly desirable for migratory and nomadic species; surely it is no coincidence that a majority of bovids which do regularly move in mixed groups display minimal sexual dimorphism, while a good number are highly conspicuous as well: *Damaliscus* and *Connochaetes, Oryx* and *Addax*, the springbok and Dama gazelle. All these, and the eland, which though neutrally colored and not very conspicuously marked, present an unmistakable silhouette, are migratory and/or nomadic. The buffalo is not exactly migratory but lives in mixed herds. The most notable exception is the lechwe, which forms mixed aggregations and is highly dimorphic. De-emphasis of sexual dimorphism could account for the otherwise puzzling penile tuft borne by female as well as male wildebeest (*C. t. mearnsi*), and the inconspicuousness of the sheath in oryx bachelor males (whereas it is bicolored and pendant in related sable and roan), which makes it difficult to determine sex in either species from the ventral outline (Estes, in prep.). Conceivably selection for de-emphasis could also explain the fact that females of the southern race of the sable (*H. n. niger*) become almost as dark as males, when elsewhere they are chestnut. This subspecies forms the largest herds, inhabits comparatively open country and shows a tendency to be migratory.

### The Difficulties of Comparing Stages of Social Development

The foregoing analysis bears out the existence of a dichotomy between bovids of closed and open habitats, solitary and gregarious habits, and provides evidence that progressive increase in body and horn size, conspicuousness, etc. goes together with increasingly elaborate social behavior. Accordingly anatomical and morphological traits offer a rough index as to how far a species has advanced from the primitive condition. If sufficiently detailed behavioral information were also available, it might be possible to arrange the African bovids in a series from least to most advanced. But this would be difficult and probably meaningless biologically, because (1) the various traits of a species are rarely evolved to the same degree: e.g. a socially advanced species like the eland retains a rather primitive (concealing) coloration, while a socially backward relative, the greater kudu, has perhaps the most elaborate horns; and (2) a well-marked trend from primitive to advanced types is evident in most tribes, with the result that a number of species are at comparable stages of development (see Table 3). Therefore a linear arrangement would be less biologically meaningful than an intertribal grouping of species at roughly equivalent levels of social organization. Even such a simple arrangement as the one presented in Table 5 must be regarded as provisional until much more behavioral information becomes available.

## THE SOCIAL ORGANIZATION OF SOLITARY SPECIES

Although the dichotomy between forest and plains bovids exists, there is no corresponding dichotomy of social systems, such that one may speak of *a* solitary and *a* gregarious type of social organization. Even asocial species appear to have at least two basically different organizational plans, and others may emerge with further study of the as-yet-poorly known solitary antelopes.

1 a. *The pair territory*—A recent field study of Kirk's dikdik (Hendrichs and Hendrichs, 1971), and extended observations of captive blue duikers (Aeschlimann, 1963; Rails, 1971 and this volume) point to a similar type of organization: a male and female live together and maintain a small territory (as little as 2. 5 ha, 6 acres, in dikdik). Except for its permanency, this type of arrangement resembles the pair territories so common in passerine birds. Observations of grey duiker (Wilson and Clarke, 1962; Wilson, in prep.), steinbok (Chalmers, 1963), oribi (Hediger, 1951; Roosevelt and Heller, 1914; Tinley *in lit.)*, and klipspringer (Wilson and Child, 1965; Wilson, 1969) indicate that this is the typical pattern in the two tribes of small, cover-dependent antelopes. However, some interesting differences are discernible, particularly in the territorial role of the female.

The territory is maintained and advertised by ceaseless olfactory marking, in which both partners participate, although the male plays the leading role. Duikers seem to rely primarily on their uniquely constructed preorbital glands, which are well-developed in both sexes. Neotragines also deposit a pitchy secretion on twigs and grass stems all over the territory, but only the male—the female's preorbital glands are apparently less developed. Dung middens, which both sexes—at least in dikdik, oribi, steinbok and klipspringer, and even the young (dikdik)—help to maintain in a regular dunging ceremony, tend to be at least as important for territorial demarcation in this group (Hendrichs and Hendrichs, 1971; Tinley, 1969 and in lit.; Walther, 1968a; Hediger, 1951). Mutual licking and nibbling about the head, usually initiated by the male (also as a courtship preliminary), probably functions to maintain the pair bond; duikers also press their preorbital glands together (for details of blue duiker marking and grooming behavior, see Rails' account in Paper 4). When confined with other conspecifics, paired blue duiker, Phillips' dikdik and steinbok continue to show a preference for each other, even though the extra females may be courted (Aeschlimann, 1963; Rails, 1971; Simonetta, 1966; Chalmers, 1963).

It seems that male blue and grey duikers tolerate other females, at least in captivity, but that their mates behave aggressively when other adult females are introduced

(Wilson and Clarke, 1962; Rails, pers. comm.). In Rails' experiment with trios consisting of a male and two females, the females in each case were mother and daughter, which lived peaceably although with minimal interaction as adults. Conversely, dikdik females were found to take no active part in territorial defense; the male drove out males and strange females alike (Hendrichs and Hendrichs, 1971). Male offspring are driven out as soon as they reach adolescence (at seven to nine months), probably in all small antelopes. Female offspring also leave during this period, but why is unclear. It would be most interesting to know whether one parent or the other is responsible or whether perchance it leaves on its own. The presence of horns in female forest duikers may have some bearing on their apparently more aggressive treatment of conspecific females. Female Neotragini are hornless (except for the East African klipspringer *O. o. schillingsi*—Roosevelt and Heller, 1914). Considering that females of early forest bovids were hornless (Pilgrim, 1939), conceivably the duikers represent specializations for territorial defense.

The tolerance of extra females shown in captivity (and even of other males in the case of four male and three female suni that lived amicably in the same pen—Izard *et al.* 1971), suggests a certain potential to form herds even in the least social species. More indicative is the tendency to form occasional temporary groups in the wild shown by some neotragines, particularly klipspringer (up to eight on a common feeding ground—Stevenson-Hamilton, 1947) and oribi (parties of up to a dozen on short grassland—Roosevelt and Heller, 1914). The rare and unstudied beira is reported to live in small troops as well as in pairs on rocky hilltops of the Somali Arid Zone (Walther, 1968a; Dorst and Dandelot, 1970). On this basis it was tentatively placed in the category of antelopes with a rudimentary social system (Table 5). But it may well be like the oribi, which maintains typical pair territories on the periphery of floodplain grassland during the rainy season, hides from danger and runs off with a pig-like rush when flushed (Tinley, *in lit.;* Roosevelt and Heller, 1914). But in the dry season the flush of new grass following the annual fires attracts them into the open, where they may band together and behave very much like gazelles, sometimes actually fleeing in the open when alarmed, instead of hiding (Roosevelt and Heller, 1914). They even have a gazelle-like stotting display. Under the same conditions, most other solitary species immediately run for cover (including steinbok, grey duiker, dikdik, bushbuck, Sitatunga and reedbuck). While such groupings resemble herds, they break up at the slightest disturbance, as the individuals scatter in all directions (*ibid.;* Verheyen, 1951; Stevenson-Hamilton, 1947). This response is the hallmark of the most elementary stage of socialization, whereas group cohesion distinguishes an advanced level of organization.

1 b. Bohor and Common reedbuck, the two solitary Reduncini, do not demarcate their territories with dung middens and have lost their preorbital glands. Nevertheless, Jungius (1971) describes a conspicuous defecation posture, adopted by both members of a pair (with tail curled up to reveal the white undersurface) which he interprets as a territorial advertising display. But aggressiveness between females on adjacent territories was never observed. Nor was mutual grooming of the kind seen between male and female Cephalophini and Neotragini observed, and it may be doubted whether an equally close pair bond exists between reedbucks. Beginning a month before and for up to four months after parturition, the female seeks isolation on the outskirts of the territory. Her previous offspring may meanwhile associate with the male. According to Jungius (1970), female offspring usually leave the territory at around 1. 5 years, being then mature, whereas males may remain a year longer, despite the father's mounting belligerence. Such tolerance is uncommon even in gregarious species (but see discussion of sable on p. 185).

During the dry season, common reedbuck often come together on choice pastures in temporary herds of up to a dozen head, typically including two or more females with their offspring of six months and older, perhaps accompanied by one adult male. Jungius (1971:71) considers the loss of cover (through annual fires) to be primarily responsible for this grouping tendency which 'can be linked with desire to obtain better defence against predators.' Conversely, the presence of cover inhibits group formation, mainly because of the difficulty of keeping in visual contact (see also Einsenberg. 1966). Even more interesting is Jungius' observation that, having joined a group, related individuals cease to associate with one another in preference to members of other families (see p. 197).

In Sudan' Dinder National Park, where Bohor reedbuck are unusually numerous, W.N. Holsworth (pers. comm.) observed what appeared to be the largest reedbuck herds ever recorded: in an 88-km (55-mile) circuit along the east and west sides of the Dinder River at the end of the 1967 dry season, he counted about 1700 reedbuck, including five aggregations of over 100 head, three of which contained between 200 and 300 animals. The largest number seen together, on another trip, was estimated at ± 400: These aggregations were socially integrated to the extent that they fled as a group before the observer's vehicle. Nevertheless, large herds were the exception; of 199 groups counted, 118 numbered five or less, with 59 containing one to two animals. In general, the groupings of *R. redunca* are comparable to those of *R. arundinum,* reflecting their typically low population density. But it is enlightening to see that a species with a dispersed distribution pattern and concealing habits during the better part of the year has the potential to form large social gatherings in open habitat.

2. *Solitary, non-territorial*—The bushbuck is perhaps the most truly solitary African antelope, since even pairs are relatively seldom encountered (Bourliere and Verschuren, 1960; Wilson and Child, 1964). Thus, Elder and Elder (1970) found a male and female associated in only 12 out of 167 sightings, and saw only 10 groups of over two head, compared to 120 singles (50 females and 55 males, 15 unsexed). The only stable pairs seen by Verheyen (1955) were females with young of the year. The fact that bushbuck are also extremely sedentary, each frequenting a small covert which it leaves (always by the same paths) only to feed in nearby glades shared by other bushbuck, led Verheyen to suppose that females as well as males defend individual territories. But studies in Nairobi and Chobe national parks indicate that it does not demarcate nor defend a specific area against conspecifics (Allsop, 1971, as reported by Leuthold, in Paper 9 of this volume; D. Simpson, in prep.). Evidence from recent studies of other *Tragelaphus* spp. (discussed below) tends to support this finding. However, the bushbuck apparently frequents an extremely small core area: an average of 0. 56 ha for adult males and 0. 25 ha for females in Nairobi Park, compared to 2.0 ha for sub-adult males (Allsop, *op. cit.*). Considering the known pugnaciousness of the males (Stevenson-Hamilton, 1947) and the lack of clearcut evidence that male core areas are undefended, it may be premature to conclude that the bushbuck is non-territorial.

The closely related Sitatunga (which freely hybridizes with bushbuck in captivity-Pitman in Maberly, 1962; A. von Nagy, pers. comm.) is less solitary and might be considered close to the rudimentary stage of organization of other *Tragelaphus* spp. (Table 5). It is regarded here as a transitional species roughly equivalent to the reedbuck, since one to two animals accounted for over 80 per cent of all those observed by Owen (1970) (cf. lesser kudu, p. 206 this volume). On the other hand, of the nearly 46 percent of all sightings that were of single animals, only 18 percent were adult males, while 49 percent were females; most males were found associated with at least one other Sitatunga—generally an adult female. A tendency for adult females to join together was also noted: 27 percent were found in company with one or more others. 'Family groups' of up to 9 head, including an adult male, a maximum of 4 adult females, juveniles, subadults and occasionally younger calves, were not uncommon. There were no sightings of two adult males in the same group, indicating mutual intolerance and/or exclusive home ranges—or territories (see p. 338): of 11 individually known males that were seen more than once, none was more than 500 m from previously recorded positions.

As a further indication of incipient herd formation by the Sitatunga, Walther (1964a) records that eight females and immatures kept together in an enclosure established a stable rank hierarchy, the oldest female being number one. Until his removal, an adult male had held the alpha position (cf. sable, p. 343).

### The transition from solitary to social habits

A tendency to group formation has been noted in all tribes of solitary antelopes, least in duikers (admittedly on the basis of very sketchy information), in which females seemingly play an active part in territorial defense, and greatest in the reedbucks, females of which show almost no sign of territoriality. It would seem to be only a short step from the seasonal groupings of reedbuck or oribi to the more-or-less-permanent small herds of the mountain reedbuck and other antelopes at the most rudimentary level of gregarious organization. Such herds appear to represent fairly loose associations between females (with or without offspring) that share the same home range (see Waterbuck and sable accounts). Simply by prolonging the association between mothers and their female offspring, a permanent herd could be created. Yet the evidence is against the continuance of such associations in any but the most socially advanced bovids; as discussed later, the maternal bond appears notably short-lived and weak in the great majority. More likely, the individual is attached to the herd and often initially to a peer group.

Thus, the transition from temporary to permanent herds may be less straightforward than appears at first glance. There are also other obstacles to overcome and conditions to meet in the evolution of the true herd:

(1) The pair territory, if it was characteristic of the ancestral forest antelopes, is one complication. The female would have to be divested of territorial drive and pair bond alike before becoming sociable. Of course, it is possible that the pair territory is a later specialization peculiar to the Cephalophini and Neotragini. On the other hand, the existence of well-developed preorbital glands in the early bovids, apparently in both sexes (Pilgrim, 1939), is indirect evidence of marking—probably in a territorial context—by females, and hence of pair territories. These glands have since atrophied in both sexes of all or nearly all Reduncini, Tragelaphini, Bovini, and a few other species (Pocock, 1910), and may be non-functional in females of other social antelopes except for *Connochaetes* and *Damaliscus;* at any rate I know of no evidence of their employment for demarcation—nor of any other indication of territorial behavior—by females of any gregarious antelope.

(2) A change in habitat and food preferences, hence probably in morphology, would presumably accompany or precede a change in social organization; i.e. change of behavior must be correlated with change of niche, otherwise there would be no stimulus to alter already adapted behavior patterns. Antelopes that practise concealment would continue to hide as long as they remained in habitats that afforded adequate cover. On the other hand, a change of niche is possible without drastically altering social behavior, as demonstrated by the successful exploitation of arid environments by the bush duiker, steinbok, dikdik, klipspringer, etc. By keeping to cover and becoming water-independent, such species are able to live in much the same way as related forest antelopes.

(3) Only two of the three social classes distinguished below as common to the systems of gregarious bovids are formed by 'transitional' solitary species. Bachelor herds containing more than one adult male or numbers of immature animals have not been reported.

It may be said, accordingly, that a line between solitary and rudimentarily gregarious species, though not sharp, seems nevertheless to exist.

### The Psychological Basis of Herding

While important questions about the steps leading to the establishment of permanent herds remain unanswered, the selective pressure to form herds seems clear enough: it enabled antelopes to emerge from hiding and live in the grasslands.

The fact that virtually all bovids which live away from cover are social, while virtually all solitary species depend on concealment, suggests that gregariousness is an essential adaptation for life in the open. Eisenberg (1966) and others have observed that adaptation to open habitats favors group formation, but one might go further and postulate that group formation was a prerequisite to abandoning concealment.

It may be argued that antelopes band together in the open for a purely psychological reason: the herd takes the place of cover for the individual. The same hypothesis has been advanced by Williams (1964) to account for schooling in fishes (and subsequently extended to mammals by Hamilton, 1971): each fish is motivated to join others of its kind to become less conspicuous and to place others between itself and external sources of danger. The fact that 'transitional' antelopes only group together when they venture into the open, and typically onto neutral ground—i.e. outside of any occupied territory—seems particularly significant. Similarly, Hamilton showed experimentally that fishes which normally live dispersed in cover could be induced to school when the cover was removed. Human beings may be motivated to associate by the same desire for security.

Anyone who has ever acted knows that to emerge from the wings onto the stage is far easier in a chorus than all alone. To be alone and unsheltered at night in a wilderness inhabited by predators drives home the need for companions.

The obvious distress of a highly social animal when separated from its herd may be viewed from this perspective. The urge to be with the herd can be stronger than the maternal drive: females of the most gregarious species have often been known to abandon their young rather than be left behind by the group (e.g. a buffalo whose newborn calf bogged down at a crossing—Ludbrook, 1963). Even in the less social species where females sometimes occur singly, lone animals appear far less relaxed than those in herds. Thus an undisturbed sable cow feeding by itself looked up 17 times in 10 minutes, whereas a female in a herd observed an hour later looked up only 4 times in the same interval (Estes, 1972). Furthermore, animals in large groups are less easily disturbed than those in small groups—this is particularly easy to observe in the wildebeest of Ngorongoro Crater (Estes, in prep.). These are indications of how important the herd is to the well-being of gregarious bovids.

At the same time, the drive to associate is opposed by a degree of intolerance or fear of bodily contact (possibly a legacy from asocial ancestors), which causes herd members to maintain a fairly regular spacing (Hafez and Schein, 1962). This individual or social distance (Hediger, 1961), which usually exceeds the distance an animal can reach with horns or teeth, is species-typical, and is one measure of gregariousness, since reduced social distance—particularly bodily contact—indicates greater individual tolerance and group cohesion. In most social bovids there is little non-aggressive contact other than between mother and young and during courtship. Relatively few engage in social grooming (licking and/or nibbling), notably buffalo (and other bovines), impala, some gazelles and—at least in captivity—*Tragelaphus* spp. (Walther, 1964a). Alcelaphini and Hippotragini rub their heads (especially the preorbital region) and horns on one another, but this may be a display of dominance and/or symbolic marking, or otherwise, comparable to rubbing against inanimate objects (see p. 185).

## THE SOCIAL ORGANIZATION OF GREGARIOUS SPECIES

### Common Features

For all their diversity, the great majority of gregarious antelopes share a basically similar, territorial type of organization. Tragelaphine antelopes appear to be the exceptions that prove the rule—seven out of 41 social species. Two of them, the elands, are the only antelopes known to have a bovine type of organization, in which adult males associate in a dominance hierarchy and often live in mixed herds with females and young. Tragelaphini and Bovini both belong to the Bovinae subfamily, and may represent a separate phylogenetic line that branched from the bovid stock earlier than the other lines. Accordingly they will be treated separately (p. 194), following a review of territorial organization.

In all gregarious bovids, three different social classes are discernible: nursery (or female) herds of females and young, bachelor herds of juvenile to mature males, and a small class (usually less than 20 percent of the population) of single adult males. Perhaps the most important difference between territorial and non-territorial systems is in the behavior and biological role of these single males: in territorial species all breeding males belong to this class, membership in which entails individual and exclusive rights to a piece of property. In many instances, such animals are solitary only so long as there are no females in the territory. None of this holds true for non-territorial systems.

## TERRITORIAL SOCIETIES

In a territorial organization, all areas utilized by females are parcelled out among property-holding males. Nursery herds are contained, and to some extent restrained, within this territory-mosaic. The aggressiveness of the landlords toward non-territorial males of adolescent age and older keeps them largely segregated from the rest of the population. As a rule, one and only one adult male is found in a nursery herd, being the owner of the territory in which the herd happens to be. Among sedentary species, each herd frequents a traditional home range, which may encompass a few to many territories. Since it virtually never happens that a herd spends all its time in one territory (except possibly at very low population densities, e.g. tsessebe in Kruger National Park–Joubert, *in lit.*), the term harem, which implies exclusive ownership by one male, is misleading (Estes, 1967a). Among African ungulates, true harems may only occur in the two non-territorial equids, the Plains and Mountain zebras *Equus burchelli* and *E. zebra* (Klingel, 1967, 1968, and this volume)

This basic organizational plan is subject to wide variation, both interspecifically and intraspecifically. The climate, season, terrain, type of habitat, food preferences and population density are all interrelated factors that bear on herd size and spacing, degree of mobility, territory size and permanence. However, the degree of intraspecific variability is species-specific, reflecting the broadness or narrowness of the ecological niche, and the potential to achieve high population densities.

Several examples chosen from well-studied species will serve to illustrate the range of variation within the three social classes, and what makes one species socially more advanced than another. Examples proceed from relatively simple to more complex organization (see Table 5).

## The Nursery Herd

### *Gerenuk* (Antilopini)

The gerenuk is the only territorial antelope of rudimentary social organization (as here defined) that has been studied systematically in the field (Leuthold, 1970a, 1971). Water-independent and exclusively a browser, this apparently primitive, yet highly specialized member of the Antilopini is sparsely distributed in *Acacia-Commiphora* thornbush habitats of the eastern Somali Arid Zone. The average group (including single animals) seen by Leuthold (1971) in Tsavo National Park consisted of two animals and the largest numbered 10 head. Associations between females were casual and nearly half of the adults seen were on their own, with or without offspring. An adult male was found associated with females in only 23. 9 percent of the groups. The only stable social unit appears to be between a mother and her immature offspring (*op.cit.*). Known individuals remained within sizeable home ranges measuring from 3-6 $km^2$ (1.9-3.8 $mi^2$).

### *Waterbuck* (Reduncini)

Although the Waterbuck is here considered to be at an intermediate level of organization, it remains a loosely grouped, sedentary species still somewhat dependent on cover. Widely but locally distributed in the savanna biome, this large antelope (males up to 600 lbs) prefers the ecotone between woodland and grassland in areas affording permanent water. Nursery herds average from 3-6 females and young in Queen Elizabeth Park, Uganda (Spinage, 1969a) to 8 in Chobe National Park, Botswana (Child and von Richter, 1969). Temporary gatherings of up to 46 head have been recorded in the eastern Congo (Verheyen, 1955). Herds are so unstable that it is unusual to record the same composition from morning until evening (Hanks *et al.*, 1969). Waterbuck tend to spend their days in the open on some favored pasture but to shelter in dense woodland by night (*ibid.*; Kiley-Worthington, 1965) or when alarmed. Hanks *et al.* (1969) could find no evidence of continuing association between any two cows, suggesting that female offspring do not stay with their mothers after reaching maturity. Spinage detected a tendency of certain females to associate part-time, but without regard to age. In his view, what draws Waterbuck together is a common attachment to the same area, within which they tend to move more as individuals than as herds. Nevertheless, group activities like grazing and ruminating appear to be as synchronized as in other antelopes (Spinage, 1969a; Hanks *et al.*, 1969).

In Uganda's Queen Elizabeth Park, where environmental conditions are comparatively stable and Waterbuck breed throughout the year, home ranges remain rather constant, averaging ca. 3.4 $km^2$ (2.1 $mi^2$), and herd size does not vary seasonally (Spinage, 1969a). In Kafue National Park, Zambia, where Waterbuck are seasonal breeders, home range and herd size vary according to the time of year and fire history. In the dry season most of the females and young from a given locality congregate in the open on burns (Hanks *et al.*, 1969). In the wet season, when calving occurs, nursery herds are always small, localized, and largely restricted to woodland.

In keeping with such a loose social structure, interaction between herd members, either in the form of mutual grooming or aggression, is apparently minimal (Spinage, 1969a). The effective expression of aggression is limited by the absence of horns; however, females sometimes threaten to bite ('champing'—Spinage, 1969a), may butt and charge, and such behavior seems to be responsible for separating a percentage of weaned female calves from the herd, which may subsequently form 'spinster' groups.

*Sable* **(Hippotragini)**

Nursery herds of sable tend to be larger and more stable from day to day but subject to greater seasonal and geographic variation, and they have larger home ranges. Mean herd size (based on sampling of all four subspecies) is around 18, including one adult male, six adult females, four calves, three yearlings and four subadults (Estes and Estes, in prep.). In a two-year study (*op. cit.*), the smallest recorded home range was about 4. 8 km$^2$ (3 mi$^2$) over a 5-month period (Shimba Hills Reserve, Kenya), and the largest range over the course of a year was over 40 km$^2$ (Luando Reserve, Angola). This species has a pronounced tendency to disperse in *Brachystegia* woodland during the wet season and to concentrate during the dry season around permanent water points on the edge of edaphic grasslands, especially on postburn flushes. In the driest part of its range (southern Mozambique, Rhodesia and northern Botswana), the seasonal movements of *H. n. niger* may extend to 40 km (25 mi) (K. Tinley, J. Anderson, pers. comms.), and could be characterized as small-scale migrations.

In fact, the distinction between migratory and sedentary species is not sharp, since almost any gregarious grazer will move at least a few miles to reach better pasture, while the tendency to wet-season dispersal and dry-season concentration is widespread.

The sable's dry-season range tends to be relatively small: e.g. an exceptionally large and stable herd of 125 *H. n. niger* stayed within an area of about 1. 3 km$^2$ (½ mi$^2$) in Victoria Falls National Park, Rhodesia, from June at least until August (Estes and Estes, unpubl. report). The largest herd of sable yet reported, numbering about 300 head, was also from Rhodesia (Mushandike National Park—unpubl, report). Child and Wilson (1964) claim that a herd of *H. n. kirkii* made an annual circuit covering an area of some 320 km$^2$ (200 mi$^2$) in an eastern Zambia Tsetse Control Hunting Area, and Joubert (pers. comm) confirms that sable in Kruger National Park move equal distances. Disturbance due to hunting could have been a factor in the first case, while the low stocking rate in northern Kruger Park, near the southern limit for the species, may be a factor. There is some suggestion, especially in the assertion that the same adult male accompanied the Zambian herd on its peregrinations, that the normal territorial network and traditional home ranges had broken down. A similar breakdown could account for the decidedly large range (25-40 km$^2$) of the even scarcer Kruger Park roan and the atypical behavior of the accompanying 'herd bull', as described by Joubert (in Paper 35 of this volume). Schaller (pers. comm.) thinks this distribution pattern may also be applicable to the few roan herds in the Serengeti National Park. Here perhaps is another illustration of how different the same species distribution, movement and behavior patterns can be at low and high densities.

In the Shimba Hills, a sizeable but otherwise representative nursery herd of 48 that was observed daily for two months proved to have a definite rank hierarchy based on age; the oldest cows were rank-dominant and usually led, while yearling and two-year males were subordinate to all adult females. Superiority was manifested by rubbing the horns or head on another animal's neck or rump, by ducking the head, by hooking, giving a lateral intimidation display, and by charging, each representing a higher level of aggression. Reproductive status had no apparent bearing on rank.

When an adult male was present (about half the time) he dominated all the rest (as usual in bovids), but invariably brought up the rear instead of leading. The herd's range included approximately four territories. The lowest-ranking females often remained at a slight distance from the herd and their activity cycles appeared to be less synchronized than the cycles of other herd members; they might start feeding while the others were resting, and vice versa. They also tended to be more alert—or nervous. Accordingly they were often the first to spot a possible source of danger. This fact suggests that it may be the less cohesive members of a herd, these being often the lowest-ranking members, who commonly play the role of so-called sentinels. It sometimes happened that one of these semi-detached animals acted as leader simply by moving away on its own in a purposeful manner; the same thing has been reported in domestic cattle (Hafez and Schein, 1962). Rank and file members tended to follow blindly and to pay less attention to their surroundings than either regular or occasional leaders.

Sable have annual rutting-calving seasons from Zambia southward, and fairly well-defined bi-annual seasons in Kenya. Age-groupings are very pronounced for calves through three-year olds, and grouping by sex is evident from two years onward. Herds are thus highly structured. Nevertheless, a herd not infrequently splits into two or more groups that go different ways for a matter of days or months before reuniting. The question then arises as to whether it is actually a single herd that splits up sometimes or different herds that occasionally join forces. Using the criterion of attachment to a common home range that Spinage (1969a) applies to the Waterbuck, it would appear that all belong to the same herd, particularly since the main group rarely splits the same way twice in a row. Evidence that the individuals are well-enough acquainted to have stablished a stable rank hierarchy suggests long familiarity. In the Shimba Hills, five distinct home ranges were mapped, between which there was little or no overlap, and no appreciable mixing of the resident herds. There was evidence that the same home ranges had been occupied for many years.

It begins to appear that this kind of arrangement, in which a number of mutually acquainted females in varying combinations (but least often singly) share the same traditional home range, may be widespread, particularly among sedentary antelopes with a highly clumped distribution and typically variable herd composition. Thus Hanks *et al.* (1969) speak of four Waterbuck population units along a 12-mile stretch of river, each consisting of 4-5 territorial males, a bachelor herd and 20-odd females with their offspring. He found 'remarkably little movement from one unit to another in spite of the fact that there are no physical barriers.' The impala of Nairobi National Park are also divided up into more or less distinct units (Leuthold, 1970b), while the roan closely resembles the sable (though usually more sedentary in smaller herds—Child and Wilson, 1964). No doubt there is interchange between units, perhaps chiefly through the wandering of subadults, as Spinage (1969a) and Leuthold (1970b) record in Waterbuck and impala respectively. The principle enunciated by Wynne-Edwards (1962:141) that 'any given stock tends to persist generation after generation in the same locality', seems entirely applicable to sedentary antelopes.

### *Gazelles* **(Antilopini)**

Grant's and Thomson's gazelles display interesting differences in social organization and behavior between congeneric, sympatric species which reflect differences in ecological niche (Walther, 1964b, 1965; Estes, 1967a). Thomson's gazelle, a highly migratory grazer dependent on water in time of drought, is specialized to exploit the short-grass plains of the Somali Arid Zone and adjacent tree savanna, where it tends to be the most numerous ungulate. It concentrates in thousands on green pastures. The Grant is a water-independent and semi-desert-adapted browser that is less committed to migratory habits and is far less numerous, although migratory populations may form sizeable concentrations (e.g. on the Eastern Serengeti Plain).

In Ngorongoro Crater, Tanzania, where *G. granti* is exceptionally plentiful (approximately 1500 Grant's to 3500 Thomson's gazelles in 1964-65), *granti* nursery herds are spaced out at intervals of roughly half a mile in *Themeda/Andropogon* hill grassland and are largely sedentary, each herd frequenting its own home range (Estes, 1967a). Nevertheless, herds often split and apparently there is interchange between those on neighboring ranges. Since territories are as large as a square mile, a herd may spend much of its time with the same male. The average of 100 herds was 16.4 head.

Thomson's gazelle nursery herds are much more variable in numbers and distribution, both of which largely depend on seasonal changes in the grassland habitat; they concentrate during the long rains in a relatively small area of short alkaline grassland, and disperse widely over the Crater floor when the *Cynodon* grassland is generally low during the dry season. The average of 100 herds was 22. 9 head, but there was a continual interchange of herd members in the middle of concentrations, where the spacing between groups was as little as 100-200 yards, corresponding to the spacing between territorial males—which indeed appeared to be mainly responsible for fragmenting concentrations. The existence of any rank order in the absence of distinct groups would appear very unlikely. The greater stability of the Grant herds would favor a hierarchial arrangement (but its existence awaits confirmation). Both species herd more closely than sable, but less closely than wildebeest or impala. The two gazelles breed through the year, with rainy-season peaks. Females with concealed fawns often form 'mother groups removed from the main herds' (Walther, 1965).

### *Wildebeest* **(Alcelaphini)**

The wildebeest, one of the most advanced antelopes, has a notably flexible social organization (Estes, 1966, 1969a and b). Where permanent water and good pasture occur, it exhibits a typical sedentary pattern, including a permanent territorial network, bachelor herds and small nursery herds averaging about 10 head in Ngorongoro Crater. These herds often combine to form temporary aggregations on burns and reclaimed marshland during the dry season. Between the acacia savanna and the arid zone, wildebeest form migratory populations which spend the rainy season on the short-grass plains and the dry season in the savanna, within reach of water. The main Serengeti population, numbering up to 400,000 head (Watson, 1969), spends virtually the whole year moving about in search of fresh green pasture (Talbot and Talbot, 1963). Concentrations of over 10,000 head within a few square miles are commonplace, and over 190,000 were once counted in an area of 40 $km^2$ (25 $mi^2$) (Talbot and Stewart, 1964). Wildebeest of all classes join these 'armies', although the main concentrations of males, and females with young generally remain segregated. When migrating (and even on the way to water) wildebeest usually trek in single file, a formation typical of perhaps most social antelopes when moving from one place to another, which, to cite just one advantage, reduces the individual's risk of blundering into a predator in ambush (Schaller, 1972). At night aggregations rest in linear bedding formations up to a dozen animals across, spaced sufficiently to permit individuals to move freely in and out (Estes, 1966, 1969b). This arrangement retains the advantage of close grouping and at the same time allows the herd to stampede instantly in the same direction, if necessary, without any animals being trapped in the rear (as would happen to those in the center of a circular formation). The same arrangement may be seen in resting assemblies of other bovids (e.g. buffalo, eland, oryx).

Except for a few months of the dry season, when territorial behavior may all but cease in migratory populations, adult bulls establish a territorial network whenever an aggregation settles down and proceed to break it up into what Watson (1969) terms 'pseudo-herds', as there is no evidence (yet) of any continuing association between adults. At the same time, non-territorial males from yearlings onward are cut out and shunted to the side-lines of the network. When the concentration moves on, the bulls abandon their territories rather than remain alone, though sometimes one or more will linger if water is available (Estes, 1969a). Watson (*ibid.*) also refers to these territories as 'pseudo', but here the term is inappropriate, since they only differ from other wildebeest territories in being temporary.

In the sedentary phase, wildebeest nursery herds tend to be rather stable in composition for at least five months after the calving season, reflecting semi-closed associations between adult females; outside females that attempt to join are usually harassed and/or excluded. There is a definite rank hierarchy, which is maintained in much the same manner as in sable. Month after month, known Ngorongoro herds were observed to keep to core areas often of less than 20 ha (50 acres), encompassing fewer than a dozen territories, which they seldom left except to go to water (and sometimes to join passing concentrations overnight). The spacing between herds in prime habitat was as little as 100-200 yards. Although social distance is minimal, with some animals touching, when a herd is resting (typically in *Sternformation*—Walther, 1958) wildebeest do not pack together nearly as closely as buffalo or cattle.

Herd composition begins to vary more during the dry season, when females and young aggregate on the best remaining pastures. At first the herds tend to separate at the end of the day and return each to its core area, but later they merge and apparently lose their identity in bigger groupings. With the onset of the next rainy season, however, apparently many of the same individuals get together again in the area they frequented previously, although usually in different combinations. There is also some evidence of continuing association between cows and their female offspring; for instance, one female marked as a yearling kept company with an easily recognized older cow for at least the following two years. However, this was not a typical case, in that the old animal was apparently barren, and therefore less likely to rebuff her previous offspring than the mother of a new calf.

The wildebeest's variable social system enables it to alter its distribution pattern to fit a wide range of environmental conditions. Populations can follow any pattern from completely sedentary to migratory and more or less continually nomadic. The arrangement can be varied seasonally and from year to year in response to regular or irregular changes in rainfall distribution. Sedentary and migratory patterns often coexist within the same population, and even at the same time and place, as in Ngorongoro Crater, a remarkably rich ecosystem with a carrying capacity of at least 14, 000 wildebeest (along with 10, 000 head of zebra and gazelles), but space sufficient for only a quarter that many in the form of small, independent herds (Estes, 1966, 1969b).

The black wildebeest, topi (particularly Guinea Savanna-Sudanese Arid Zone populations), and blesbok—all related species—have much the same system. In fact, probably most migratory and even highly nomadic antelopes can become sedentary, at least part-time, under favorable conditions—just as most water-independent species will drink if given the choice (see e.g. species accounts in Dorst and Dandelot, 1970). However, it seems that most antelopes are more committed than the Alcelaphini to either a sedentary or nomadic existence: depending on whether they inhabit a wetter or a drier climate, either they need move little or tend to keep moving most of the time.

### *Oryx* **(Hippotragini)**

Although a major study has yet to be undertaken of the oryx, it may serve as an example of a desert-adapted antelope with a social organization specialized for nomadism. The most unusual feature of its organization is that adult males and females regularly associate in mixed herds, a practise which has caused some doubts as to whether oryx are territorial. However, there is a certain percentage of solitary males which are apparently attached to definite small ranges. In Etosha National Park, South West Africa, where the oryx population is unusually numerous and sedentary in the dry season, adult bulls were spaced out (in August) in what appeared to be a typical territorial network, and a similar, though wider-spaced, network was seen in the Subdesert of Iona National Park, Angola (in October). Moreover, on several occasions when solitary bulls have been seen to join mixed herds, they proceeded to dominate all the other males by means of threat displays (unpubl. observations). Finally, it seems to be the rule that the scrotums (and also the sheaths) of most apparently adult males in the herds are decidedly smaller than those of solitary bulls. The evidence suggests that most of the bulls in herds are not in reproductive condition, that they are, in fact, simply bachelor males which in this species remain integrated with the nursery herds.

## The Bachelor Herd

Bachelor herds are composed of juvenile to adult males, numbering from two head into the hundreds (and even thousands). Male groups presumably result from the same social attraction that brings females together, although the male's attachment appears weaker, since individual spacing in male herds is usually greater than in female herds (Estes, 1969a). Probably this reflects naturally greater male aggressiveness induced by androgenic hormones (Etkin, 1964b). Nevertheless, bachelor herds offer males the same mutual security that nursery herds offer females and young; their main significance in antelope society is that they provide a haven for males from the time they are expelled from nursery herds until they mature and become territorial. In advanced species at high density, bachelor herds also provide sanctuary for adults, which may include unfit and old as well as fit but supernumerary individuals and spent territorial males. But male-herd organization too differs greatly from species to species, and also intraspecifically, in terms of size, age composition, structure and particularly in the degree of interaction between members. Again, a few examples will serve to illustrate the range of variation.

### *Gerenuk*

In the gerenuk observed by Leuthold (1971), over one-third of all subadult males were seen alone. But often from two to four were found associated, sometimes alone, sometimes with a female group, whereas associations between adult males were never seen.

### *Sable*

In the sable, with its naturally low population density, notably clumped distribution and large territories (usually more than one square mile), separate bachelor herds are uncommon and rarely number over 10 head (Estes and Estes, in prep.). By adopting the typical female *Demutshaltung* in the presence of territorial bulls, males are tolerated in the nursery herds until they are over three years old. Even when not actively chased out, however, they show a progressive tendency to break away from the herd, especially when there is more than one juvenile in the same age class. The typical sable bachelor herd probably consists of subadults from the same nursery herd, which remain within the traditional home range at least part of the time and periodically try to rejoin the main herd. In the absence of contemporaries, rejected subadults live alone, often frequenting closely wooded areas, where they are less likely to be seen than sable in groups. Since bulls mature in their fifth year, and are already subadult by the time they leave the nursery herds, the period of association in all-male groups is relatively brief, and bachelor herds are thus relatively unimportant in this species.

A rank hierarchy based on age is established between males, and may persist even after maturation, with younger territorial males satellite to a few master bulls that dominate over wide areas. Sparring is seen, but with decreasing frequency and vigor in older age classes. The full sable fighting repertoire is practised from infancy through the third year, but is largely limited to frontal pushing by the age of four, as the horns approach their maximum curvature and length, making the other hippotragine technique (parallel stance with over-the-shoulder-hooking) dangerous (Estes, 1972).

### *Waterbuck*

Waterbuck males mature as slowly as sable, but leave the nursery herds beginning at 8-9 months (Spinage, 1969a). Bachelor herds (averaging five head in Queen Elizabeth Park) are accordingly more important for this species, more in evidence, and contain more age classes, which tend to associate in sub-groups in the kob genus (de Vos and Dowsett, 1966). Male herds appear to be more stable than nursery herds. Within the framework of a rank hierarchy, associations may continue until maturity, strangers attempting to join are sometimes harassed, and a herd may keep to the same home range through succeeding generations (e.g. in Queen Elizabeth Park a herd of 7-10 frequented an area of ca. 100 ha (250 acres) within the territory of one or more adult bulls—Spinage, *ibid.*).

### *Gazelle*

Bachelor herds of Grant's gazelle in Ngorongoro Crater average about 10 head and contain yearling-class to young adults (Estes, 1967a). Male groups are tolerated within territories and even permitted to mingle with nursery herds. Bachelors are notably active and aggressive in this species, often engaging in display and sparring 'tournaments', whereby they probably learn to judge their strength relative to their peers. A strict age hierarchy is in evidence (Walther, 1965). In adult life, a display of neck development largely substitutes for combat (Estes, 1967a).

### *Impala* **(Aepycerotini)**

Male impala herds stay as close to nursery herds as territorial males will allow—which is closer than in most other antelopes. In southern Africa, all social classes intermingle during the dry season following the annual rut (Stevenson-Hamilton, 1947).

In East Africa, where breeding continues year-round, such breakdowns of social structure occur only during exceptional droughts (Jarman, 1970). Bachelors are decidedly less belligerent toward one another than Grant males, and even engage in mutual grooming (social licking being an impala trait) (Schenkel, 1966). Many juveniles join bachelor herds before they are half a year old, remain until mature at about 28 months (Kerr, 1965) and rejoin as adults after abandoning or losing their territories (Jarman, 1970).

### *Kob* **(Reduncini)**

In the Uganda kob (*Kobus kob neumanni*), a large bachelor herd is associated with each territorial ground or lek, and consists partly of exhausted territorial males that are recuperating before attempting to regain places in the arena (Leuthold, 1966).

### *Wildebeest*

Compared to many other antelopes, interactions between bachelor wildebeest are infrequent and sedate. Conversely, interactions between territorial bulls are exceptionally frequent, spirited and elaborate (Estes, 1969a). Because of the short annual calving peak, age classes are very distinct. No evidence of rank order was noted within age groups. Wildebeest join bachelor herds as yearlings and remain until they mature fully in their fourth year, or about as early as kob (Buechner, Morrison and Leuthold, 1966) and a year earlier than lechwe (Robinette and Child, 1964), both smaller animals. Ngorongoro bachelor herds, often numbering in the hundreds, are found in the same areas year after year, typically in taller grassland that is substandard wildebeest habitat and consequently occupied by few territorial males. Male herds can be distinguished from nursery groups at a distance by their wider, more regular individual spacing. Although males marked as yearlings were often resighted in the same quarter, the accumulated evidence from resightings indicated considerable movement about the Crater and unstable groupings. This reflects the fact that bachelor herds are tolerated in and are usually attached to every sizeable aggregation of females and young—an evident adaptation to migratory habits. Even in small sedentary populations, bachelors—and also territorial males—thereby gain access to green pastures when aggregations form in the dry season. Thus in the wildebeest too, bachelor herds may contain not only non-breeding juvenile to adult bulls (including old ones past their prime), but also 'off-duty' and sojourning territorial males. In fact herds composed entirely of 'off-duty' bulls form daily during the dry season on neutral ground, usually near waterholes. Regardless of age or status, the common denominator of wildebeest in bachelor herds is sociability and non-belligerence.

## The Territorial Male

In animals with a territorial system, mating opportunities are limited almost exclusively to propertied males. Aggressive and sexual behavior, both dependent on testicular-hormone production (Marler and Hamilton, 1966), are identified with and largely restricted (in adults) to the individual's territory, the one place where he is dominant over all conspecifics (Estes, 1969a; *in lit.*). Thus competition for territory comes ahead of and largely substitutes for direct competition over mates. Territorial competition is proportional to population density, stability of the territorial network and favorableness of location within it. Strong competition exerts pressure in favor of year-round territoriality—even with a restricted breeding season—because it is far easier to hold onto than to win a place in an established network. At the same time, average tenure is likely to be reduced as active rivalry increases. A case in point is the wildebeest, which has a short rutting season throughout its range (see below), yet many bulls in sedentary populations remain on territory and ready to mate the whole year (Estes, 1969a). Predictably, the greatest turnover occurs during the rut. However, as already noted, the territorial drive tends to wane during an extended dry season, and may cease altogether in migratory populations, as well as in sedentary populations of species which become seasonal breeders at higher latitudes (Ansell, 1960; Skinner, 1970). Nevertheless, going by the incidence of solitary males, apparently the great majority of antelopes are territorial throughout the year.

The psychophysiological factors that govern the territorial drive at the same time suppress sociabilty and make it possible for adult males to live alone in the absence of nursery herds. (The maternal drive has a comparable, though temporary, effect on females with concealed calves.) Yet the moment a male leaves the vicinity of his property, the gregarious drive reasserts itself and he reverts to the status of bachelor male. Nothing could better demonstrate the psychological component of territoriality. On the other hand, continuing isolation from conspecifics apparently creates a growing appetite for social contact in the most gregarious species, that leads territorial males to attach themselves, sometimes for days at a time, to nearby individuals or herds of practically any available ungulate (Estes, 1969a). Completely isolated wildebeest eventually abandon their grounds (*ibid.*).

The onset of the territorial drive is linked to maturation of the testes, which in turn closely corresponds with attainment of adult weight and size (Talbot and Talbot, 1963; Kerr, 1965;Brooks, 191; Robinette and Child, 1964; Hvidberg-Hansen, 1970). Sexual maturity, meaning simply puberty (a less ambiguous term), or the age of spermatogenesis, is reached during the second year, if not before, probably by most antelopes. Full maturity comes early for small antelopes (e.g. to yearling blue duiker—Aeschlimann, 1963) and takes up to five years or more for large species (e.g. waterbuck, sable, roan, kudu), while medium-sized species take two (Thomson's gazelle, impala) to three years (kob, Grant's gazelle). Except in small antelopes, females almost invariably begin reproducing at least a year earlier than males, and even species as big as wildebeest may calve by their second birthday, although this probably happens a year later in most large species (e.g. sable apparently do not calve before they are three).

Territorial spacing, while obviously subject to great intraspecific variation, is nevertheless species-specific as regards average and minimal intervals. For instance, the average spacing between Ngorongoro wildebeest in prime habitat (120-145 m) is less than between associated Thomson's gazelle (250-350 m) and much less than between Grant's gazelle (500-1000 m) (Walther, 1964b, 1965; Estes, 1969a, 1967a) or than the related black wildebeest (von Richter, 1971) and hartebeest (Gosling, 1969). Sable bulls are rarely spaced less than one mile apart, whereas Waterbuck often occur at much closer intervals (see Spinage in Paper 33).

The frequency and intensity of interactions between territorial neighbors, tolerance toward bachelor males, and the vigor with which females are herded all seem to be related to territory size. As a rule, the smaller the area and the closer the spacing, the harder the owner works to keep potential rivals outside and nursery herds inside his grounds. In at least some species with large territories, males may only actively herd females and young when they approach the border, and bachelor males are tolerated; herds of sable may actually be unattended by any adult male, sometimes over a period of weeks (Estes and Estes, in prep.).

But just why species A defends a larger area than species B is far from obvious. Clearly body size is not a major factor, nor openness of the habitat, at least not as between the wildebeest and the other plains species mentioned (for a discussion see Estes, 1969a:297). In Leuthold's (1970b:716) words, 'It is clear that the expression of territoriality is affected to a large extent by the size, density and dispersion of an animal population', these in turn being largely governed by the quality of the habitat. But then territorial spacing itself may be a factor in dispersion (see below). It is difficult to distinguish between cause and effect. It would be fair to say, however, that the smallest territorial spacing is found in those species that form large, dense aggregations, notably *Connochaetes, Damaliscus* and *Kobus* (kob and lechwe). It is evidently density that is the determining factor here, since spacing within aggregations is much reduced compared to adjacent areas with only small herds. Thus, when a wildebeest concentration moves into an area occupied by resident territorial males, 'migratory' bulls with the concentration succeed in establishing themselves between the residents for as long as the concentration stays put (and no longer), thereby more than halving the spacing. In the Uganda kob, which has perhaps the most specialized territorial system of any bovid, breeding arenas, where the average diameter of a territory is about 33 meters, are best developed at the heart of large, concentrated populations, and are inevitably surrounded by conventional territories of increasing diameters (average 100-200 m) going away from the arenas (Buechner, 1963;Leuthold, 1966). Where they occur, the arenas tend to persist over long periods—one was known to have been in use for over 30 years. However, there is evidence that the system breaks down temporarily if adverse climatic conditions cause nursery herds to move to distant pastures (Leuthold, 1966). The arena system is thus seen to be adapted to a relatively constant tropical-savanna climate capable of sustaining large, sedentary populations and year-round breeding.

Yet population density alone does not explain such close territorial spacing; there also seems to be a minimum distance that males of a given species will tolerate. For instance, it is doubtful whether Waterbuck males would accept such near neighbors as kob or lechwe do, under any conditions, or that the tremendous populations of black wildebeest that once roamed the South African Highveld ever had such close territorial spacing as one sees in concentrations of blue wildebeest (*C. taurinus*).

### The Territorial Male's Role in Population Dynamics

Of the three social classes discussed above, only that of the territorial male is common to both solitary and gregarious systems. In fact territoriality seems to represent a direct holdover from the primitive condition, having originated in solitary ancestors as a means of securing exclusive rights over a fixed home range. It must be rare in gregarious antelopes that the territory includes a male's entire home range (the gerenuk may be one example—Leuthold, 1971), whereas it may only rarely not include all, or nearly all, of a solitary antelope's normal range. That so many antelopes have retained their territorial heritage is not only a remarkable demonstration of conservatism of a behavioral trait, but also a measure of its adaptability to all sorts of conditions. To a very large extent, antelope social systems have been built around the territorial male, whose role is by no means limited to inseminating females, as sometimes portrayed. Indeed the other two classes owe their separate identities very largely to territorial behavior. The broader implications of territoriality for population dynamics should not be overlooked.

1. *The expendability of males*—In theory a polygynous system requires only a few males for reproduction, so that 'a high survival rate for the males is of small consequence to the survival of the species' (Etkin, 1964b:112). In practise, the number of males in a territorial system that have a chance to reproduce depends on the number of territories that can be established within habitat utilized by females. This number is automatically adjustable to absolute numbers and population density, within the species-specific limit of territory compression. The greater the competition over a limited number of places—the greater the excess of males to the available space—the more certain it becomes that the fittest males will be selected. In large populations of Uganda kob and wildebeest, probably no more than half the adult males take part in reproduction at any given time (Leuthold, 1966; Estes, 1969a). Adults in bachelor herds could accordingly be considered expendable. However, removal of apparently surplus adult and young males—say by game cropping—would not only reduce territorial competition but also eliminate replacements for vacancies in the territorial network. This is particularly clear in Uganda kob bachelor herds, where 'the adult males form a reservoir for continuous exchange with territorial males' (Leuthold, 1966:219).

2. *The unequal adult sex ratio*–To the extent that non-reproducing males are segregated from nursery herds, they are kept from competing and interfering with females and young. Being forced into often inferior habitat on the outskirts of the territorial network may subject bachelors to greater nutritional stress and predation pressure. This could partially explain why, in most populations of gregarious antelopes sampled up to now, adult females outnumbered adult males, usually by a ratio of from 3:2 to 2:1 or more, despite natal sex ratios that are probably generally close to unity (Leuthold, 1970b; Dasmann and Mossman, 1962; Bourliere and Verschuren, 1960; Allen, 1963; Foster, 1966; Estes, 1969a). However, pressure from territorial males must not be the only factor, since a similar inequality has been found to exist in at least some non-territorial ruminants, including, among African bovids, the greater kudu (Simpson, 1968; Wilson, 1965—but cf. Leuthold's nearly equal sex ratio for lesser kudu in Paper 9). Factors such as the sex-linked tendencies of males to be bolder, more careless and independent and to have a higher metabolism, must also be taken into account (Taber and Dasmann, 1954). Whichever is more important in the greater male mortality rate among territorial antelopes, it seems clear that bachelor males *are* treated as the most expendable members of the population and that the surplus is culled through natural processes.

By cutting juvenile males out of the nursery herds, keeping bachelors away from them and off the best pastures, territorial males promote the reproductive success of the population.

If membership in nursery herds is in some degree responsible for a higher female survival rate, then an adult sex ratio close to unity might be predicted for solitary species, since juveniles of both sexes presumably face much the same risks after leaving the territory. In fact there is evidence, though still fragmentary, of an equal or higher male sex ratio in the grey duiker (Wilson and Roth, 1967), dikdik (Kellas, 1955; Kurt, 1964), klipspringer (Wilson and Child, 1965), and bushbuck (Wilson and Child, 1964; Elder and Elder, 1970). But Tinley (*in lit.*) reports an adult ratio of about 3:2 in favor of female oribi.

3. *Spacing out the population*—In species that form large, dense aggregations, competition between territorial males, by breaking up concentrations into small units and spacing them out, one to a territory, helps to prevent overutilization of any one part of the range (Koford, 1957; Buechner, 1963). Speaking more generally, it may be said that the minimum spacing tolerated by territorial males sets limits to the size and spacing of nursery herds. Where males are closely spaced, there will generally be no more than one herd to a territory, since each male attempts to herd all the females on his property into a single group; the herd becomes increasingly difficult to defend against invading males as its membership increases (Estes, 1969a).

4. *Reproduction*—Considered purely from the standpoint of reproduction, the efficiency of the territorial system becomes apparent when there is a sharply defined rut in a large population, as in wildebeest or topi. The disruption and confusion created by hundreds of highly excited bulls is spectacular enough, but at least the activities of each male are confined to the immediate vicinity of his own property. If instead, contending males of equal rank congregated around every herd containing a female in estrus, it could well lead to chaos. Intimations of what might happen in the absence of restraints—either a territorial network or a dominance hierarchy between males—can sometimes be gained when a herd is left unguarded: it may be raided from all sides by territorial neighbors, or invaded by a bachelor herd, whose members take it in turns to pursue and harass the females (for examples see Leuthold, 1966 and 1970b).

## The Socialization Process

In the last analysis, the adult male has had to change his ways very little to accommodate to a polygynous system. Crucial as his role may be in that system, he plays it by remaining true to type. The only major concession required of the territorial male was tolerance of females in herds, toward which the male libido predisposed him. It did not require him to become gregarious. In fact, territorial males of gregarious species probably spend more time in solitude, on the average, than those of solitary species, which are typically paired with a female (Estes, 1969a).

Since the territorial drive inhibits or suppresses gregarious tendencies, the question arises whether, in pair-forming species, it is territoriality, as evidenced directly by aggression toward outside females or indirectly by scent-marking activities, that keeps females from associating with one another (assuming their mates are tolerant at least toward other females in estrus). If so, the first step toward sociability entailed leaving the territory and we may postulate that the precursor to true herds was small, temporary gatherings on neutral ground, like those of the reedbuck or oribi. Females that continued to associate gained freedom, both from dependence on cover and on a particular male, and the opportunity to share an enlarged home range, including several territories. The owners who proved most tolerant of females in groups would be favored with the most opportunities to reproduce. Beginning then, female offspring no longer needed to go through a solitary wandering stage, but could continue to enjoy the security of a group within a familiar range. Juvenile males could also improve their chances of survival by forming all-male associations after being ejected, inevitably, from their nursery herds at adolescence.

Once social groupings were begun, natural selection would have favored the evolution of increasingly gregarious, complex organizations as the means of achieving maximum population densities and so succeeding in the competition to be the dominant herbivore in the ecosystem. But large herds and high densities developed only among those species that moved out into the grasslands, for as Ewer (1968:99) observes, 'Large societies are only able to exist in situations where the members can easily keep in contact ... and only if adequate food can be found for all, within an area easily covered in the normal feeding period .... Terrain and type of food are thus the two external factors which have most influence on the evolution of social relations.'

The tendency toward increasing sociability and larger groupings in open environments has been observed in such diverse phyla as primates (Crook and Gartlan, 1966), weaverbirds (Crook, 1964) and fishes (Williams, 1964), among others. Williams, for instance, points out that 'schooling is a conspicuous phenomenon in pelagic oceanic waters, scarcely detectable in weedy or rocky shallows and of intermediate development in intermediate habitats.' This is exactly parallel to the situation among African bovids.

The bovid socializing process led to reduced social distance in herds, especially when promoted by the practise of mutual grooming (e.g. social licking between impala and bovines-Sambraus, 1969). It led to the establishment of the most experienced animals as leaders, and to the formation of rank hierarchies. According to Etkin (1964a), there are strong evolutionary pressures in favor of dominance hierarchies as a principle of social organization, because the advantages enjoyed by dominants in time of privation 'enables them and, with them, the species to survive.' On the other hand, Eisenberg (1966) argues that loose and therefore flexible social systems are the rule for species adapted for unstable niches (e.g. arid biomes), while species with more closed social systems are specialized for more predictable, stable niches (e.g. wet savanna). (In the wildebeest both closed and open systems occur interchangeably in one species.)

As information on more bovids becomes available, it will be of great interest to explore further the relationship between social system and niche, specifically, to determine whether a rank hierarchy is characteristic of gregarious antelopes that live in sedentary small herds, and whether presence or absence of horns is correlated to some degree with a dominance hierarchy and social distance. Horns should make a difference, if Etkin (1964a) is correct in saying that 'dominance patterning .. is clearest in those group-living animals which show a high level of individual aggression,' since aggression between females seems to be most pronounced in horned species.

## NON-TERRITORIAL SOCIETIES

The Bovinae subfamily includes three tribes: the essentially African Tragelaphini (Gentry, 1968b), the wholly Eurasian Boselaphini and the Bovini of Eurasia (primarily), North America and Africa (the latter two with but one recent species each). The Bovini are the most recent and advanced bovid tribe, having arisen in south Asia during the Lower to Mid-Pliocene from the Boselaphini (Pilgrim, 1939: see Fig. 2). The latter tribe contains the most primitive living bovid, the small four-horned antelope, and the large nilgai (*Boselaphus tragocamelus*), which retains primitive horns but is moderately advanced socially. The Tragelaphini, which separated from the Boselaphini as early as the Mid-Miocene, may also be considered a generally primitive group—with the notable exception of the elands—on the basis of comparatively limited forebrain development (Ronnefeld, 1970), elementary social organization, dependence on closed habitats and browse. The eland, as every Masai herdsman knows, is more like an ox than an antelope, which Pilgrim (1939) attributes either to convergence or deferred inheritance.

Major features of bovine social organization include the integration of males and females in mixed herds (truer of some species than others), precocial young, group defense (notably a mobbing response released by the distress call), social licking and minimal social distance (e.g. buffalo regularly lie touching). Although nearly all are grazers (and use the tongue to gather grass, unlike any known antelope), most species inhabit well-watered woodland interspersed with glades and live in small to medium-sized herds of fluid composition. In terms of population density and aggregating tendency, the American bison—the only plains species—and the African buffalo rank as the most advanced and successful members of the tribe.

One outstanding feature of the bovine system that sets it apart from all antelopes except the eland (as far as we know), is the existence of a dominance hierarchy between adult males. Accordingly two rank hierarchies exist in a herd which are quite separate, with males from subadults onward all ranking above females (Schloeth, 1961; Schaller, 1967). There is evidence of a similar male rank hierarchy in eland herds (author's observations).

Until recently, I had imagined that the bovine organization evolved from a territorial system, representing the complete integration of the sexes in nomadic herds freed finally from all restraints on their movements and composition. Thus the eland seems to be the most completely nomadic of the antelopes. The fact that female rank hierarchies are common in gregarious territorial species made the establishment of a male rank hierarchy in place of territoriality seem the logical next step up in bovid evolution. Even more to the point, male rank hierarchies already exist in bachelor herds of many species. New evidence is emerging, however, suggesting that: (a) the ancestors of the Bovini may not have been territorial; and (b) male rank hierarchies are based on differential size achieved through prolonging growth in adults—i.e. depend on a specialized physiological mechanism.

(a) Recent findings indicating that Tragelaphini may be non-territorial raise the possibility that the ancestors of the oxen did not go through a territorial stage. Tragelaphini and Boselaphini seem so different from other antelopes, both in morphology and behavior, that it is quite conceivable this line is distinct from all the other bovids, as Leuthold (p. 231 this volume) also suggests. The two tribes likewise differ greatly from one another (especially in horns and markings), but share one morphological peculiarity that clearly demonstrates their relatedness: very similar scent glands between the false hoofs of the hind feet, which are unique both in position and structure, are found in both Boselaphini and so far in the two kudus, the nyala and eland (but not in bushbuck and Sitatunga—Pocock, 1910, 1918; Ansell, 1968).

In social organization *Tragelaphus* spp. and seemingly also the Boselaphini share a cervid-like tendency toward sexual segregation except when breeding. Males of social tragelaphines may associate in bachelor herds, but fully mature bulls are most often solitary (Leuthold, Paper 9 of this volume; Maberly, 1962; Steinhardt in Walther, 1964a; author's observations). In the absence of exclusive home ranges or territories, the false-hoof glands, of unknown function but apparently better adapted for diffusing scent through the air than for scent deposition (thereby resembling cervid metatarsal glands?), could function for spacing out individuals (and vice versa).

The bovine social system could have arisen equally well from a social tragelaphine prototype, in which a number of adult males and females with overlapping home ranges occasionally combined in small herds. This seems to have happened, in fact, in the eland, an undoubted tragelaphine despite its conspicuously bovine appearance and social organization, as an adaptation to nomadism in more open habitats.

However, there is one serious flaw in the argument that the ancestors of the oxen were non-territorial: according to Schaller (1967), rutting nilgai bulls are territorial. Supposedly Bovini arose from ancestors of the nilgai and not the Tragelaphini (Pilgrim, 1939).

(b) The bovine dominance hierarchy has generally been conceived as based on mutual familiarity between individuals in closed herds, rather than on such objective criteria as relative size of horn development (Schloeth, 1961;Geist, 1966). This may be true for females and not for males. Schaller (1967) has pointed out that meetings between presumably unacquainted gaur bulls, which wander widely in the breeding season, continually joining and leaving nursery herds, are frequent. They 'probably determine their status in most instances by assessing each other's physical attributes visually without overt interaction.' Dominance is determined mainly through the lateral display, the predominant bovine threat posture, which is enhanced by the gaur's dewlap and tremendously developed dorsal ridge (cf. Lott's paper on the bison's lateral display, no. 19 below). Schaller concludes that size determines dominance and there is evidence that this may apply to bovine males in general.

In the African buffalo, Pienaar (1969) reports that bulls continue to grow and put on weight even during old age. Females, in contrast, attain adult weight in their fourth year and grow little thereafter. Males become adolescent at 2. 5-3 years and attain full adult dentition at five years, but are not fully armed before 6-7 years old, when the horny shield growing around the base of either horn finally joins. Bulls are estimated to be at least 7-8 before they are powerful enough to compete successfully for breeding opportunities with older animals. Although the sample is small, average weights, shoulder heights and horn spans of males in different age classes suggest a substantial increase with age (*op. cit.*):

| Age Class | 4 yr | 5 yr | 6-7 yr | 8-15 yr | >15 yr |
|---|---|---|---|---|---|
| Weight (kg) | 508.2 | 539.5 | 589.9 | 643.8 | 717.6 |
| Shoulder height (cm) | 135.6 | 135.9 | 139.9 | 143.5 | 148.3 |
| Maximum horn span (cm) | 82.3 | 86.4 | 88.9 | 91.9 | 100.6 |
| No. in sample | 6 | 4 | 6 | 13 | 6 |

Such an extended size range, apart from promoting an orderly and evolving rank hierarchy in closed herds, should facilitate the visual assessment by strangers of bulk and power. The disproportionately greater bulk attained by males—up to two/ times female weight—in the whole tribe supports the hypothesis that the bovine male rank hierarchy is based on body size as a function of age.

That the same principle may apply to other species in which reproductive success is based on absolute dominance rather than territorial dominance is suggested by the fact that rank in elephants (*Loxodonta* and *Elephas*) and giraffe (*Giraffa camelopardalis*) is also evidently based on continuing growth of the male, not only in body size but also in armament (see e.g. Laws, 1966 and Spinage, 1968). Geist (1966, 1971) has shown that relative horn development is decisive in determining status among male sheep (*Ovis* spp.). In all these cases, apparently selective pressure in favor of larger size (especially horns in sheep and bulk in bovines) has resulted in neoteny = extending the growth period of the male (discussed in Geist, 1971).

If the above hypothesis proves correct, the male rank-hierarchy system would appear to be basically unlike the territorial system, in which the available evidence suggests that growth virtually ceases at the time of maturation (e.g. in lechwe—Robinette and Child, 1964; wildebeest—Watson, 1969; impala—Kerr, 1965; and Thomsons's gazelle-Hvidberg-Hansen, 1970). Although the size range between adult males is considerable, here it is based on individual differences existing at maturity rather than on seniority.

## CONCEALED VS. PRECOCIAL YOUNG

Another holdover perhaps even more ancient than territoriality is the instinct to hide, which has been retained by the young of all but a few recent antelopes. A single offspring is the rule among African bovids, authentic cases of twins being rare. The concealing habit, which adults had to lose before social plains dwellers could evolve, continued to have survival value for the newborn, and therefore persisted with only minor modifications in savanna species. Very much the same mechanisms that make for effective concealment are employed both solitary and gregarious species (cf. Hendrichs and Hendrichs, 1971; Jungius, 1970; Walther, 1965, 1969; Gosling, 1969; Lent, Paper 1 in this volume).

The calf chooses its own hiding place and lies still until summoned by its mother. The very young may show no flight reaction whatever, even when handled. Later, calves will bolt if closely approached, but immediately seek another place of concealment (Estes, 1967a). The mother usually remains watchfully in the neighborhood but only approaches once or twice a day (in some cases only alter dark), and summons the calf to suckle from a little distance. While the calf suckles, she licks its genitalia and anus, thereby stimulating it to eliminate metabolic wastes, which she consumes. A brief activity period follows, after which the calf chooses a new hiding place, watched intently by the mother, who then again leaves it. While offspring of the hider type can be induced to follow during the concealment period (and may do so on their own initiative), they rarely move at the mother's side like the young of true follower species (Walther, 1968b; Lent, Paper 1 in this volume)

The main variation in this system is in duration of the concealment period, which lasts anywhere from a few weeks (Waterbuck—Hanks *et al.*, 1969) to several months (reedbuck—Jungius, 1970). In social species, the sooner the calf joins the herd and/or a creche of other calves, the earlier its social life begins. Thereafter it has even less contact with its mother than before, but tends to spend all its time with its peers apart from brief interruptions for suckling. The socialization process is thus facilitated by the formation of age-classes. Since young of the same age are most likely to occur when there are large herds, a high population density and/or a definite breeding season, social evolution should proceed most rapidly under these circumstances. It would appear that the concealment system, while making for a rather weak bond between mother and offspring, may thereby actually facilitate attachment to the herd. By the same token, a continuing bond between a female and her offspring would seem inherently unlikely.

Alone of all antelopes, it seems, Alcelaphini have precocial young, which are able to run within 10 minutes of birth, show a well-developed following response and accompany their mothers from the time they first gain their feet (Estes, 1966, 1969b). However, hyenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*) can easily run down a newborn calf; its best chance of surviving—just as for hidden offspring—is to escape the notice of predators. Since the hiding response has been lost, the calf is utterly dependent on the presence of conspecifics for concealment and protection. Here there can be no doubt that the herd takes the place of cover. The more animals there are, in particular the more calves, the harder it becomes for a hyena—the ranking predator on the young of large antelopes—to single out newborn individuals (Estes, 1967b). Natural selection thus favors the evolution of a short calving season, which is characteristic of alcelaphines at all latitudes. A short birth peak offers the additional, better-known advantage of producing more young than predators can handle at one time, and not enough to sustain a large predator population for the rest of the year. The evolution of this system can be traced within the tribe, beginning with the hartebeest, in which the young are concealed (Gosling, 1969)—but for a few days at most in Lichtenstein's hartebeest, according to Mitchell (1965). In sedentary wildebeest and topi/blesbok populations, the young are completely precocial, but are born in small herds, where the initial mortality rate may be high (up to 50 percent in Ngorongoro Crater wildebeeste during the first month—Estes, 1969b). Apparently the system operates most effectively in migratory populations in which large numbers of cows foregather on calving grounds outside the range of most of their predators (Kruuk, 1970; Schaller, 1972). Here the mortality rate tends to be much lower (ca. 20 percent on Ngorongoro calving grounds), although there is a tendency for losses due to separation of mothers and offspring to increase in such large aggregations as those of the Serengeti (Talbot and Talbot, 1963).

A rather puzzling aspect of this system is that in *Connochaetes* and *Damaliscus* the newborn are a completely different color from older calves and adults, retaining the tawny coat seen in varying shades in virtually all savanna antelopes. This hue is well-adapted to concealment in high grassland, but it makes young wildebeest, topi and blesbok decidedly conspicuous in the company of older conspecifics. Accordingly a short peak calving season is really essential to minimize loss due to predation—as the almost total mortality of early calves in Ngorongoro Crater clearly demonstrates (Estes, 1969b). One possible explanation is that the system has developed so recently that there has been no time for the evolution of young that assume the adult coloration earlier than usual (between the first and second month). Nevertheless it seems to represent an advance over the older system and, together with a comparatively early minimum breeding age, has helped alcelaphine antelopes achieve preeminence in certains plains ecosystems. Probably, as Ewer (1968) suggests, precocial young represent an adaptation to migratory habits in this tribe.

### Defense against Predators

Females of most antelopes defend their offspring against predators smaller than themselves, often by direct attack, primarily in response to the young's distress calls.

Jungius (1970) recounts how a female reedbuck intercepted a dog as it was pursuing her fawn, jumped over it and kicked at it in passing, which caused it to desist. Another put a baboon troop to flight, while a Waterbuck cow was courageous enough to chase a car after its calf was caught and tagged (Spinage, 1969b). A wildebeest cow will turn and charge hyenas and wild dogs when her calf is overtaken (Estes and Goddard, 1967). In every case it is the mother that defends; cooperative defense by the herd, a characteristic of the bovine social system, has not developed in antelopes. The nearest approach to it is the teaming of two gazelle females to defend a hidden fawn against jackals (Estes, 1967a). Because more than two females are seldom involved, Walther (1969) believes that the second female is the offspring of the fawn's mother, rather than the unrelated mother of another nearby fawn. The tendency of most plains antelopes to bunch when approached slowly by wild dogs, and to approach and form a front while staring at a resting or passing predator, could be interpreted as incipient group defense, but is hardly to be compared with the mobbing response of cattle or buffalo.

Active defense of the young by antelopes has not evolved beyond the level of the Cervidae, whose offspring are concealed and tended in much the same manner (Bubenik, 1965; Lent, Paper 1 of this volume). In the bovines, and also in equids (e.g. the Plains zebra) group defense goes together with precocial young, making a short birth season unnecessary.

## TRIBAL ORIGINS

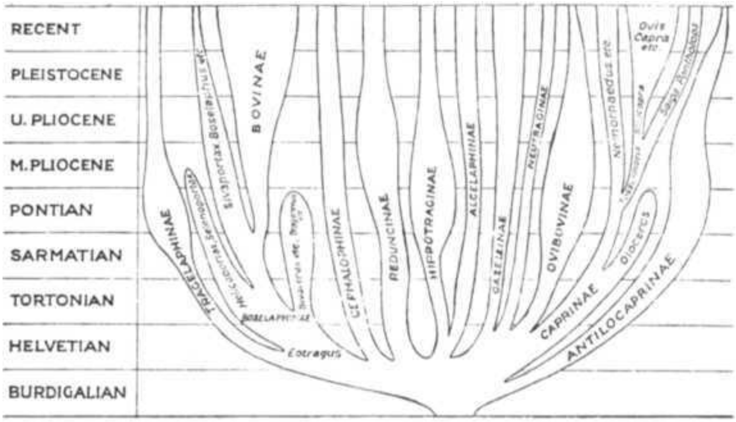

Fig. 2. The first bovid radiation (Pilgrim, 1939)

The extraordinary radiation of African bovids from late Pliocene to late Pleistocene, during which all the present species or their immediate ancestors appeared (Wells and Cooke, 1956;Cooke, 1968), has been so well documented that the comparatively ancient lineage of the tribes tends to be overlooked. According to Pilgrim (1939), all the existing tribes except the Bovini became differentiated during roughly the same period in the Middle Miocene (Fig. 2). *Eotragus* was too specialized (compressed horn cores, boodont molars) to have been the first bovid; it seems rather to have been ancestral to the Boselaphini/Tragelaphini. The first antelope may well have been already in existence during the Oligocene, having branched off from common traguloid ancestors of the ruminants not unlike the surviving water chevrotain (*Hyemoschus aquaticus*) of the West African rain forest (Young, 1962).

Thus the first great bovid radiation took place some 20 million years ago, not long after the spread of grasslands, with the differentiation of antelopes recognizably like today's tribal representatives. Niche differentiation, including the appropriate type of social organization, must also date from this period. In short, by the Middle Miocene, the ancestors of the present dominant savanna and arid-zone antelopes must have already been living in herds on the open plains. The recent discovery of a *Gazella* sp. in Upper Miocene deposits at Ft. Ternan, Kenya (Gentry, 1970), shows that gazelles, at least, have roamed the arid plains of East Africa for the last 14 million years.

Despite huge gaps in the African fossil record—notably almost the whole Pliocene—it is clear that anatomical and behavioral adaptations to the different African biomes have evolved over a much longer period than is commonly realized. The commitment to one type of biome or another which is seen in most groups (Fig. 3) dates back to the differentiation of tribes: the Cephalophini to forest; Tragelaphini and Neotragini to a variety of forest and bush habitats; the Reduncini to mesic savanna; the Alcelaphini to acacia savanna, etc.

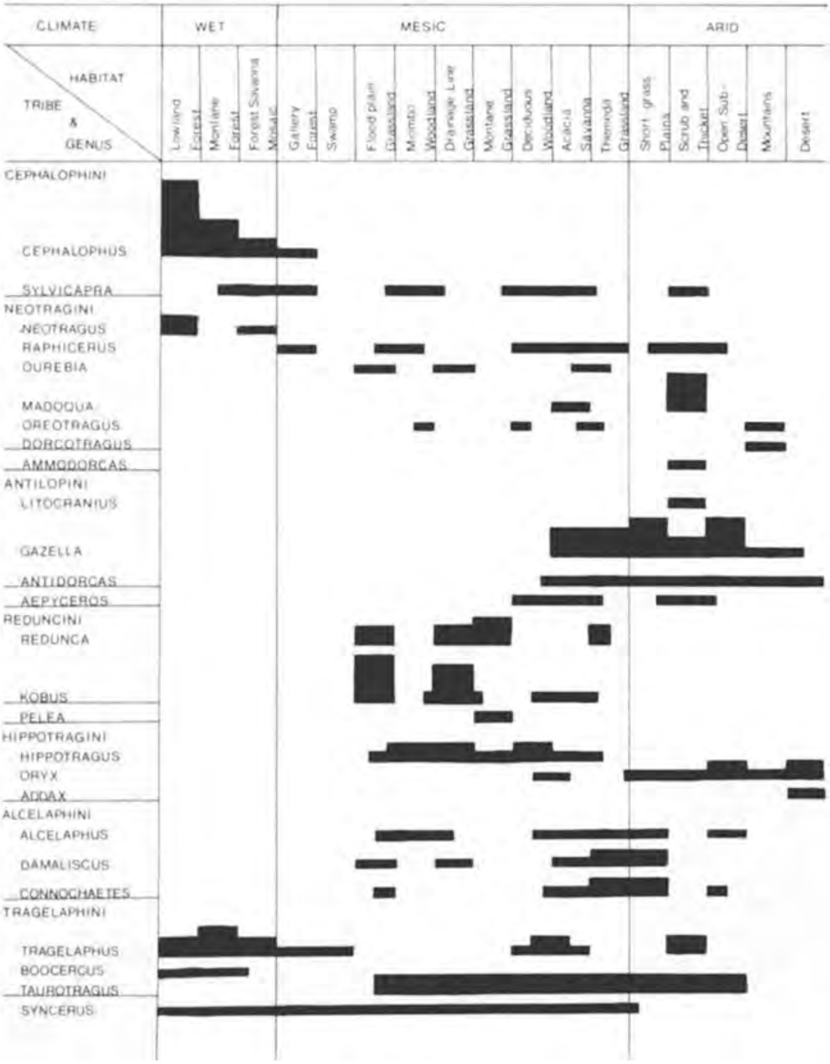

Fig. 3. Tendency to environmental specialization by tribe and genus

To discover the phylogenetic origins of the basic bovid social organization, it may be necessary to go back all the way to the traguloid ancestors of the early ruminants. A North American representative, *Hypertragulus*, may already have lived in large herds by the Oligocene, in association with early camels and oreodonts (Colbert, 1969), while the vicuna (*Vicugna vicugna*), which is not even a true ruminant, has much the same social system as most sedentary antelopes, including territorial males, separate nursery herds and bachelor herds (Koford, 1957; Franklin in Paper 24 of this volume).

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Paper No. 9

# Observations on Home Range and Social Organization of Lesser Kudu, *Tragelaphus imberbis* (Blyth, 1869)

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## ABSTRACT

Home range and social organization of lesser kudu were studied in the context of a more comprehensive ecological research project in Tsavo National Park (East), Kenya. Individual animals could be recognized on the basis of variations in their natural stripe pattern. Lesser kudu appear to be quite sedentary; individual home ranges measure around 2 km$^2$, with slight differences between sex and age classes. Subadult ♂♂ have the largest home ranges; this suggests that they may wander more than other animals. Small-scale seasonal movements, related to the cyclic changes in the condition of food plants, enable lesser kudu to make full use of a seasonally abundant food supply in areas with mostly deciduous vegetation. Group size and composition vary considerably, but a large majority of groups consists of 1-4 animals (average group size over one year was 2.39 and 3.14 in two areas). Small groups may join temporarily to form larger units; the maximum number of kudu seen together was 24. Four group types are described and distinguished in the analysis. Pure ♂-groups are the smallest on average, including a large proportion of single ♂♂. Mixed groups, containing ♂♂, ♀♀ and young, are generally the largest groups; the two other types (pure ♀-groups and 'harem' groups, i.e.♀-groups with one adult ♂) are intermediate in size. Larger groups are unstable in composition, but there appear to be small 'nuclear' groups, consisting of 1-3♀♀ (and their surviving offspring), that are fairly stable over a period of time. When giving birth, ♀♀ tend to leave their group

PLATE 1

Lesser kudu, adult male and two females. Note the horns, thick neck and darker color of the male.

and live alone with their young for some time, rejoining a ♀-group later on. Young ♂♂ grow up in their mother's group to about 1½-2 years of age when they leave it to become solitary or join other subadult ♂♂. Adult ♂♂ are usually either solitary or with a ♀-group; associations with the latter are, on the whole, temporary only. Home ranges of several adult ♂♂ may overlap. Two or more adult ♂♂ may utilize the same area simultaneously, and no defense of area has been found. Their social relationships are ill-defined and do not readily fit into one of two categories prevalent among bovids; territoriality or a dominance hierarchy. The possible influences of environment on the social organization are pointed out. Available information on the social organizations of other *Tragelaphus* species and the place of the lesser kudu and its allies in relation to the social organizations of other bovids are discussed.

## I. INTRODUCTION

### A. Aim of study

Within the multitude of African antelopes the Tragelaphines or 'spiral-horned antelopes' constitute a relatively homogeneous group that has been variously treated as a tribe (*'Strepsicerotini',* Simpson, 1945) or a subfamily (*'Tragelaphinae',* e.g. Allen, 1939; for a detailed characterization of the group see Walther; 1964). Except for the eland (*Taurotragus oryx*), they all inhabit 'closed habitats' (Dorst and Dandelot, 1970), 1970), i.e. dense bush or forest, or papyrus swamps in the case of the sitatunga (*Tragelaphus spekei*). This may be the reason why, apart from some generalities (e.g., Lydekker, 1926; Astley Maberly, 1960), little is known about the biology of these species, particularly their spatial requirements and social organization. Only in the last few years have attempts been made at studying some of these antelopes in their natural habitats (sitatunga: Owen, 1970; bushbuck, *Tragelaphus scriptus:* Allsopp, 1971; mountain nyala, *T. buxtoni:* Brown, 1969). Walther (1964) observed the behavior of several *Tragelaphus* species in captivity.

The lesser kudu (*Tragelaphus imberbis*) is one of the medium-sized members of the group, with a pronounced sexual dimorphism, adult ♂♂ reaching just over 100 kg in body weight, ♀♀ being considerably smaller (60-70 kg), hornless and lighter-colored (Plate 1). The species is endemic to the 'Somali Arid Zone' (Bigalke, 1968), occurring from the lower areas of Ethiopia through southern Somalia, most of Kenya below 1200 m (Stewart and Stewart, 1963), northeastern Uganda (Karamoja) and much of Tanzania, reaching its southern limit in the area of the Ruaha National Park (ca. 8° S lat.). It inhabits the dry bush savanna (*Commiphora-Acacia* and related types) characteristic of much ot its geographical range and is rarely seen in open country.

In the context of a more comprehensive research project I had the opportunity to study the social organization of lesser kudu in Tsavo National Park (East), Kenya. This paper is a preliminary report on results obtained between 1 November 1968 and 30 April 1971. As the study was primarily ecologically oriented and involved work on other species as well (Leuthold, 1970a, 1971a), only part of my time was devoted to the sociological aspects. This, coupled with various difficulties in field observation (see below), has rendered progress of the study relatively slow, and important gaps remain in the information available to-date. The research is to be continued.

### B. Ecological background and study area

Over the past 10-15 years the vegetation of Tsavo National Park (East) has changed profoundly. The combined effects of heavy utilization by elephants and frequent bush fires have converted an originally dense dry woodland (*Commiphora-Acacia* type) into more open bush and, locally, grassland with scattered trees (Napier Bax and Sheldrick, 1963; Laws, 1969; Leuthold, 1969). These large-scale vegetation changes inevitably affect the fauna of the park, and for animals depending on woody plants for food, cover, etc., the effects are likely to be detrimental. This situation has prompted various ecological studies, within the framework of the Tsavo Research Project, among them one on the lesser kudu (Leuthold, 1971b), typically an animal of dense woodland (Lamprey, 1963).

Figure 1 shows the portion (ca. 4000 km$^2$) of Tsavo National Park (East) lying to the south of the Galana River, the only permanent river in the park. It includes most of the areas in which the transformation of the original vegetation has progressed farthest. In those, lesser kudu have declined substantially in numbers or disappeared altogether (Sheldrick, pers. comm.). However, the degree of change varies locally to a large extent, being highest near permanent water supplies, and considerable areas still provide suitable kudu habitat.

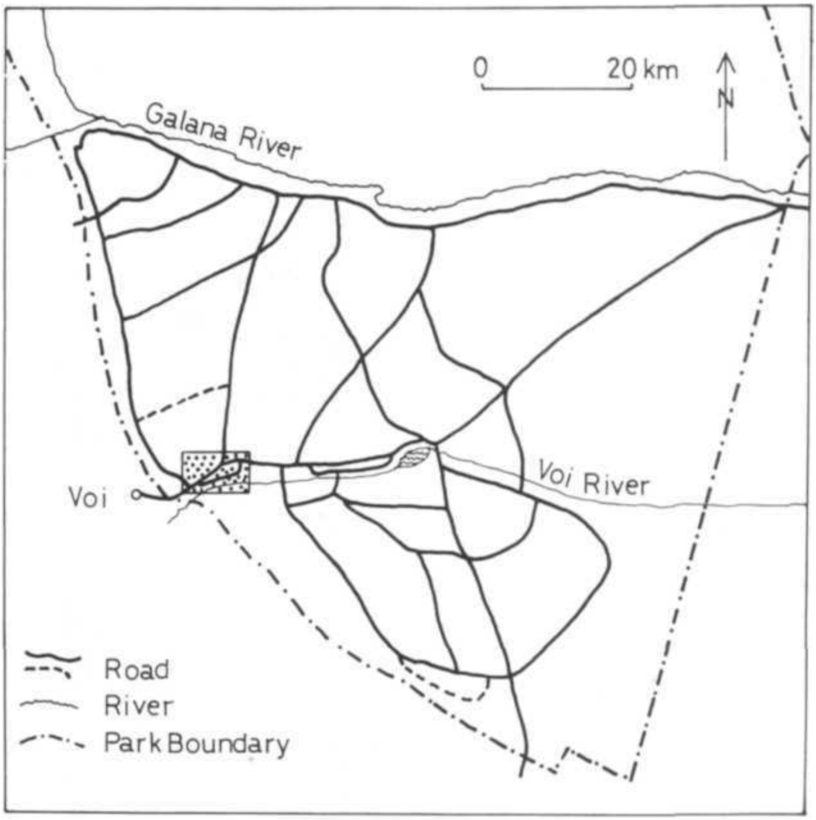

Fig. 1. Southern portion of Tsavo National Park (East)

——— Roads travelled during road counts
- - - - Other roads not included in counts
▨ Main Study area

One such area is the immediate vicinity of park headquarters near Voi, including the slopes of Mzinga Hill and the country adjacent to part of the Voi River (Fig. 2). Being conveniently located and easily accessible by roads, it was chosen as the main study area (ca. 30 $km^2$) for detailed observations on ecology and behavior of lesser kudu. In the west, on the slopes of Mzinga Hill, there is some *Commiphora* -woodland with a dense understorey of deciduous shrubs such as *Premnn* spp., *Grewia* spp., *Bauhinia taitensis*, etc., resembling the original vegetation, though considerable tree destruction has occurred here lately. To the east of the airfield and along the Aruba Road (Fig. 2) woody cover has been substantially reduced, the vegetation now being primarily grassland with scattered bush (mostly deciduous) and some large trees (*Delonix elata*, *Melia volkensii*). Along the Voi River there is a belt, 300-500 m wide, of evergreen bush and riverine forest that offers good cover and food supply throughout the year and appears to be a preferred kudu habitat. For this very reason, however, conditions in the main study area are not typical of those prevailing in the park as a whole, and conclusions drawn from observations made in this area may not apply elsewhere.

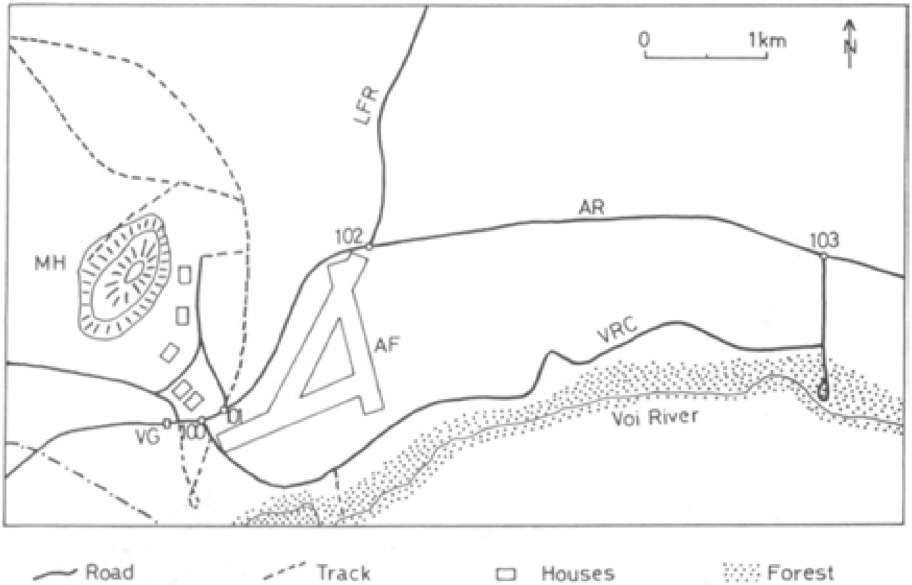

Fig. 2. Main study area

MH = Mzinga Hill
LFR = Lugard Falls road
AR = Aruba road
VG = Voi Gate (Park entrance)
AF = Airfield
VRC = Voi River Circuit
Numbers indicate numbered signposts at road junctions

## C. Methods

The study was carried out at two levels of intensity:

1. bi-monthly road counts over a fairly large area (Fig. 1); 2. detailed observations on the population of the main study area (Fig. 2).

*Road counts*

In a landrover, driven at about 30 km/h (depending on vegetation type and resultant visibility), an observer was standing on the seat and looking out of the roof hatch, his head being about 2. 5 m above ground level. Animals seen from this position were checked with 10 × 50 binoculars, counted and classified with regard to sex and age (see below). In this way, some 650 km of park roads in the area south of the Galana River (Fig. 1) were covered in the course of about a week each time; lesser kudu was only one of 13 animal species recorded. These counts yielded data on group size and composition, population structure, and other aspects not considered here.

*Sex and age classes*

As only male kudu have horns, showing no distinct stages during their development, classification of animals into age groups is difficult and, by necessity, somewhat arbitrary. Also, little is known yet on the time taken by the horns to appear and to reach adult size. Ages attributed to animals in this paper are, therefore, provisional estimates subject to possible amendments later on.

Sex and age classes (and corresponding abbreviations) used in this paper are the following:

Adult ♂♂ (♂♂a) = fully grown ♂♂ with thick necks and well-developed horns (probably mostly >4 years old);

subadult ♂♂ (♂♂sa) = young ♂♂ between ♂♂a and juvenile ♂♂ (see below). Horns about half ear-length to near-adult size (estimated ages 1-3½ years);

juvenile ♂♂ (♂♂ j) = young ♂♂ with horns just visible (ca. 7-9 months) to about half ear-length (ca. 1 year);

adult ♀♀ (♀♀a) = any ♀♀ not distinctly less than fully grown;

Juvenile ♀♀ (♀♀ j) = ♀♀ distinctly less than fully grown;

juveniles (juv) = young animals, sometimes including ♂♂ j; all probably <1 year old.

*Detailed sociological observations:*

In the main study area (Fig. 2) sociological aspects were investigated along with food habits (Leuthold, 1971b). Essential for the study was the possibility of recognizing individual animals over a prolonged period of time. The coat markings of lesser kudu provide a ready-made, presumably permanent, means of identification. In a basic pattern of 10-13 vertical stripes, small variations, such as forks, joint stripes, horizontal cross-bars, etc. (Plate 2), distinguish virtually every individual in a not-too-large population.

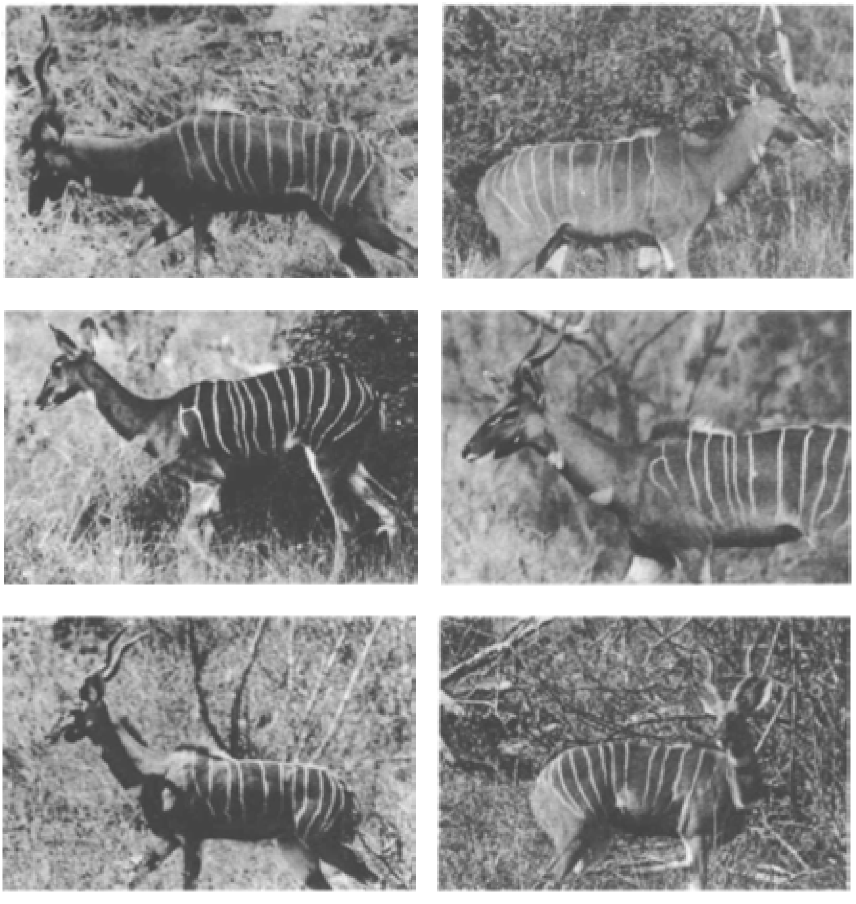

PLATE 2

Variations in the stripe pattern of the lesser kudu.

For each known animal I made up a numbered file card with a sketch and/or photograph of the stripe pattern and details on the first sighting. The collection of file cards was taken into the field and consulted for subsequent identifications of individuals. On each observation of kudu, group size and composition and known individuals were noted and the locality entered on sketch map. All observations were made from a vehicle that permitted following the animals cross-country (see below).

| Category | Number of resightings | Months under observation | | | | | | Total animals |
|---|---|---|---|---|---|---|---|---|
| | | <1 | 1-6 | 6-12 | 12-18 | 18-24 | >24 | |
| ♂♂a | 1-5 | 5 | 3 | 2 | – | – | – | 10 |
| | 6-15 | – | 3 | 2 | 2 | – | 1 | 8 |
| | 16-25 | – | – | 1 | – | 2 | – | 3 |
| | 26-35 | – | – | – | 2 | – | – | 2 |
| | Total in category | 5 | 6 | 5 | 4 | 2 | 1 | 23 |
| ♂♂sa+j | 1-5 | 6 | 7 | 3 | – | 1 | – | 17 |
| | 6-15 | – | 5 | 5 | 6 | – | – | 16 |
| | 16-25 | – | – | 1 | 1 | 2 | 1 | 5 |
| | 26-35 | – | 1 | – | 1 | – | – | 2 |
| | 36-45 | – | – | – | – | 1 | – | 1 |
| | Total in category | 6 | 13 | 9 | 8 | 4 | 1 | 41 |
| ♂♂ | 1-5 | 9 | 4 | 1 | 1 | – | – | 15 |
| | 6-15 | – | 4 | 6 | 4 | 2 | – | 16 |
| | 16-25 | – | – | 4 | 4 | 3 | 2 | 13 |
| | 26-35 | – | – | 1 | 4 | – | 2 | 7 |
| | 36-45 | – | – | – | 2 | – | 1 | 3 |
| | >45 | – | – | – | – | 2 | – | 2 |
| | Total in category | 9 | 8 | 12 | 15 | 7 | 5 | 56 |
| Juv[1] | 1-5 | 2 | 3 | – | | | | 5 |
| | 6-15 | – | 3 | 1 | | | | 4 |
| | >15 | – | 1 | – | | | | 1 |
| | Total in category | 2 | 7 | 1 | | | | 10 |
| Total | overall | 22 | 34 | 27 | 27 | 13 | 7 | 130 |

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[1] 6 animals originally recorded as juveniles are included with the ♂♂ sa + j, one with ♀♀

A total of 164 recognizable individuals (29 ♂♂a, 52 ♂♂sa + j , 66♀♀ and 17 juv) were recorded in the study area. Of these, 34 (21%) were never resighted (6♂♂a, 11♂♂ sa+j, 10♀♀, 7 juv; these include some of the very first individuals noted, whose markings were not sufficient for later recognition); for the others, the numbers of resightings and the periods over which these were made are given in Table 1. The maximum numbers of resightings of one individual in each category are as follows:

> 34 for ♂♂a, 44 for ♂♂ sa + j, 51 for ♀♀ (no figure is given here for juv, as those that survived are included in the appropriate category of older animals).

While the coat markings of lesser kudu are nearly ideal for individual recognition, their habitat preferences (Lamprey, 1963) and flight behavior are not. Kudu inhabit fairly to very densely wooded areas where visibility is often limited to 20 m or even less. Standing motionless in dense bush, camouflaged to some extent by the somatolytic effect of their stripes, they may let a vehicle approach to within 20-30 m, as long as it moves. However, as soon as it stops, they run off, usually into thick cover. It is, therefore, often a problem to detect the animals early enough and to see them well enough to recognize individuals. Also, the number, sex and age of animals in a group sometimes cannot be determined with certainty. At the onset of the study these difficulties were aggravated by the fact that the kudu, like most other animals in the park, were relatively shy, i.e. not used to vehicular traffic, the number of visitors to the park being rather low at that time. Through repeated and persistent 'harassment' from my part many kudu in the main study area gradually became habituated to being approached by a vehicle, and a few of them now permit observation at as little as 30 m under favorable circumstances.

Two other difficulties in observing and identifying lesser kudu should be mentioned here:

1. The patterns on the right and left side of the same animal vary independently (cf. Plate 2). One side may show a characteristic configuration, while the other is quite regular. Thus, a given animal may be seen but not recognized an unknown number of times (theoretically up to 50% of all possible sightings). This is perhaps the major shortcoming of this method of identification, in comparison to artificial marking by means of ear tags, neck bands, etc.

2. The nature of the vegetation and the abundance of dead trees in much of the area make cross-country driving difficult and tiresome, even impossible locally. Thus various areas where kudu might have occurred were visited only rarely or not at all, even within the relatively small study area. In addition, when I did follow some kudu cross-country the inevitable noises made by the car on the bushes and over dead wood often frightened the animals. Stalking them on foot had, however, proved even less practicable.

Thus, many difficulties impeded the progress of the study and, therefore, much of the information given below remains incomplete and the conclusions tentative.

### D. Acknowledgements

This study was conducted within the framework of the Tsavo Research Project, Kenya National Parks. I wish to thank the Trustees and Director of Kenya National Parks for sponsoring and providing facilities for my work and permitting publication of the results. The Ford Foundation supported the Project financially in its early stages. Dr. P. E. Glover, Tsavo Research Project, and Mr. D. L.W. Sheldrick, Park Warden, provided various assistance and advice throughout the study. Most of all, I am indebted to my wife, Barbara, for her valuable contributions in field work, recording of data and preparation of the manuscript, including drawing the illustrations.

## II. HOME RANGE

'Home range' here denotes the entire area within which a given animal was seen during the study.

Home ranges were determined by plotting on a map all locations where an individual animal was sighted and drawing a polygon around them. Sizes were obtained by measuring the polygons on the map and calculating their approximate areas. In most cases it is possible, even probable, that an unknown part of an animal's home range lies outside the areas regularly visited by me. This applies particularly to the Voi River Circuit (Fig. 2) where a belt of dense riverine bush precluded observations in a fairly large area of apparently good kudu habitat (see section I. B). Also, the country immediately south of the river was not readily accessible and was visited only twice. Thus, most or all of the apparent home ranges given below are probably smaller than the real home ranges of the animals concerned.

### A. Size, shape and location of individual home ranges

Figures 3-5 show the apparent home ranges of 8♂♂sa, 8♂♂sa and 8♀♀, respectively. Table 2 gives their longest dimensions in two directions, their approximate sizes,

TABLE 2. APPARENT HOME RANGES OF INDIVIDUALLY KNOWN KUDU

| | | Size of home range | | | | |
|---|---|---|---|---|---|---|
| Category | Animal Number | Length (km) | Width (km) | Area ($km^2$) | Number of Obs. | Period of observation |
| ♂♂a | 2 | 3.75 | 1.25 | 3.3 | 13 | 6.11.68–18.3.70 |
| | 7 | 3.6 | 0.5 | 1.5 | 15 | 10.11.68–19.6.69 |
| | 11 | 2.0 | 1.25 | 1.3 | 12 | 21.11.68–18.3.71 |
| | 17 | 1.75 | 1.1 | 1.3 | 26 | 1.4.69–4.11.70 |
| | 27 | 2.6 | 0.5 | 0.8 | 11 | 31.8.70–18.1.71 |
| | 28 | 3.25 | 2.0 | 4.3 | 26 | 26.6.69–11.4.71 |
| | 51 | 2.0 | 1.6 | 1.6 | 30 | 17.11.69–29.4.71 |
| | 55 | 2.75 | 1.75 | 3.7 | 35 | 12.3.70–29.4.71 |
| ♂♂ sa | 9 | 4.75 | 1.5 | 4.1 | 21 | 14.11.68–7.3.71 |
| | 20 | 1.75 | 1.6 | 1.4 | 23 | 8.10.69–20.4.71 |
| | 22 | 2.5 | 2.0 | 2.9 | 15 | 28.5.69–6.8.70 |
| | 40 | 4.25 | 2.5 | 6.3 | 7 | 1.11.69–21.2.71 |
| | 48 | 2.6 | 1.25 | 1.9 | 45 | 25.7.69–20.4.71 |
| | 54 | 1.0 | 0.6 | 0.4 | 23 | 1.11.69–22.4.71 |
| | 76 | 3.5 | 1.75 | 3.1 | 8 | 10.7.70–29.1.71 |
| | 91 | 1.75 | 1.1 | 1.1 | 27 | 5.4.70–29.4.71 |
| ♀♀ | 2 | 3.6 | 0.6 | 1.5 | 27 | 4.11.68–7.11.69 |
| | 4 | 3.75 | 1.25 | 2.4 | 32 | 7.11.68–18.1.71 |
| | 18 | 1.0 | 0.6 | 0.4 | 20 | 20.5.69–22.4.71 |
| | 25 | 2.6 | 1.25 | 2.8 | 51 | 29.5.69–23.4.71 |
| | 29 | 4.0 | 0.75 | 1.8 | 14 | 7.10.69–30.4.71 |
| | 37 | 2.75 | 2.5 | 3.5 | 39 | 25.11.69–28.3.71 |
| | 38 | 1.4 | 0.6 | 0.6 | 20 | 5.3.70–9.4.71 |
| | 46 | 1.8 | 1.0 | 1.3 | 27 | 28.3.70–29.4.71 |

the numbers of sightings for each animal and the period of time over which they were obtained.

*Size:* Individual home ranges vary substantially in size, from 0.4 $km^2$ (♀18, ♂54) to 6. 3 $km^2$ (♂40), with an average of 2. 2 $km^2$ for the 24 animals considered here (for variations related to sex and/or age see below).

*Shape:* As a result of the method used in determining them, the home ranges shown in Figs. 3-5 do not take into account any features of the environment that might influence their shape, e.g. obstacles to free movements of kudu such as houses at park headquarters.

Several home ranges located along the Voi River appear particularly long and narrow, compared with the majority of the others. The following factors may account for this:

(1) the oblong shape may be real, but exaggerated due to the impossibility of observing animals in the riverine bush; (2) this particular area was inhabited by a number of individuals often seen together in one group (♂7, ♂9, ♀2, ♀3, ♀4, ♀6, and others, see Table 5

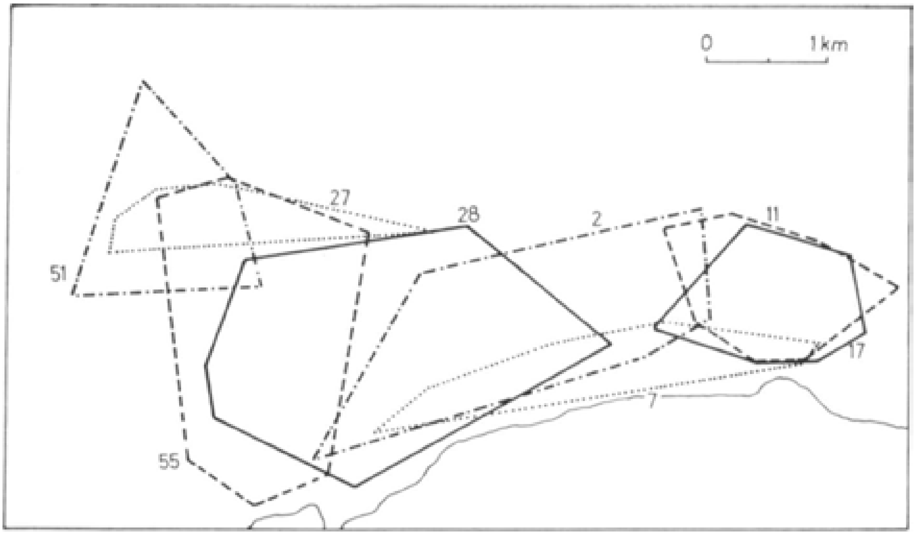

Fig. 3. Apparent home ranges of eight ♂♂ a. The numerals indicate the number assigned to each individual. The frame includes the same area as Fig. 2.

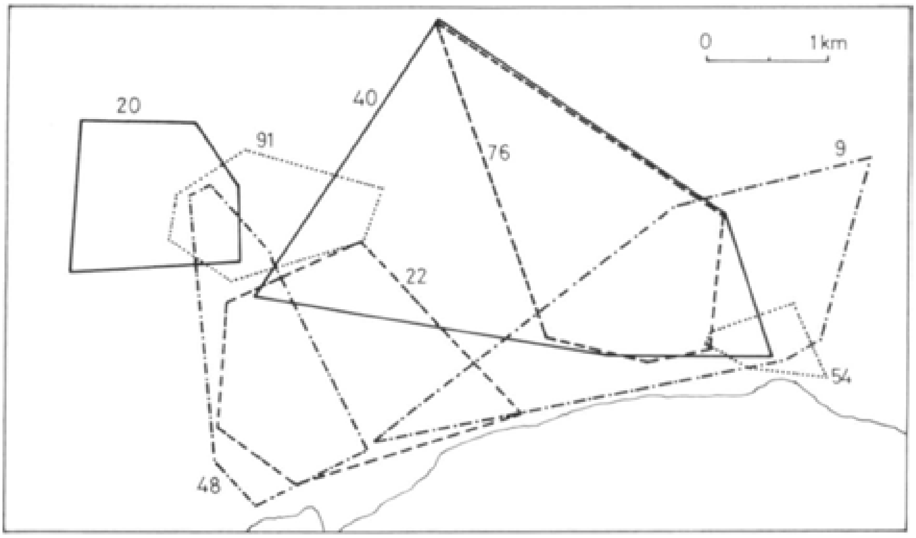

Fig. 4. Apparent home ranges of eight ♂♂ sa. (Arrangement as in Fig. 3).

below); the shape of their home ranges may reflect a special case of individual variation. Other animals living partly in the same area show more 'normally' shaped home ranges (e.g.♂ 11, ♂ 17 in Fig. 3; ♀ 18 in Fig. 5), at least as far as the available data indicate.

*Location:* The home ranges shown in Figs. 3-5 suggest four 'core areas' of kudu activity within the main study area:

(1) north and north-east of Mzinga Hill (Fig. 2): ♂ 27, ♂ 51, ♂ 20, ♂ 91, ♀ 38, ♀ 46;

(2) the east side of Mzinga Hill and the western extremity of the Voi River Circuit: ♂ 28, ♂ 55; ♂ 22, ♂ 48; ♀ 25, ♀ 29, ♀ 37;

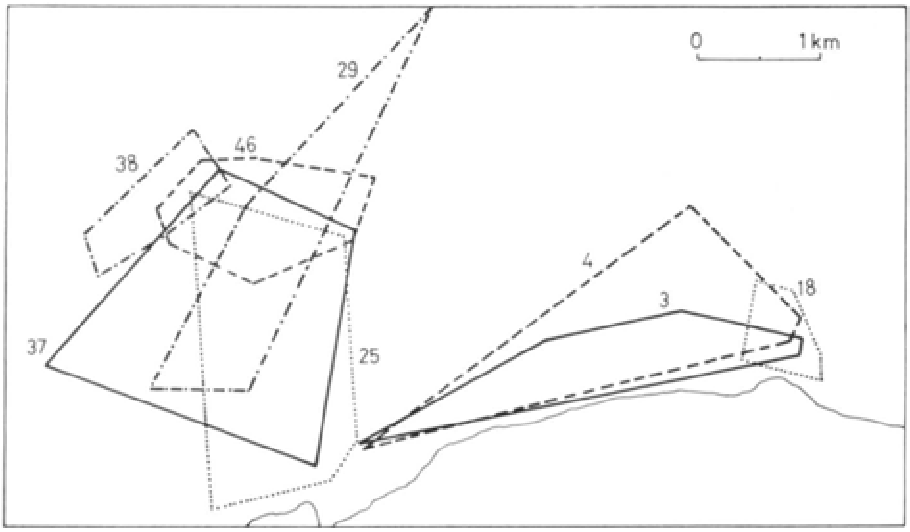

Fig. 5. Apparent home ranges of eight ♀♀. (Arrangement as in Fig. 3).

(3) most of the length of the Voi River Circuit: ♂2, ♂7; ♂9; ♀2, ♀4;

(4) the easternmost part of the Voi River Circuit: ♂11, ♂17; ♂54; ♀18 (their home ranges possibly extend farther eastward)

Only 2 ♂ sa (♂40, ♂76) do not quite fit this picture. Their home ranges may include substantial areas to the north of the Aruba Road (Figs. 2,4) that were not readily accessible by vehicle (the same may apply to a few other animals).

Most of the individuals living within one 'core area' were occasionally seen together, but animals from different 'core areas' very rarely joined in one group (cf. Tables 5-7). This suggests that some of the individual home ranges considered here might actually be 'communal home ranges', inhabited by a given group of kudu. However, as will be shown later (III. B), few if any groups were stable over a prolonged period of time; it would, therefore, be more appropriate to speak of certain 'population segments' inhabiting largely the same home range. The formation of social groups within such population segments would depend on various, partly environmental, factors. The different population segments are, however, not strictly separated; their respective home ranges overlap considerably.

### B. Sex- and age-specific characteristics of home ranges

On the whole, the home ranges of ♂♂ a, ♂♂ sa and ♀♀ are similar in size and shape. Also, there is substantial overlap of home ranges within and between all sex and age classes. This is particularly noteworthy in the case of ♂♂ a and will be discussed later (III. D).

The data in Table 2 indicate slight differences in the size of home ranges between sex and age classes. The home ranges of ♂♂ sa are largest, both on average and individually (2.6 and 6.3 $km^2$, respectively); in ♂♂ a they are slightly smaller (average 2.2 $km^2$, largest 4.3 $km^2$), while ♀♀ have the smallest ranges of all (average 1.8 $km^2$, largest 3.5 $km^2$). The longest distance between two observations of the same individual is 4.75 km for ♂♂ sa, 3.75 km for ♂♂ a, and 4.0 km for ♀♀ . If these differences are of any significance at all, they might suggest that ♂♂ sa tend to wander about more than ♂♂ a and ♀♀ or, conversely, that ♀♀ are more sedentary than ♂♂ generally. However, the degree to which such differences can develop depends to some extent on environmental conditions, particularly the quality and quantity of the food supply in a given area and its seasonal variations.

From this point of view one would expect the animals living in the most favorable habitat (here: the Voi River area) to have the smallest home ranges. This holds true for ♂ 54 and ♀ 18 (Table 2), but in other cases it does not. It is impossible to decide, at this point, whether any deviations from a theoretical model are real or simply a result of the inadequacy of available data. Further research will have to show if social factors also play an important part in this context.

## C. Seasonal variations

While some animals remained in a given area throughout the year (as far as could be ascertained), e.g. in 'core area 1' (see above), others undertook small-scale seasonal movements between dry-season and wet-season feeding grounds, particularly in 'core area 2'. A considerable number of kudu inhabited the western slope of Mzinga Hill (Fig. 2) during and after the rainy season, but when the deciduous trees and bushes of this area (see I. B; cf. also Leuthold, 1971b) lost their foliage, many of them moved to the south and south-east, to the western portion of the Voi River Circuit.

Fig. 6. Seasonal variations in the home range of two ♀♀

○ = ♀24, dry season    △ = ♀4, dry season
● = ♀24, wet season    ▲ = ♀4, wet season
Dotted lines indicate movements within a particular observation period (i.e. usually within 1-3 hours)

Figure 6 shows plotted observations of two known ♀♀ , distinguished as to season. With ♀ 24, the separation of dry-season and wet-season areas is readily evident, despite a few observations out of line with the general trend (this may be merely a consequence of the impossibility to clearly delimitate dry and wet seasons). The distance between the approximate centers of dry-season and wet-season ranges is about 1.5 km. In the case of ♀ 4, no seasonal pattern of home range utilization is immediately apparent. However, the preponderance of wet-season over dry-season sightings and the single observation near the Aruba Road (also wet season) suggest that animals living along the Voi River disperse temporarily northward, into the more open bush/ grassland (see I.C),to feed during the wet season, and withdraw into the evergreen riverine bush in the dry season (hence the relative scarcity of dry-season sightings).

These seasonal movements, however small-scale they may be, are ecologically important in that they enable the animals concerned to make full use of a copious but only temporary food supply during part of the year, while at the same time allowing the vegetation in the dry-season habitat to recover from heavy utilization.

## III. SOCIAL ORGANIZATION

'Lesser kudu associate in small herds, ranging from pairs to four or six—the latter probably consisting of a ram and five ewes. Old rams often lead solitary lives, while 4-6 rams of varying ages may sometimes be seen together' (Astley Maberly, 1960). This description is essentially correct, but it gives no indication of the frequency of different group sizes and types, nor of the stability of individual groups and of the relationships between and within different sex and age classes. One of the main aims of this study was to collect more detailed information on these aspects of the social organization of lesser kudu.

### A. Group size and composition

With regard to their composition, the following group types are distinguished here (the term 'group' includes single individuals):

I. ♂-groups, consisting of ♂♂ a and/or ♂♂ sa exclusively;

II. ♀-groups, made up only of ♀♀, with or without juveniles;

III. 'harem groups', i.e. ♀-groups with one ♂ a only;

IV. mixed groups, including ♀♀, with or without juveniles, and one or several ♂♂ sa and/or ♂♂ a.

Strictly speaking, group types III and IV are just different combinations of types I and II, but in view of their relative importance (see below) they warrant treatment as separate types.

Data on the frequency of different group types and their sizes were obtained from two sources:

(a) from the bi-monthly road counts (see I.C., Fig. 1);

(b) from observations in the main study area (Fig. 2).

In both cases, size and composition of all groups encountered were noted (under the limitations discussed in section I.C). To minimize the influence of chance variations in the data, these were totalled over a year (see Tables 3 &4). Both sets of data represent near-random samples of the kudu populations in the two areas, obtained while travelling along a fixed route given by the existing roads. The samples from the main study area are more likely to be somewhat biased, because the same itinerary was not always strictly followed and because the study area includes some particularly favorable kudu habitat that is inhabited the year around (the Voi River forest, see section I.B). To what extent this affects the comparability of the two sets of data is unknown.

Table 3 presents an analysis of 157 groups recorded during six series of road counts between May 1970 and April 1971. Table 4 gives corresponding data for 625 groups seen during the same period in the main study area.

One immediately obvious difference between the two sets of data concerns group size: mean group size was considerably higher in the main study area (3.14 vs. 2. 39). Also, the largest group recorded in the road counts consisted of nine animals, while in the main study area 19 (= 3% of all) groups numbered over nine, the largest one 24 animals.

The total proportion of groups containing 1-4 animals was 90% in the road counts (involving 74% of all animals); in the main study area it was 80% (53% of all animals). These differences can be explained, at least partly, as consequences of two main factors: (a) Habitat: the proximity of the evergreen forest along the Voi River (see I.B) and relatively favorable local rainfall conditions allow a considerable number of kudu, including a high proportion of ♀♀ and juveniles (see below), to remain within a relatively small home range the year around (see II.A);the resultant high density probably favors formation of larger groups; and (b) Methods of observation: while the road counts were relatively cursory and some animals hidden in dense bush may have escaped detection, observations in the main study area often involved following the animals around for some time; this reduced the chances of additional animals remain-

TABLE 3. GROUP SIZE COMPOSITION: DATA FROM GROUND COUNTS, MAY 1970-APRIL 1971.

| No. of animals in group | Group type* |  |  |  |  | No. of groups | % of all groups | No. of animals | % of all animals |
|---|---|---|---|---|---|---|---|---|---|
|  | I |  | II | III | IV |  |  |  |  |
|  | a | sa |  |  |  |  |  |  |  |
| 1 | 29 | 26 | 12 | – | – | 67 | 42.67 | 67 | 17.86 |
| 2 | 12 |  | 13 | 6 | 2 | 33 | 21.02 | 66 | 17.60 |
| 3 | 6 |  | 10 | 4 | 3 | 23 | 14.65 | 69 | 18.40 |
| 4 | 2 |  | 5 | 4 | 8 | 19 | 12.10 | 76 | 20.27 |
| 5 | – |  | – | 2 | 4 | 6 | 3.82 | 30 | 8.00 |
| 6 | – |  | 1 | – | – | 1 | 0.64 | 6 | 1.60 |
| 7 | – |  | 1 | – | 3 | 4 | 2.55 | 28 | 7.47 |
| 8 | – |  | 1 | 1 | 1 | 3 | 1.91 | 24 | 6.40 |
| 9 | – |  | – | – | 1 | 1 | 0.64 | 9 | 2.40 |
| No. of groups in group type | 75 |  | 43 | 17 | 22 | 157 | 100.00 |  | 100.00 |
| % | 47.77 |  | 27.39 | 10.83 | 14.01 | 100.00 |  |  |  |
| No. of animals in group type | 105 |  | 109 | 58 | 103 |  |  | 375 |  |
| % | 28.00 |  | 29.07 |  | 15.47 | 27.46 |  |  | 100.00 |
| Mean group size | 1.40 |  | 2.53 |  | 3.41 | 4.68 |  | overall 2.39 |  |

*see text

ing undetected and also, while moving along, one group sometimes met and joined with another, making it difficult to define either group as a discrete entity. In such cases, the combination of the original groups was usually counted as one group, on the assumption that the 'second' group had been present all along but escaped notice initially. This procedure obviously tends to give a higher average value for group size.

Another difference lies in the proportions of pure ♂-groups: 48% of all groups in the road counts (28% of all animals seen), vs. only 36% in the main study area (17% of all animals). Correspondingly, the combined proportion of group types II-IV is higher in the main study area. This difference is tentatively explained as follows. Probably as a consequence of favorable habitat conditions the main study area contains relatively more ♀♀ than other areas. The sex ratio—(♂♂ a + ♂♂ sa) : ♀♀—for the data in Table 3 (road counts) is 104 :100, for those in Table 4 (main study area) it is 62 :100. It is difficult to judge to what extent this difference is real or a result of bias inherent in the sampling procedure. It is possible, for instance that the park roads travelled during the counts accidentally traverse a higher proportion of habitat favored by ♂♂ (or avoided by ♀♀), or that ♂♂, being larger and bearing horns, are more readily detected than ♀♀ under the circumstances of the road counts.

In addition, it should be pointed out that all but one of the groups numbering over nine animals in the main study area were seen between January and March 1971, when feed-

TABLE 4. GROUP SIZE AND COMPOSITION: DATA FROM THE MAIN STUDY AREA, MAY 1970-APRIL 1971

| No. of animals in group | Group type* |  |  |  |  | No. of groups | % of all groups | No. of animals | % of all animals |
|---|---|---|---|---|---|---|---|---|---|
|  | I |  | II | III | IV |  |  |  |  |
|  | a | sa |  |  |  |  |  |  |  |
| 1 | 92 | 69 | 43 | – | – | 204 | 32.64 | 204 | 10.40 |
| 2 | 35 |  | 62 | 4 | 10 | 111 | 17.76 | 222 | 11.31 |
| 3 | 17 |  | 57 | 18 | 33 | 125 | 20.00 | 375 | 19.11 |
| 4 | 4 |  | 27 | 9 | 20 | 60 | 9.60 | 240 | 12.23 |
| 5 | 4 |  | 15 | 3 | 17 | 39 | 6.24 | 195 | 9.94 |
| 6 | – |  | 6 | 7 | 11 | 24 | 3.84 | 144 | 7.34 |
| 7 | – |  | 9 | 5 | 11 | 25 | 4.00 | 175 | 8.92 |
| 8 | 1 |  | 1 | 2 | 8 | 12 | 1.92 | 96 | 4.89 |
| 9 | 1 |  | 1 | 2 | 2 | 6 | 0.96 | 54 | 2.75 |
| 10 | – |  | – | – | 4 | 4 | 0.64 | 40 | 2.04 |
| 11 | – |  | – | – | 4 | 4 | 0.64 | 44 | 2.24 |
| 12 | – |  | – | 1 | – | 1 | 0.16 | 12 | 0.61 |
| 13 | – |  | – | – | 1 | 1 | 0.16 | 13 | 0.66 |
| 14 | – |  | – | 1 | 2 | 3 | 0.48 | 42 | 2.14 |
| 15 | – |  | – | – | 2 | 2 | 0.32 | 30 | 1.53 |
| 16 | – |  | – | – | 1 | 1 | 0.16 | 16 | 0.82 |
| 18 | – |  | – | – | 2 | 2 | 0.32 | 36 | 1.83 |
| 24 | – |  | – | – | 1 | 1 | 0.16 | 24 | 1.22 |
| No of groups in group type | 223 |  | 221 | 52 | 129 | 625 | 100.00 |  |  |
| % | 35.68 |  | 35.36 | 8.32 | 20.64 | 100.00 |  |  |  |
| No. of animals in group type | 335 |  | 637 | 250 | 740 |  |  | 1962 | 99.98 |
| % | 17.07 |  | 32.47 | 12.74 | 37.72 |  |  | 100.00 |  |
| Mean group size | 1.50 |  | 2.88 | 4.81 | 5.74 |  | overall 3.14 |  |  |

*see text

ing conditions were favorable locally. The data in Table 4 may well be unduly biased in favor of large groups.

With regard to the mean size of each group type, Tables 3 and 4 are in good agreement on general trends, though not on actual values (for reasons just explained). Pure ♂-groups are by far the smallest on average, followed by pure ♀-groups, 'harem' and mixed groups (as mentioned earlier, group types III and IV are really combinations of types I and II). Particularly noteworthy is the high incidence of single animals in group type I; nearly three-quarters of all ♂-groups recorded consisted of a single ♂, as follows:

| | | | | |
|---|---|---|---|---|
| Road counts: | single ♂♂ a | = 38.7% | of ♂-groups | = 18.5% of all groups |
| | " ♂♂ sa | = 34.7% | " " | = 16.6% " " " |
| Study area: | " ♂♂ a | = 41.3% | " " | = 14.7% " " " |
| | " ♂♂ sa | = 30.9% | " " | = 11.0% " " " |

By contrast, single ♀♀ make up only 7.6% of all groups in the road counts and 6.9% of all groups in the main study area. The differences in the frequency of single ♂♂, as between the road counts and the main study area, can probably be explained by the

TABLE 5. GROUP COMPOSITION AND STABILITY: ALL OBSERVATIONS OF ♀ 2

(Figures = individual numbers of known animals: X = animal unknown or not seen well)

| Obs. No. | Date | ♂a | ♂♂ sa + ♂♂ j | ♀♀ | Juv | No. of animals in group |
|---|---|---|---|---|---|---|
| 1 | 4.11.68 | X | 3 | X | X,X | 7-9 |
| 2 | 9.11. | – | — | 3,X,X | X | 6 |
| 3 | 10.11. | 7 | 3 | 3,X | X,X | 7 |
| 4 | 13.11. | 7 | 3 | 3,6,9 | X,X | 8 |
| 5 | 17.11. | — | — | 3,5,6,9 | ? | 8 |
| 6 | 20.11. | 7 | 3 | 3,4,X,X,X | X,X | 10 |
| 7 | 21.11. | – | 3 | 3,4,6,X | X,X | 8 |
| 8 | 22.11. | — | – | 3,X | X,X | 5 |
| 9 | 22.11. | – | 3,9 | 4,6,9,X | X | 8 |
| 10 | 24.11. | – | 3 | 3,4,X | X,X | 7 |
| 11 | 25.11. | – | 3,9 | 9,X,X | X | 7 |
| 12 | 27.11. | 7 | 3 | 3+? | ? | 8 |
| 13 | 14.3.69 | – | X | X | – | 3 |
| 14 | 15.3. | – | X,X | X | – | 4 |
| 15 | 12.5. | 7 | 9,19 | 3,6 | 1 | 7 |
| 16 | 14.5 | – | X,X | 3,6 | X | 6 |
| 17 | 15.5. | 7 | X,X | 3,6 | X | 7 |
| 18 | 16.5. | — | X | 3 | – | 3 |
| 19 | 19.5. | 7 | 9,X | 3,6 | X | 7 |
| 20 | 25.5. | — | — | — | — | 1 |
| 21 | 3.6. | 7 | 9,X | 3,6,9,X,X | 1 | 10 |
| 22 | 19.6. | 7 | 3,9,19 | 3,6,9 | 1 | 9 |
| 23 | 2.7. | – | – | – | – | 1 |
| 24 | 12.10. | – | X,X | 4,X,X | – | 6 |
| 25 | 31.10. | X | X | 17,19,X,X,X,X,X | X,X | 12 |
| 26 | 5.11. | 30 | — | 4,9,X,X | — | 6 |
| 27 | 7.11. | 30 | – | — | — | 2 |

fact that, with proportionately more ♀♀ in the main study area (see above), there are more opportunities for ♂♂ to join a ♀-group. This would account for the generally lower proportion of single ♂♂ in this area. It is also interesting to note that among ♂♂ sa the frequency of single animals is lower than among ♂♂ a. (see Tables 8 & 9 below)

On the whole, the data from the road counts are probably more representative of the kudu population of Tsavo National Park than the data from the main study area which, in turn, illustrate the possible range of variation under favorable environmental conditions.

### B. Relations between ♀♀

As a large proportion of the animals inhabiting the main study area were known individually, it was possible to analyze the composition and stability of ♀-groups, at least to some extent (subject to the limitations of the method used). To illustrate this aspect of the social organization I tabulated all observations of some of the known ♀♀ sighted most frequently. Two selected examples of these records are given in Tables 5 and 6. They were chosen because (a) they represent conditions in different habitat types (see I.B) and (b) they show the general tendencies evident from the main body of relevant data.

Table 5 gives data on 27 sightings of ♀ 2 in the area of the Voi River Circuit (Figs. 2 and 5). Prominent among the animals accompanying ♀ 2 are ♀ 3 and ♀ 6, to a lesser extent also ♀ 9. ♀ 3 and ♀ 6 were seen last on 2.8. 69 and presumably died soon afterwards, so only observations 1-23 of Table 5 need be considered. Out of these, ♀ 2 was associated 16 times with ♀ 3, and possibly another 5 times when ♀ 3 may have been present but was not recognized. ♀ 6 was first identified on 13.11. 68, so only observations 4-23 are relevant. Out of these 20 occasions, ♀ 6 was with ♀ 2 certainly in 10 cases, and possibly in another 8 (but not identified). While the total number of ♀ in groups including ♀ 2 varied from 1-9, and at least seven other known, and some unknown, ♀♀ were seen associated with ♀ 2, the data in Table 5 suggest that there may have been a 'nuclear group', consisting of ♀ 2, ♀ 3 and ♀ 6, which was fairly stable over about 8 months (there are, of course, considerable gaps between subsequent observations, precluding final conclusions). Members of another group living partly in the same area behaved similarly: ♀ 19 was seen 17 times between 20. 5. 69 and 22.4. 71. On 10 occasions she was certainly, on another 4 possibly, associated with ♀ 18.

Table 6 lists 45 observations of ♀ 41, spread over nearly 18 months. During this time, ♀ 41 was seen in groups of 1-24 animals (including ♂♂), in the company of at least 22 other known ♀♀ and some unknown ones. However, she associated most frequently with ♀ 24 and ♀ 25, as follows: out of the 45 observations, she was accompanied 21 times by ♀ 24 and 23 times by ♀ 25 (on 16 of these occasions by both). This association was much more consistent after 31. 8. 70 than before. The following details from the life history of ♀ 41 may explain this. On 4. 12. 69 a small young one, estimated about a week old, followed her (J10 in Table 6); during the next 8 months she was always accompanied by J10 and usually by ♂ 48, presumably her previous young. Only on 5 out of 17 occasions between 4. 12. 69 and 9. 8. 70 was ♀ 41 associated with other ♀♀. However, on 7. 8. 70 J10 was seen for the last time; it probably died soon afterwards. On 28.8.70 ♀ 41 gave birth to another young, but it was killed by Martial Eagles (*Polemaetus bellicosus*) on its first day of life. After that, ♀ 41 accompanied other ♀♀, particularly ♀ 24 and ♀ 25, in all but one of the 24 subsequent sightings (Table 6). These observations suggest that a ♀ having a young at heel leads a more solitary life but joins other ♀♀ when the young is lost. But this is not invariably so. Other ♀♀ may rejoin a ♀-group as soon as the young is able to follow, or sometimes even earlier, while the young is 'lying out' (Gosling, 1969; *'Abliegen'* of Walther, 1964; see also Leuthold, 1971c).

More data on relations between ♀♀ are available but cannot be treated in detail here. On the whole, they confirm the general picture emerging from the above examples. We may thus summarize relations between ♀♀, as follows.

While a given ♀, over a period of time, associates with a considerable number of other ♀♀, within her 'core area' (see II. A), she may have a few 'close friends' with which she forms a temporarily stable 'nuclear group'. Factors of the habitat are probably

TABLE 6. GROUP COMPOSITION AND STABILITY: ALL OBSERVATIONS OF ♀ 41
(Figures = individual numbers of known animals: X = animal unknown or not seen well)

| Obs. No. | Date | ♂ a | ♂♂ sa + ♂♂ j | ♀♀ | Juv | No. of animals in group |
|---|---|---|---|---|---|---|
| 1 | 4.11.69 | – | 22,48* | 12,22,24,25 | 5,X | 9 |
| 2 | 4.12. | – | – | – | 10† | 2 |
| 3 | 11.3.70 | – | 48 | – | 10 | 3 |
| 4 | 16.3. | – | 48 | – | 10 | 3 |
| 5 | 22.3. | – | 48 | – | 10 | 3 |
| 6 | 3.4. | – | 48,X | 15,22,36,37, X,X,X | 8,10,X | 13 |
| 7 | 12.4. | – | 48 | – | 10 | 3 |
| 8 | 14.4. | – | 48 | – | 10 | 3 |
| 9 | 15.4. | – | 22,48 | – | 10 | 4 |
| 10 | 16.4. | – | 48 | – | 10,X | 4 |
| 11 | 5.6. | – | – | 22,24,25,X | 10,X,X | 8 |
| 12 | 6.6. | – | – | 22, 24, 25, X | 10,X | 7 |
| 13 | 28.6. | – | – | 12,22 | 10 | 4 |
| 14 | 16.7. | – | 48,78 | – | 10 | 4 |
| 15 | 6.8. | – | 48,79 | 24 | 10,X | 6 |
| 16 | 7.8. | – | 48 | – | 10 | 3 |
| 17 | 8.8. | 66 | 48,78,79 | – | – | 5 |
| 18 | 9.8. | – | 48 | – | – | 2 |
| 19 | 28.8. | X | 48,79 | – | X‡ | 4 |
| 20 | 29.8. | – | 48 | 24,25,36,49 | 15,X | 8 |
| 21 | 31.8. | – | – | – | – | 1 |
| 22 | 6.9. | – | – | 24 | 15 | 3 |
| 23 | 19.9. | – | 48,79 | 25 | – | 4 |
| 24 | 20.10. | – | 48,79 | 24,25 | – | 5 |
| 25 | 20.10. | – | 48,79 | 25 | – | 4 |
| 26 | 4.11. | – | – | 24,25 | 15 | 4 |
| 27 | 4.11. | – | – | 24,25 | 15 | 4 |
| 28 | 6.11. | X | 48 | 24,25 | 15 | 6 |
| 29 | 20.11. | 55 | 48, X | 24,25 | – | 6 |
| 30 | 23.11. | – | – | – | – | 1 |
| 31 | 2.1.71 | – | – | 12,24,25 | X | 5 |
| 32 | 11.1. | – | X, X,X | 15,24,37,50,57 | 22 | 10 |
| 33 | 11.1. | – | – | 15,24,37,50,57 | 22 | 7 |
| 34 | 17.1. | 28 | X | 22,25,35,42,X,X | 29,30, X,X,X | 14 |
| 35 | 18.1. | 27,55 | 20,61,91,122, X,X | 12,24,25,37,43, 47, 50, 87, 89, X, X, X,X | 22,23 | 24 |
| 36 | 19.1.71 | – | 48 | 12,25,50,89,95 | 22,23, 29 | 10 |
| 37 | 27.1. | 28 | 79 | 25 | – | 4 |
| 38 | 23.2. | – | 48,79 | 25,49,88 | – | 6 |
| 39 | 4.3. | 85 | 91 | 24,25,42,46, 47,49,57,58, 59,88,89,X,X | – | 16 |
| 40 | 13.3 | – | 108,122 | 24,25,49,88 | – | 7 |
| 41 | 17.3. | – | – | 24,X | – | 3 |
| 42 | 18.3. | – | – | 25,25,49,88 | – | 5 |
| 43 | 28.3. | – | – | 25,96,X | X, X,X | 7 |
| 44 | 19.4. | 55 | – | 24,25 | – | 4 |
| 45 | 23.4. | 55 | – | 24,25 | – | 4 |

* ♂ 48 probably young of ♀ 41
† J10 certainly " " "
‡ newborn young of ♀ 41 (dying).

important in determining the degree of group stability that can be achieved, e.g. the area of the Voi River Circuit with its evergreen vegetation presumably favors the formation of relatively stable groups. At the time of parturition a ♀ may separate from her companions and remain alone with her offspring for a variable period of time. When the young is older, or when it dies, she rejoins the other ♀♀. A few observations suggest that at least some of the 'nuclear groups' consist initially of mother-daughter or sister-sister units. This kind of group formation probably occurs in many ungulates (e.g. Schloeth, 1966).

### C. Relations between ♂♂ and ♀♀

Two basic types of relationships between ♂♂ and ♀♀ are distinguished here: (a) a 'family bond' between a ♀ (and her group) and her male offspring; (b) 'sexual attraction' between ♂♂ a and/or ♂♂ sa on one hand, and a ♀ or a ♀-group on the other hand.

While these two types may not encompass or adequately describe the entire range of possible relations between ♂♂ and ♀♀, they can at least serve as useful working categories. In the course of a young male's maturation, the two types may temporarily exist side by side and thus become blurred. These limitations must be kept in mind during the following discussion of ♂-♀-relations.

#### *1. Relations of type (a)*

A newborn young depends on its mother for survival during a certain period of time. It will usually associate with her beyond the stage of actual dependence, forming part of her 'nuclear group'. This relationship is essentially the same for male and female offspring. But while a young ♀ presumably remains in her mother's group later on (actual proof of this is still lacking for lesser kudu), a young ♂ eventually separates from it and either joins other young ♂♂ or remains solitary for some time (see Tables 7 & 8). The exact age at which this happens probably varies considerably; a few observations suggest that young ♂♂ leave their mother's group at about 1½ to 2 years of age. They may, on occasions, rejoin the group temporarily, but their relation has then usually changed from type (a) to type (b), as far as may be concluded from their behavior towards the ♀♀. Familiarity with the individuals in the mother's group could also be an important factor influencing association with a ♀-group.

The development just outlined is documented by the observations on ♂ 9 (Table 7). When first seen, he was estimated to be 6-8 months old and, during the following 9 months, was always seen with the same ♀-group which presumably included his mother (see also Table 5). Of the following 11 occasions, he was with a ♀-group only 3 times, once alone and 7 times with other ♂♂ sa (cf. Table 8). There is, unfortunately, a large gap in sightings of ♂ 9 between December 1969 and November 1970.

To further illustrate this change of association in young, I tabulated observations of 18 known ♂♂ sa according to group types (Table 8). The ♂♂ sa are subdivided into a 'younger' and an 'older' class. The 'younger' ones are those first seen as juveniles in a ♀-group. For each of them a point in time was chosen after which he was treated as a ♂ sa rather than a ♂ j, around 1-1½ years of estimated age (the choice of this point was somewhat arbitrary, as ages were not accurately known for any of these ♂♂). Two things are evident from Table 8: (1) there is considerable individual variation in the frequency of occurrence in the three group types distinguished, even within the two age classes; (2) the younger ♂♂ sa associated much more frequently with ♀-groups than the older ones, which tended to join other 'independent' ♂♂ more often. These differences illustrate the gradual nature of the separation of a ♂ sa from his mother's group.

#### *2. Relations of type (b)*

Table 8 shows that the older ♂♂ sa were seen with ♀-groups in about one-third of all observations. While some of these associations may have had other motivations, the majority presumably resulted from sexual attraction. When in company of ♀♀, a ♂ sa often approaches one of them from behind, induces her to urinate then shows 'Flehmen'; he may also rub his head against her hindquarter or flank as in premating behavior (Walther, 1964). Essentially the same behavior is shown by ♂♂ a accompanying a ♀-group (actual mating has not yet been observed).

In fact, there is no obvious difference between ♂♂ a and ♂♂ sa in their visible relations to ♀-groups. Also, ♂♂ a and ♂♂ sa cannot always be clearly distinguished, as the development of physical traits characteristic of adult ♂♂ (horn length, thick neck) is gradual.

Table 9 summarizes all sightings of 14 known ♂♂ a with regard to group type. As with ♂♂ sa, there is mucn individual variation but, on average, the ♂♂ concerned were with ♀-groups in nearly 50% of all observations. Some individuals were almost always seen with the same ♀-group, e.g. ♂ 7 (cf. Table 5; note that the group with ♀2 was also seen *without* ♂ 7 quite often); others seemed to 'drift about' between different groups. On the other hand, the ♂♂ considered in Table 9 were alone in over 40% of all sightings. It would, however, lead too far to discuss all relevant observations in detail.

We may summarize relations between ♂♂ and ♀♀ as follows. Once the initially strong 'family bond' between a ♀ and her male offspring is loosened, associations between individual ♂♂ (a + sa) and ♀-groups become relatively casual, and there is no evidence indicating a firm bond between a given ♂ and a given ♀-group. The formation and dissolution of such associations may be influenced considerably by environmental factors such as feeding conditions and resultant movements of individuals or groups, as described in section II. C.

TABLE 7. GROUP COMPOSITION AND STABILITY: ALL OBSERVATIONS OF ♂ 9

(Figures = individual numbers of known animals: X = animal unknown or not seen well)

| Obs. No. | Date | ♂a | ♂♂sa+♂♂j | ♀♀ | Juv | No. of animals in group |
|---|---|---|---|---|---|---|
| 1 | 14.11.68 | 7 | — | 5,6,X,X | X | 7 |
| 2 | 22.11. | — | 3 | 2, 4, 6, 9, X | X | 8 |
| 3 | 25.11. | — | 3 | 2,9,X,X | X | 7 |
| 4 | 12. 5.69 | 7 | 19 | 2,3,6 | 1 | 7 |
| 5 | 19.5. | 7 | X | 2,3,6 | X | 7 |
| 6 | 21.5 | — | ? | 3,6, ? | X | 4(?) |
| 7 | 23.5 | — | 19 | 3,4,6 | X | 6 |
| 8 | 2.6. | 7 | X | 2,3,6,9,X,X | 1 | 10 |
| 9 | 19.6. | 7 | 3,19 | 2,3,6,9 | 1 | 9 |
| 10 | 2.8. | 30 | 19 | 3,6,9,X,X | 1 | 9 |
| 11 | 3.11. | — | 3 | — | — | 2 |
| 12 | 7.11. | — | — | 4,9,X,X,X,X,X | 4,X | 10 |
| 13 | 9.12. | — | — | — | — | 1 |
| 14 | 13.11.70 | — | 119 | 84,X,X,X | — | 6 |
| 15 | 24.12. | 121 | X | — | — | 3 |
| 16 | 15. 1. 71 | — | 40,124 | 9, 27, X | 28,X | 8 |
| 17 | 18.1. | — | 124 | — | — | 2 |
| 18 | 26.1. | 11 | 40, 76, 77, 119,124,X | — | — | 8 |
| 19 | 27. 1. | — | 40,76,119 124 | — | — | 5 |
| 20 | 23.2. | 11 | 124 | — | — | 3 |
| 21 | 7.3. | — | 124 | — | — | 2 |

## D. Relations among ♂♂

The social organization of most ungulates is expressed primarily by the behavior and relationships between ♂♂a, within the framework of a given environment. Studying the interactions between ♂♂a is, therefore, essential for understanding the social organization. Unfortunately, only few encounters between ♂♂a, or even between ♂♂a and ♂♂sa, were witnessed during this study; also, no fight has been seen to-date. The following account is, therefore, provisional.

A comparison of the data in Tables 8 and 9 indicates that ♂♂sa, particularly the older ones, tend to associate with other ♂♂ considerably more than do ♂♂a. The latter are, in turn, found singly much more often than ♂♂sa. Groups including more than one ♂a are very rare; in the few cases I saw (e.g. ♂2, ♂7 and an unknown ♂a together on 4. 6. 69; ♂ 28 and ♂ 55 together on 3. 4. 71) relations between the ♂♂a concerned were not clear. No overt antagonism was evident but, possibly, they were too disturbed by the presence of a vehicle to show 'their real feelings' toward each other.

Most ♂-groups numbering two or more animals consist of ♂♂sa with, at the most, one ♂a. The same applies to mixed groups (type IV). Within these it is also rare to find a ♂a and a relatively old, i.e. nearly adult, ♂sa together. If it does occur, the ♂a usually tries to chase away the ♂sa and, in the few cases I have seen, the latter gave way and either disappeared or kept at some distance. The same happened in the only instance

TABLE 8. GROUP TYPES IN WHICH 18♂♂ sa WERE SEEN, AND PERIODS OVER WHICH RECORDS WERE OBTAINED

| ♂ No. | Alone | With other ♂♂ | With ♀-group or mixed group | Total | Months under observation |
|---|---|---|---|---|---|
| 3 | 3 | 2 | 1 | 6 | 6 |
| 9 | 1 | 7 | 3 | 11 | 17 |
| 22 | 1 | – | 6 | 7 | 9 |
| 41 | 1 | – | 8 | 9 | 13 |
| 48 | 8 | 2 | 19 | 29 | 9 |
| 54 | – | – | 17 | 17 | 6 |
| 71 | 1 | – | 16 | 17 | 4 |
| 119 | 1 | 2 | 3 | 6 | 2 |
| Total 'younger'* | 16 | 13 | 73 | 102 | |
| % | 15.69 | 12.74 | 71.57 | 100.00 | |
| 20 | 4 | 11 | 8 | 23 | 18 |
| 40 | – | 4 | 3 | 7 | 15 |
| 53 | 4 | 6 | 5 | 15 | 13 |
| 61 | – | 6 | 1 | 7 | 12 |
| 73 | 4 | – | 3 | 7 | 2 |
| 76 | 1 | 7 | – | 8 | 6 |
| 101 | 3 | 2 | 2 | 7 | 6 |
| 102 | – | – | 7 | 7 | 7 |
| 108 | 1 | 4 | 3 | 8 | 6 |
| 124 | 1 | 6 | 1 | 8 | 3 |
| Total 'older'* | 18 | 46 | 33 | 97 | |
| % | 18.56 | 47.42 | 34.02 | 100.00 | |
| Total overall | 34 | 59 | 106 | 199 | |
| % | 17.08 | 29.65 | 53.27 | 100.00 | |

*See text

TABLE 9. GROUP TYPES IN WHICH 14♂♂a WERE SEEN AND PERIODS OVER WHICH RECORDS WERE OBTAINED

| ♂ No. | Alone | With other ♂♂ | With ♀-group or mixed group | Total | Months under observation |
|---|---|---|---|---|---|
| 2 | 8 | 1 | 4 | 13 | 16 |
| 7 | 1 | 1 | 13 | 15 | 7 |
| 11 | 5 | 4 | 3 | 12 | 28 |
| 17 | 17 | – | 8 | 25 | 19 |
| 27 | 3 | 4 | 4 | 11 | 5 |
| 28 | 15 | 1 | 10 | 26 | 21 |
| 30 | 2 | – | 11 | 13 | 17 |
| 31 | 8 | – | 1 | 9 | 6 |
| 44 | 3 | – | 2 | 5 | 1 |
| 51 | 7 | 2 | 21 | 30 | 17 |
| 55 | 16 | 5 | 14 | 35 | 13 |
| 66 | 5 | 2 | 7 | 14 | 6 |
| 85 | 3 | 3 | 15 | 21 | 8 |
| 121 | 6 | 2 | 1 | 9 | 3 |
| Total | 99 | 25 | 114 | 238 | |
| % | 41.60 | 10.50 | 47.90 | 100.0 | |

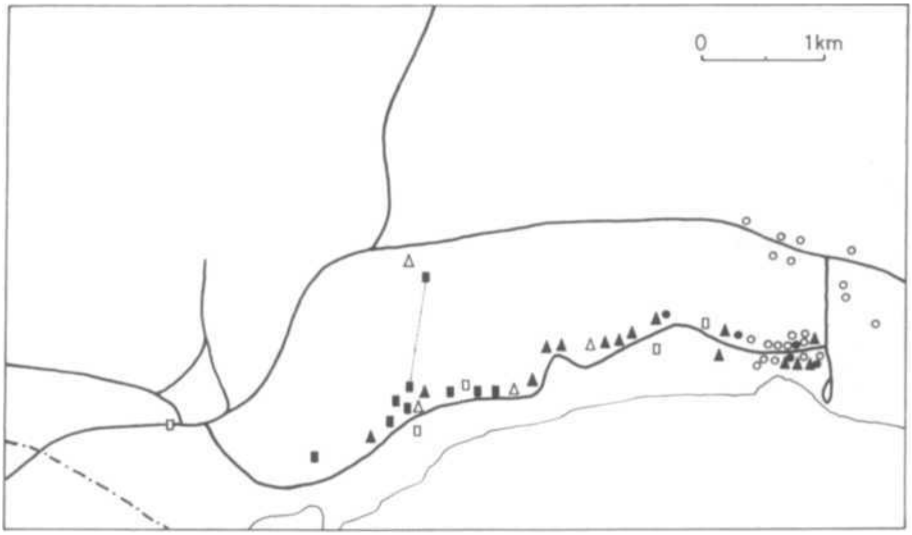

Fig. 7. Sighting locations of four known ♂♂a on the Voi River Circuit.

▲ = ♂7, up to 19.6.69 △ = ♂28, 26.6.69 - 18.3.70
■ = ♂2, up to 19.6.69 □ = ♂2, 19.6.69 - 18.3.70
● = ♂17, up to 19.6.69 ○ = ♂17, after 19.6.69

For further explanations see text.

in which I saw two apparently adult ♂♂ accompanying a mixed herd (♂27 and ♂55 on 18. 1. 71, see Obs. No. 35 in Table 6); ♂55 avoided contact or interference with ♂27 who was probably the older of the two.

From the above, it appears that ♂♂a do not associate with one another but tend to keep separate. Also, they restrict their activities to relatively small home ranges (Table 2, Fig. 3) and usually stay within their respective 'core areas' (see II. A). However, as shown earlier (Fig. 3), the home ranges of several ♂♂a overlap considerably, some nearly entirely. To explore the possibility that the overlap in space might be compensated for by some degree of separation in time, I plotted sighting locations of four ♂♂a inhabiting the Voi River Circuit area, taking into account the dates of observations (Fig. 7). The four were seen as follows (cf. Table 2):

♂7: 15 times up to 19. 6. 69, he probably died soon afterwards;

♂2: 8 times before 19. 6. 69, 5 times afterwards, up to 18. 3. 70;

♂17: 5 times before 19.6.69,21 times afterwards;

♂28: 4 times between 26. 6. 69 and 18. 3. 70 (for comparison with ♂2; he was seen another 22 times later on).

Figure 7 shows that ♂2 and ♂7 utilized partly the same area between 10. 11. 68 and 19. 6. 69, thus overlapping in time as well as in space. The same applies to ♂7 and ♂17 between 1. 4. 69 and 19. 6. 69, and to ♂2 and ♂28 between 26. 6. 69 and 18. 3. 70. A similar situation involved three other ♂♂a in another area (♂27, ♂51 and ♂55, cf. Fig. 3 and Table 2).

The main difficulty in interpreting these data are: (a) the small number of sightings of each ♂a within the period considered; and (b) the fact that the different ♂♂a were only rarely seen on the same day or within only a few days. Their separation — in time or in space — may have been more complete than is evident from the data in Fig. 7 (and others). But even if sightings of two or more of them on the same days are compared individually, no clear-cut trend emerges. Possibly, the ♂♂a in question 'know' their status relative to others in the same area and actively try to avoid meeting each other when they become aware of another one's presence near-by.

As far as the available data permit conclusions, the social organization of lesser kudu appears to be rather indistinct (or very flexible) and does not readily fit one of the two types prevalent among other bovids, viz. territoriality or a dominance hierarchy. This will be discussed further below (IV. C).

## IV. DISCUSSION

### A. Environment and social organization

Attention has repeatedly been drawn to the possible influence of the environment on the social organization (e,g. II. B,III. A,B). Variations in the social organization of a given species in differing habitats have been described, among African antelopes, on the largest scale in wildebeest: (*Connochaetes taurinus:* Estes, 1969; Watson, 1969), and to a lesser extent in impala (*Aepyceros melampus:* Leuthold, 1970b; P. J. and M. V. Jarman, pers. comm. and in preparation) and in the Uganda kob (*Adenota kob:* Leuthold, 1966). Under adverse conditions a well-defined social organization may break down temporarily, as in impala (M. V. Jarman, 1970) or Uganda kob. For many species, including lesser kudu, the extent of such variations and their expression are not yet known, for lack of comparative studies of the same species in different habitats.

In most cases, the proximate factor influencing the social organization appears to be the available food (and water) supply. If food is scarce or seasonally limited, home ranges must be larger or shifted seasonally, leading to movements and migrations. In areas with less favorable environmental conditions than my study area (see I. B), lesser kudu may well have larger home ranges and more pronounced seasonal movements than those described in this paper. This assumption is supported by a few cases in which unknown but well-marked kudu suddenly appeared within the study area but were seen only once or for a short time. Group size and composition, too, may vary locally and/or seasonally. In a habitat with scarce or erratic food supply, flexibility of the social organization is vital to survival. It would be interesting, in this context, to know more about the sociology of desert ungulates.

One aspect of environmental influences on social organization is closely linked to reproduction, especially its seasonal distribution. In tropical areas, this may take one of three forms: (1) strictly seasonal, i.e. breeding limited to a particular, usually fairly short, period of the year; (2) partly seasonal, i.e. breeding throughout the year but with seasonal peaks; (3) non-seasonal, i.e. breeding more or less continuous the year around. The environmental agents responsible for a particular breeding pattern, and the ways in which they act, are not yet fully understood. On occasions, strictly and partly seasonal breeders share the same habitat in which species with non-seasonal reproduction may occur as well. The social organization of any species can be considered as a system providing a framework within which reproduction can take an orderly course. In seasonal breeders, it is best defined during the mating season and may, but need not, break down or be replaced by some other system at other times. It is, therefore, essential to have at least a general idea of the breeding pattern of a species whose social organization is to be studied. However, such information is often difficult to obtain beforehand. The few observations available for lesser kudu suggest that, in Tsavo National Park, it breeds throughout the year, but it is uncertain whether there are seasonal peaks. This would mean that the social organization is unlikely to change significantly in the course of a year and, indeed, no evidence for such changes (except on a very small scale, see II. C) has been found so far.

### B. Comparison with other Tragelaphines

As indicated earlier (I. A), little information is available on the social organization of free-ranging Tragelaphines (eland and bongo, *Boocercus euryceros,* are not considered here). This is, for the most part, due to the habitat preferences of these species, which render observation of undisturbed individuals or groups difficult and very time-consuming. To my knowledge, only one field study involving detailed observations on sociology of a *Tragelaphus* species has been carried out so far (Allsopp, 1971). The following comparison is, therefore, by necessity, somewhat fragmentary and limited in scope.

#### Greater kudu (*T. strepsiceros*)

Except for the bushbuck, the greater kudu is most widely distributed. Its social organization may, therefore, vary in different parts of its range, perhaps more than in the other species. For the northern races Drake-Brockman (1910) mentions groups of one ♂a and 3-4 ♀♀ and young, also mixed groups of several ♂♂sa and ♀♀. Astley Maberly (1960) gives herd sizes of 6-20 animals, usually mixed (♂♂sa, ♀♀, juv), sometimes accompanied by one ♂a; other ♂♂a and ♂♂sa form groups of up to 10 individuals, while 'very big old bulls are often solitary' (p. 37). In the southern parts of the species' range greater kudu occur usually in groups of less than 10 which occasionally—in the dry season—join to form herds of nearly 30 animals; ♂♂a are usually seen alone (F.C. Selous, quoted in Lydekker, 1926). More recent information was gathered during tsetse control operations in Zambia (Wilson, 1965) and Rhodesia (Simpson, 1968). Wilson recorded groups of 1-11 animals, many mixed (type IV in this paper), with an average size of 4. 2. In Rhodesia, group size varies seasonally, apparently in relation to reproduction (Simpson, 1968).

As far as can be concluded from this limited information, group structure in greater kudu is similar to that in lesser kudu, but groups are apparently somewhat larger. As for the social organization, the few general accounts available suggest that it may also be similar to that of the lesser kudu, but probably subject to more pronounced seasonal variations in the southern part of the species' range.

#### Mountain nyala (T. *buxtoni*)

The only recent account dealing with field observations on this rare and local species (Brown 1969) gives group sizes of 1-13, with an average of 5.7 (49 groups). Usual group size is said to be 4-6, herds of over 10 animals being rare. 'Mature, but not old, bulls' (presumably older ♂♂sa) form small groups, while 'really old bulls' generally remain alone. About half of the ♀-groups seen were accompanied by 'a bull'. Obviously, no conclusions regarding the social organization can be drawn from these data.

### Nyala (*T. angasi*)

Although this species lives in somewhat more accessible areas than the preceding one, even less is known about its biology and, particularly, sociology. Lydekker (1926) quotes accounts by several early authors indicating that nyala form small herds, partly mixed, of up to 16 animals. The only recent publication on nyala (Vincent *et al.,* 1968) does not refer to the social organization.

Dorst and Dandelot (1970) state that herds of up to 30 head may occur and that the nyala's 'habits in general resemble those of the lesser kudu' (p. 196, original source not quoted).

### Sitatunga (*T. spekei*)

The only report on this species published to-date (Owen, 1970) indicates group sizes and composition very similar to my data on lesser kudu, except that groups are slightly smaller (average 1. 9, range 1-9; one group of 11 reported in addition). Also, single ♂♂a (8. 4% of all groups) and single ♂♂sa (8. 6%) are less common than in lesser kudu (see III. A), while single ♀♀ are considerably more frequent in sitatunga (22.6% of all groups).

On the basis of these data one might assume the social organizations of sitatunga and lesser kudu to be quite similar. However, in view of its very specialized habitat and way of life, the sitatunga cannot be compared to other species without reservations.

### Bushbuck (*T. scriptus*)

The bushbuck is generally considered to be a solitary animal, groups of over three being very rare. In the Albert National Park, Congo, 36 out of 44 sightings (= 82%) concerned single, the remainder two animals (Bourlière and Verschuren 1960). In a sample of 74 groups in Zambia, 53 (= 72%) were single animals, 19 (= 26%) consisted of two, and one each of three and four animals (Wilson and Child, 1964; see also Elder & Elder 1970). Bushbuck are also closely attached to a given locality (Astley Maberly, 1960);Verheyen (1955) considered them to be territorial.

Allsopp (1971) studied the social organization of bushbuck in Nairobi National Park, Kenya, using the same method as I did for lesser kudu. His main findings are as follows: 54% of all groups consisted of one animal, 33% of two; two groups (= 0. 5%) contained five animals. Home ranges measured 0. 25 ha in ♀♀, 0. 56 ha in ♂♂a and 2. 0 ha in ♂♂sa. These sizes are only a fraction of those found in lesser kudu (the difference in body size between the two species and factors of the habitat may account for much of this discrepancy), but the differences between sex and age classes show the same trends, being perhaps more pronounced in bushbuck. Overlap of home ranges is evident in ♂♂sa (Fig. 15 *op. cit.*), but not in ♂♂a; however, this point does not appear to have received particular attention. Also, 'male bushbuck do not defend an area but rather an association with a ♀' (p. 64 *op. cit.*).

Most of Allsopp's observations and conclusions with regard to the bushbuck are in line with my own on lesser kudu. This suggests that, apart from group size, the social organizations of the two species are very similar.

### Conclusion

It must be emphasized that none of the studies quoted above, except for Allsopp's on bushbuck, used known individuals to determine their use of space and their social habits. The limited information available suggests that group structure is similar in all *Tragelaphus* species, while group size decreases from greater kudu/mountain nyala through lesser kudu/nyala (exact sequence unknown and perhaps not fixed) and sitatunga to bushbuck. Whether the similarities in group structure extend to the social organization as a whole, including the use of space, remains uncertain. Further field studies are needed to clarify this point.

## C. Comparison with other bovids

The social organizations at rutting time of most bovids studied so far readily fit into one of two categories: territoriality or a dominance hierarchy. Although there are important differences between the two, they can be regarded as aspects of the same phenomenon. In a territorial system, dominance is restricted to a given locality or area, the territory, which the occupant tries to keep free of rivals. In a hierarchy, dominance is distributed among individuals regardless of location.

Assuming that further studies will not reveal substantial deviations from the picture presented in this paper, we may characterize the social organization of lesser kudu as follows. On the one hand, it lacks the main characteristic of a dominance hierarchy, i. e. the simultaneous presence of several fully adult ♂♂ together with ♀♀ in the same herd. On the other hand, several features do not conform to conditions typical of territoriality either, e.g. the substantial overlap of home ranges of ♂♂a and the apparent lack of aggressiveness between lone ♂♂a which, if present, might indicate competition for space (the few aggressive encounters witnessed by me occurred in the presence of ♀♀). Also, olfactory skin glands and marking behavior, as well as ritualized urination and/or defecation, all of which are often—but far from always—associated with territoriality, are absent in lesser kudu and, to my knowledge, in the other *Tragelaphus* species as well. In a habitat as that of most Tragelaphines, which largely precludes constant surveillance of a given area, olfactory marking would appear to be virtually indispensable to maintain a territorial system. The social organization of lesser kudu thus does not fit into either of the two categories mentioned above; for want of a better term I call it 'intermediate' in the present context.

It is tempting, at this point, to speculate about the evolution of social organizations in bovids and their mutual relationships in general, and about the lesser kudu's place in a wider context in particular. In view of the considerable gaps still existing in our relevant knowledge, any such attempt can be neither comprehensive nor final at this stage. A possible way of illustrating the relations referred to is shown in Fig. 8. It is not meant to reflect physical phylogenetic relationships, nor does it take into account local and seasonal variations, as discussed in section IV. A.

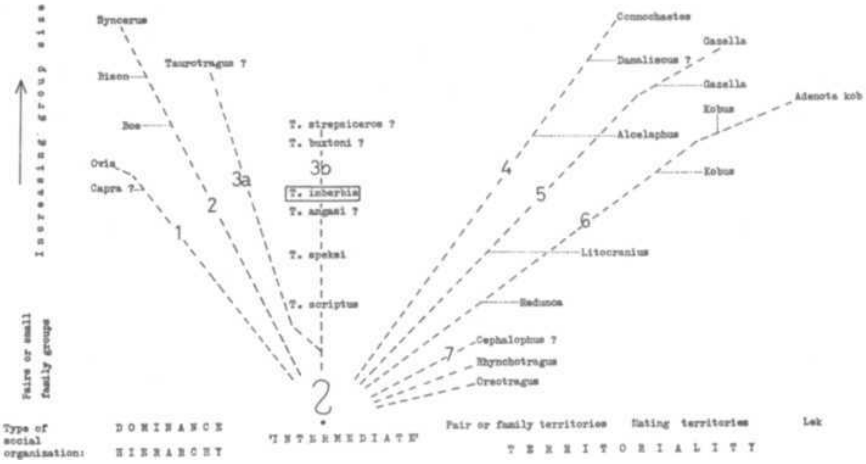

Fig. 8. Types of social organizations in bovids, and their distribution within the family.

1 = Caprinae 2 = Bovinae
3 = Tragelaphinae 3b = Tragelaphus
4 = Alcelaphinae 5 = Antilopinae
6 = Reduncinae 7 = Cephalophinae

Several subfamilies (e. g. Oryginae, Aepycerotinae, Allen, 1939) are not included, partly for want of relevant information and partly to keep the Figure reasonably clear.

Species accompanied by ? have not been studied yet in detail; their position in the Figure is based on my personal impressions or only limited information in the literature.

Figure 8 implies that the type of social organization, i.e. the distribution of territoriality and dominance hierarchy among bovids, is to some extent group-specific. While it is too early to generalize too much, available information suggests that this is largely true. In the Bovinae and Caprinae (subfamilies here according to Allen, 1939) a hierarchical organization appears to be the rule (e.g. Schloeth, 1961; Geist, 1968). On the other hand, all species of Reduncinae studied so far have been found to be territorial, viz. the waterbuck (*Kobus defassa:* Kiley-Worthington 1965; Spinage 1969; Hanks *et al.,* 1969), red lechwe (*K. leche:* de Vos and Dowsett, 1966), puku (*Adenota vardoni:* de Vos, 1965; de Vos and Dowsett, 1966), Uganda kob (*Kobus kob:* Buechner, 1961, 1963; Leuthold, 1966) and southern reedbuck (*Redunca arundinum:* Jungius, 1970). The situation appears to be similar among the Alcelaphinae (e.g. Estes, 1969; Gosling, 1969) and Antilopinae (= Gazellinae; Walther, 1968; Leuthold, 1971a). In fact, among African antelopes studied to-date territoriality is much more common than the dominance hierarchy, which probably occurs in the eland and possibly in the oryx (*Oryx beisa*), although neither species has been the subject of sociological research.

Ungulate territories can be broadly divided into three types (Fig. 8):

(1) Pair or family territories, inhabited by a single pair and its offspring, often throughout the year. This type appears to prevail among small antelopes, such as dikdik (*Rhynchotragus = Madoqua* spp.: Simonetta, 1966;Hendrichs and Hendrichs, 1971), klipspringer (*Oreotragus oreotragus:* Hendrichs, 1972), oribi (*Ourebia ourebi:* Hediger, 1951) and duikers (Cephalophinae: Rails, 1971), but little documented information is available for many of these species (cf. Walther, 1967). Reedbuck (*Redunca* spp.) approach this type (Jungius, 1970).

(2) Mating territories, held only by ♂♂a, with ♀♀ coming and going 'at will'. All the larger antelopes mentioned above (e.g. Reduncinae, Antilopinae, etc.) exhibit this type.

(3) Leks or arenas, i.e. tightly clustered mating territories in certain locations. This is known only in the Uganda kob so far; it may be considered a special case of (2).

Among the species showing a dominance hierarchy the only differentiation made is one regarding group or herd size. Even here only very general trends are indicated, and no detailed discussion of this type of social organization is intended.

Keeping in mind the reservations put forward in section IV. B, the social organizations of all *Tragelaphus* species are tentatively treated as being essentially like that of lesser kudu; they have been included in Fig. 8, accordingly, as the 'intermediate' type. The eland, although not studied yet in detail, has been entered among the species with a dominance hierarchy, departing from the pattern assumed to prevail in the Tragelaphinae (this is based on my personal impression of the eland's social organization).

The arrangement of taxa in Fig. 8 suggests a common origin of all social organizations from the 'intermediate' type represented by the Tragelaphines. This should not be construed as reflecting my firm conviction on the subject, although the possibility cannot be excluded. Some authors (e.g. Ronnefeld, 1970) consider the Tragelaphinae as a relatively 'primitive' group among the bovids. However, even if this were accepted, it does not necessarily follow that their social organization is also primitive and provided the starting point for the evolution of all other social organization in bovids. Other subfamilies, e.g. the Cephalophinae, and their social organizations might be regarded as primitive with equal justification. Also, convergent evolution in several fairly independent lines is a strong possibility.

In conclusion, it must be emphasized again that the above discussion of social organizations is largely speculative, and much more field research is required before conclusions can be reached on a more reliable basis.

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**Paper No. 10**

# On the Relationship of Ecology and Behaviour in the Evolution of Ungulates: Theoretical Considerations

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## ABSTRACT

It is possible to show from paleontological data that ungulates evolved in a predictable fashion. Lineages which evolved, changed in pre-Pleistocene epochs towards larger body size, larger and complex horn-like organs, and often greater dental specialization. Other forms remained frozen in evolutionary development over long geologic time spans. The Pleistocene accelerated evolution in the direction indicated and produced many large-bodied species with huge and bizarre horn-like organs unequalled in earlier times. An examination of the zoogeography of living and extinct forms, a consideration of bioenergetic factors impinging on the biology of periglacial and warm-climate ungulates, and a short examination of a theory explaining ungulate evolution during re-colonization of areas after glacial withdrawal, allow one to explain many aspects of ungulate evolution. It can be shown that evolutionary advancement is irreversible since breeding is the prerogative of dominant males, that evolutionary stagnation occurs in ungulates living at carrying capacity, that clines of races reflect not ecological gradients but the dispersal history of that species, that ecological **and** social specialization run parallel in the tropical climates but not necessarily in the periglacial zones, that longevity of species is related to ecological and social primitiveness, that rates of evolution were accelerated in the Pleistocene due to many glacial withdrawals which gave the opportunity to disperse, and that the bizarre, large horn-like organs are a product of the seasonal superabundance of forage in the short summer in temperate or arctic regions due to the high nutritional value of forage grown in the arctic or temperate regions as well as due to selection pressures for intense combat in colonizing, post-glacial populations.

## INTRODUCTION

In the past decade the publication of such superb texts on the paleontology of mammals as the volumes by Thenius and Hofer (1960), Orlov (1962), Romer (1966) and Kurten (1968), as well as the republication of Scott's (1937) excellent work on the history of land mammals in the western hemisphere, have placed the findings of paleontology in condensed and comprehensible form into the hands of other disciplines. The past decade also witnessed a blossoming of detailed field studies on the ecology and behaviour of large mammals. This has made it possible to begin a synthesis of the findings in these fields due to two fortunate circumstances. First, the remains of large mammals are better preserved and more numerous than those of small mammals. This has permitted the reconstruction of evolutionary lineages with adequate detail. Secondly, many large mammals possess conspicuous social adaptations in the form of antlers, ossicones, horns, tusks as well as skeletal structures apparently adapted to absorb severe impacts during intraspecific combat (Walther, 1958; Geist, 1966b, c and 1971a; Schaffer, 1968). Such structures are well preserved in the fossil record and provide considerable insight into social evolution in past epochs. This paper is a condensation of a theory linking ecological and social evolution elaborated in Geist (1971a) on the basis of studies of caprid and rupicaprid biology, and Geist (1971b) on the old-world deer, the genus *Bison* and several lineages of ungulates including proboscidians and Perissodactyls. The theory, termed the *dispersal theory* was first proposed in simplified form in Geist (1966a). It was then termed 'glaciation theory', as well as in

Geist (1971a). In addition this paper will deal with aspects treated only peripherally in the earlier publications on this subject.

## PALEONTOLOGICAL CONSIDERATIONS

If we examine the adaptations of living mammals as well as the fossil history of this class we can conclude that the evolution of mammals is generally a predictable process. We find that different stocks evolved into surprisingly similar animals, and we find that certain adaptive syndromes arose repeatedly. Such adaptive syndromes as 'sabre-tooth tiger', 'cat', 'wolf, 'mole' or 'mouse' evolved not only several times in therian mammals, but in the eutherian mammals as we'll. The adaptive syndrome 'rhino' appeared at least four times, if not more, in the Perissodactyla alone, namely in the rhinos proper, the acerathers, dicerathers, brontothers and maybe teleocers; it appeared also in the embrithopods, Dinocerata and South American toxodonts. One can even make a case that the last of the dinosaurs, the ceratopsians, were good 'rhinos' also. Similarly the 'horse' was evolved in the Perissodactyls twice, once in the familiar equid lineage and once in less perfect form in the cursorial rhinos (Hyracodontidae), as well as in the unrelated South American litopterans, in the family Proterotheriidae. In view of the great morphological similarities of the end products of convergent evolution that we encounter so often in mammals, the great behavioural similarities of convergent rodent lineages (Eisenberg, 1967), or the striking similarities in the behaviour of some African gazelles (Walther, 1964, 1965) with that of American pronghorns (*Antilocapra americana*) (Bromley and Kitchen, Papers 17 and 18 in this volume) should not be surprising.

An examination of individual ungulate lineages reveals that some have changed progressively in geologic time in a predictable, irreversible manner while others, illustrating Cope's rule, remained frozen in their primitive form and did not change markedly over long geologic time spans; some lineages show both processes. If lineages changed, the species evolved into ever larger forms with larger and more complex horn-like organs, and often—but not always—with more specialized dentition. The Dinocerata and the Brontotheriidae as illustrated by Flerov and Osborne respectively (see Thenius and Hofer, 1960) are examples of such change. Here ever larger species replaced each other in geologic time, changing in the manner indicated, but without noticeable specialization in dentition. The Protoceratinae, a peculiar lineate of American ruminants, illustrate also progressive evolution, but here a specialization in cheek teeth from brachyodont to hypsodont types runs parallel with the evolution of horn-like organs and an increase in body size (see Scott, 1937). We notice the same in Pleistocene forms of *Dicerorhinus* when these adapted from forest to steppe to tundra (Kurten, 1968).

The best examples of lineages in which some forms froze in their evolutionary development and remained living fossils, while giving off lineages that evolved into larger and more bizarre forms, are the old-world deer and the rhino lineage represented by *Dicerorhinus* and *Coelodonta.* The Sumatran rhino of today (*Dicerorhinus sumatrensis*) appears to have changed little in size, cranial morphology and dentition from the Oligocene form of *Dicerorhinus* (Thenius and Hofer, 1960). In the northern, periglacial area *Dicerorhinus* evolved along expected lines to terminate in the large, heavy-horned woolly rhino (*Coelodonta*) that had a highly specialized skull and dentition. In the old-world deer, the Muntjacinae, are essentially primitive deer, little changed since the early Miocene. While they remained essentially frozen in their evolutionary development, the Cervinii evolved in the direction outlined earlier to produce many huge-antlered giants. I have discussed the evolution of this group in some detail elsewhere (Geist 1971b). Both of these complex lineages also illustrate the great durability of generalized, primitive forms from the tropics and subtropics, and the susceptibility to extinction of specialized or bizarre forms. The same lesson can be learned by examining other lineages such as the Tayassuidae, Suidae, Tragulidae, Rhinocerotidae, Proboscidae, Giraffidae or Dasypoda. Today we still find alive many primitive or generalized species while the fossil record is littered with extinct forms of large size, odd horns and tusks, and specialized dentition and legs—the most striking being the horned armadillo *Peltephilus* (see Scott, 1937, p. 682), the horned and large-tusked pig

*Kubanochoerus* (see Orlov, 1962, p. 487), the mid Pleistocene steppe rhino *Elasmotherium*, or the giant sivathers (*Sivatherium giganteum*) (see Orlov, 1962, p. 527). The durability of generalized forms versus the short-lived existence of bizarre forms requires explanation.

In addition to these observations we note that the Ice Ages accelerated the evolution of large mammals in an incredible manner and led to the appearance of grotesque forms unequalled in the complexity and size of horn-like organs by pre-Pleistocene forms. The direction of evolution in individual lineages towards large body size, complex horn-like organs, and specialized dentition remained the same as in pre-Pleistocene epochs, but the rate of change increased. Such pre-Pleistocene lineages as the Dinocerata, Brontotheriidae or Protoceratidae lasted 10-20 million years; Pleistocene lineages like the true elephants, old-world deer, rhinos, caprids,bovines or even the Mastodontidae reached comparable evolutionary status and often extinction in usually less than two million years. It should be noted that antlers, horns, ossicones and tusks evolved during the Ice Ages in parallel towards large size and/or complexity in cervids,bovids, rhinos, giraffes and proboscidians. This is not surprising in view of the finding that these horn-like organs are used in a similar manner, and as such are analogous organs (Geist, 1966b).

These observations on mammalian evolution leave us with a number of questions. Why should most mammals converge into a lesser number of adaptive syndromes? For the present it is sufficient to answer that similar ecological professions probably require similar tools (in our case adaptations) for efficient exploitation of a given niche. The remaining questions cannot be answered that simply.

Why should evolution in some ungulates lineages invariably and apparently irreversibly proceed towards giantism, specialized social organs and often specialized dentition?

Why do some evolutionary stages in a lineage halt in their evolutionary advancement, stagnate and remain 'living fossils'? We find such stagnation within clines of living species such as in the genus *Ovis* or among old-world deer.

Why should ecological specialization as indicated in tooth structure parallel social specialization as indicated by form and size of horn-like organs in some lineages but not others?

Why should primitive, generalized forms have such great longevity compared to large and bizarre forms?

Why should the Ice Ages precipitate an acceleration of evolution in the same direction as in pre-Pleistocene times, and lead to the most bizarre ungulates ever to evolve?

## ZOOGEOGRAPHIC CONSIDERATIONS

A first clue towards answering these questions comes from zoogeography. In the northern hemisphere, in the regions covered repeatedly by Pleistocene ice, we find ungulates of large size, bizarre horn-like organs and of recent evolutionary origin as indicated by the fossil record. In the tropics and subtropics we find many related, but relatively primitive and old species. This geographic distribution reflects Pleistocene and pre-Pleistocene evolution, as well as the complex dispersal of the animals.

Here we must deviate for a moment. A comparison of living forms considered primitive and advanced by modern taxonomic opinion, reveals that the advanced forms tend to be not only larger, have larger horns or antlers, and sometimes more specialized dentition, but also have larger rump patches, shorter and weaker tails, and occasionally enlarged skin glands. This is illustrated by the old-world deer (Geist, 1971b; Fig. 1, 2, 4), in the genera *Odocoileus*, *Ovis*—both in the Asiatic and again in the American sheep (Geist, 1971a; Fig. 43, 46), and *Capra*. We have here one of those silly correlations: in northern ungulates 'tail size' is inversely related to 'horn size'. Yet it is valid as can be seen not only in above forms but also in the living and extinct elephants, rhinos, and the genus *Bison*. Furthermore, in the genera *Ovis*, *Capra* and *Bison* there is in general an inverse relation between horn size and the amount of long hair on the body, such as manes, beards and robes (excepting *Capra falconeri*) (see Geist, 1971a, b). It can be noted that the organs which change most, i.e. horn-like organs, hair patterns, rump patches and external skin glands, are intimately connected with the social behaviour of these ungulates. Since complex teeth and horn-like organs are often found together, this leads to the conclusion that somehow ecological and social evolution are connected, a conclusion which is not new. Eisenberg reached it earlier in his studies of rodents (1963, 1967) and more recently in tenrecs (Eisenberg and Gould, 1971). (The tenrecs, in particular, illustrate well that the ecologically most specialized form is also the most bizarre in appearance and most specialized in social behaviour.) Before that Cullen (1957) had drawn attention to the above relationship in a cliff-nesting gull. However, the conclusion was reached in a manner quite different from the above authors, and as such strengthens the hypothesis that ecological and social evolution are related. Again we turn to zoogeography. Examining the distribution of advanced and primitive races of northern cervids and caprids one notes that the primitive forms are found in glacial refugia and advanced races in glaciated zones (see Geist, 1971b; Table 1). A second examination reveals that the primitive races are at the geographic beginning of the dispersal of the species in post-glacial times and the advanced species are at the end point of the dispersal of that species. Races intermediate in physical characteristics between the primitive and advanced races occupy geographically intermediate positions. Put simply, the further a species moves, the larger the individuals become in body size, horn size, rump patch size, occasionally gland size, and the shorter the tail grows. We find such geographic clines and centres of post-Pleistocene dispersal in Asiatic sheep, American sheep, in the wapiti, the mule deer and to some extent also in the reindeer or caribou (Geist, 1971a, b). Clearly there is a close relationship here between post-glacial dispersal and social evolution.

One point needs to be raised: these living northern forms show little or no ecological specialization as indicated in tooth structure paralleling social evolution. There is precious little difference in the teeth of urials and argalis, thinhorn or bighorn sheep, red deer and wapiti, blacktail or mule deer. This runs counter to the apparent correlation found in the tropical and subtropical continents where tooth structure and such social adaptations as horns, or colouration appear to specialize in common, as is also confirmed by the fossil record, as well as by Eisenberg's studies on rodents (1963, 1965) and Eisenberg and Gould's (1971) study of tenrecs. It runs counter to a positive relationship between tooth specialization and tusk size in elephants or tooth specialization and wart and tusk structure in the living Suidae, the positive relationship between ecological specialization and antler structure as found in the primitive deer of India, and the recent finding that the most specialized morphological species of baleen whales (*Megaptera*) has also the most complex song found among whales (Payne and Scott, 1971). We must now explain why the correlation between tooth structure (ecological) and social specialization is less pronounced in ungulates from the periglacial than from the subtropical and tropical zones.

## BIOENERGETIC CONSIDERATIONS

The following may appear to deviate from the line of thought followed until now, but it is nevertheless relevant. The northern, temperate or periglacial regions are characterized by extremes in both forage production and availability to ungulates; it is an annual 'boom and bust' economy. The growing season is only 6-9 weeks in the north, but plant growth is intense. The winter is long, about eight months of the year, and the snow restricts ungulates to relatively small areas of favourable habitat. The life of ungulates in the northern zones is geared to these extreme conditions. The reproductive periods are timed with great precision. The rutting seasons are very short. Consequently the males are idle from sexual activity for all but a fraction of the year. Following winter, the individuals experience a superabundance of highly nutritious forage as they scatter over wide areas of new plant growth. Freed from the reproductive activity the males are free to grow, molt, fatten and store vitamins and minerals in preparation for the coming rut. Condemned to idleness and faced with a superabundance of food, the males are free to indulge in excessive horn growth as well as in the wasteful process of fat storage since nutrients are not limited. Lipogenesis is very wasteful of food energy (Blaxter, 1961), yet in the north the superabundance of forage makes the term wasteful meaningless. The fat is used advantageously by the male during the short rutting season since it frees him from feeding in favour of engaging in courtship and dominance interactions; the large antlers or horns allow him probably to escape excessive combat since they tend to act as rank symbols.

In the tropics, and in particular in the humid forests and savannahs, forage production does not fluctuate as severely as it does in the cold regions. The caloric density of plant tissues is much lower in the tropics and the fiber content of plant matter considerably higher than in the temperate and arctic regions (Jordan, 1971). Although in the tropics there is much more plant production than in the Arctic, the arctic plants have a much greater food value to a ruminant than the tropical ones. Since the maximum daily intake of energy for ruminants is directly proportional to the digestibility of forage (Blaxter *et al.*, 1961), it would appear that a ruminant from the temperate or arctic zones would have a much higher maximum daily energy intake during the vegetative season than would a tropical one. This suggests, assuming similar maintenance requirements, that a temperate or arctic zone ruminant would have a far greater surplus of energy for fat storage or antler-horn growth than would a tropical one. Therefore, not only a superabundance of forage, but also higher forage quality would generate an energy and nutrient surplus for cold climate ruminants in excess of that expected for tropical forms. As expected we do find that tropical deer and bovids have generally smaller antlers or horns than those from temperate zones, as I have discussed in detail elsewhere (Geist, 1971b).

Whereas in the cold climates breeding seasons are sharply limited, this need not be the case for tropical ungulates. Breeding seasons may be year round, or last for several months (see Schaller, 1967). The males are therefore not free to idle and grow fat in tropical forms; rather they must be on guard during territorial defense and courtship, or—if in bachelor groups—ready to take on a territory. The males must hence be ready to fight anytime, to better their rank in bachelor groups or to become territorial. The cost of social life should therefore be higher to tropical males than to those from temperate zones during much of the year. This would reduce still further the surplus energy and nutrients available for growth and fattening. Moreover, males which would forego lipogenesis in favour of direct use of the ingested energy for reproduction would have more energy to spend for reproduction. This would be so since lipogenesis is exceedingly wasteful of energy. We would expect, therefore, that ungulates from the humid tropics and savannah would have only a very small store of body fat. This is indeed found in the Uganda kob (Ledger and Smith, 1964), where the subject has been investigated.

Furthermore, if males and females roam over the same, limited home range, it becomes adaptive for the males to have food habits different from those of the females or to segregate males and females as much as possible. A reduction in food competittion between the sexes during the female's gestation period would benefit the growing foetus, in that the female would have more net energy for foetal growth. This suggestion that males should feed on qualitatively poorer forage compared to females is less far-fetched than appears at first glance. We do know that Icelandic ptarmigan (*Lagopus mutus*) during the egg laying season have different food habits according to sex. Thus Gardarsson and Moss (1970) found that females fed on freshly growing herbs far more than did males, and thus consumed a more digestable and qualitatively better food. We also know that there are taste preferences in blacktailed deer (*Odocoileus hemionus columbianus*) (Crawford and Church, 1971). In view of the fact that exacting field studies on the food habits of ungulates of different ages and sexes during all seasons of the year are still outstanding, it is premature to discard the hypothesis that in some ungulates food habits may vary by sex and age, with the males feeding on the coarser, less digestable forage.

Another means of reducing competition for forage between sexes would be to segregate adult males and females spatially as much as possible. Some territorial systems, such as that of Thomson's gazelle (*Gazella thomsoni*), in which territorial males stake out large territories in the home ranges of females and regulate bachelor herds to secondary habitats at the forest edge (Walther, 1964), would serve the purpose. Assuming that both male and female would select for the highest quality forage possible, the reduction of males on the feeding ranges of females would clearly allow the females to feed more on high quality food. Whether the absence of non-territorial males indeed does free a noticeable amount of high quality food remains to be demonstrated.

The short rutting season in the north concentrates intense aggressive interactions between males. This puts a premium on mechanisms which clearly signal the combat potential of the dominant or breeding males. Every fight, chase or interaction saved necessarily saves fat from oxidation and allows the dominant male to use such fat to supplement his energy intake during winter. This should increase his life expectancy. At present it appears that natural mortality in males from northern ungulates is linked to the loss of body fat during rutting. That is, they go bankrupt into winter while males prevented from intensive rutting maintain fat stores and have an excellent chance of survival (see Flook, 1970; Geist, 1971a). Clearly, the better the male is at intimidating rivals the better his chances to live another year. This can be achieved not only by relatively large antler or horn size, but also by intensifying all signals that are used by the dominant males, be they sounds, odours or actions associated with dominance. This suggests that northern males should evolve not only larger antlers or horns than comparable forms from subtropical regions, but also that they should vocalize more, and spray more urine, distribute more dung or secretions and make themselves most visible during the rut. This prediction remains to be verified. Our present knowledge indicates that it will hold for old-world deer; in the caprids the horns alone increase in size.

In ungulate species living close to carrying capacity the year round and breeding the year round, mechanisms may evolve to ration rutting for each male. Theoretically this may take the form of males spending only a fraction of the year on the territories and recuperating from the strains of territorial life for the remainder of the year. One would note in such species that an individual male occupied his territory periodically and that in his absence other males occupied that territory. Leuthold's (1966) observations on the Uganda kob (*Adenota kob*) come close to this expectation.

This concept can also be applied to explain musth in Asiatic elephant bulls. Eisenberg *et al.* (1971) note that it is similar to rutting in ruminants and support this contention plausibly. According to the hypothesis suggested here, continuous rutting would place so heavy an energy drain on bull elephants as well as unduly expose the male to the hazards of intraspecific conflict, that the life expectancy of sexually mature bulls would be very short. A short annual rut coupled with continuous sexual activity throughout the year allows the male to dominate others for a short time annually, to breed uncontested females during any time of the year, as well as to recuperate from rutting and increase his life expectancy. This would, in the long run, allow a bull to sire more offspring than if the male were in rut continuously and died young. This viewpoint suggests that bulls can afford to rut only if they are in favourable energy balance and have sufficient energy available for rutting above those of maintenance. Eisenberg *et al.* (1971) support this view. First, musth appears mainly during rainy periods, that is when fresh, newly-sprouted vegetation is available that is of higher quality than old vegetation. Moreover, there should be more forage available than during the dry season. Second, to extinguish musth domestic elephant bulls are put on reduced rations by mahouts. Third, musth appears sporadically in bulls 14-20 years of age but more regularly in older bulls, implying that musth appears mainly in bulls whose growth processes are near completion and, hence, have more energy available in excess of maintenance. It is interesting in this context that African elephants may consume a much greater amount of forage per day than do Asiatic elephants (Sikes, 1971). If this is found to be valid, then it appears that Asiatic elephants may have evolved more efficient mechanisms of forage conversion in the face of chronic shortage. The predictions inherent in the above hypothesis explaining musth are as follows: musth should be found to occur most frequently in wild bulls from excellent habitats.

Bioenergetic consideration also helps in explaining why territories are found primarily in tropical and subtropical ungulates and only exceptionally in northern forms. A male can occupy a territory year round only in such regions in which the productivity and the diversity of plants is such that the male can find enough sustenance—and of the right kind—year round for himself as well as for his mates and offspring. The productivity in humid tropical climates, as well as the great diversity of plants on relatively small areas, appear to allow territorial behaviour. A territory cannot be held year round if the diversity of plants or the productivity of the territory is too low to supply the necessary sustenance, or if the productivity is highly seasonal and adequate forage available for a short time only. Furthermore, fixed living or breeding territories becomes increasingly unadaptive the greater the movement of females during migration, the more unpredictable the availability of food, whether because food supply is determined by local rains—as it is on the African plains—or its availability is affected by snow storms, cold snaps and thaws. Thus a group of females faced with little or no forage on a territory is likely to escape from the territory holding male and head towards better pastures. A male holding a territory with favourable forage conditions may find himself the next day in territory covered by a deep blanket of snow, while the females have moved several miles to a more favourable area. A male holding a territory here may find himself alone as soon as strong winds have cleared specific ridges of snow. In short, if the rut is short and the animals must often move to different regions in order to feed, a male maximizes his reproductive success by sticking with the females. It is noteworthy that the roe deer (*Capreolus*) and the pronghorn (*Antilocapra*), both of which are northern forms in which the males form territories during the rut (Kurt, 1966; Bromley, 1969), mate during the summer or early fall when vegetation is still green, relatively abundant and the likelihood of snow storms minimal.

The foregoing illustrates how the availability of forage in the habitats of ungulates from cold and warm climates could, and apparently does, reflect itself in the biology of these animals. We now turn to the circumstances which accelerate social evolution in periglacial ungulates in preparation to answering the questions posed earlier.

## THE DISPERSAL THEORY

*Evolution in periglacial regions.* The following is a short version of a theory discussed in detail elsewhere (Geist, 1971a, b).

After glacial withdrawal ungulates began to colonize the vacant habitat of the once glaciated zones. Individuals crossing or circumventing barriers, such as large melt-off channels or glacial lakes, formed colonizing populations. Until the population reached carrying capacity, the individuals would be confronted by a super-abundance of forage to which they would respond in a predictable fashion. Birthrates, birth weights and milk production would increase. Consequently neonatal survival and the growth rates of young would go up. The young would mature early and reach an adult size close to their genetic maximum. However, the adults would have a short life expectancy. Such animals would be lively, interact in play-like combat frequently, and fight intensely during serious combat at rutting time. Under such conditions large-bodied individuals as well as those with larger horns or antlers, which improved combat techniques and defense mechanisms, as well as sturdier skulls to absorb impact and stronger skull to spine connection, would have the advantage. The longer the population exists in the colonizing state, the longer selection continues for large males with improved combat techniques and adaptations.

Large body and horn size can be achieved by increasing the intensity and duration of growth. This can be done by enlarging the physiological mechanisms characteristic of juveniles. If this happened then ungulates should become not only larger, but also more juvenile-like during early post-glacial evolution. This hypothesis could be tested on American and Asiatic sheep (Geist, 1971a). It could be shown that in all parameters tested the behaviour of the advanced bighorn sheep (*O. canadensis canadensis*) was more juvenile-like than that of the more primitive Stone's sheep (*O. dalli stonei*); in Asiatic sheep evolutionary advancement was associated with the loss of the neck mane, a secondary sexual characteristic of males in primitive races.

Selection for large body size would come to a halt in the population at carrying capacity when the body size no longer reflects genotypic but phenotypic variation. Such a population is characterized by a low reproductive success, low vigour in its social interactions, but a long life expectancy of the individuals. However, the evolutionary advancement in weapons and defensive systems are maintained, since a reversal towards the primitive condition could only take place if males at the bottom of the dominance order, that is the subordinates and socially unfit, would do most of the breeding. This is most unlikely and has been reported as a rule for no species studied to date. Only if subordinates bred regularly and in the majority would evolution become reversible and thus contradict Dollo's law.

The foregoing exemplifies the simplest kind of evolution in which there is an advance in social adaptations without a concurrent advance in ecological ones, since the species only invades habitat to which it is already adapted. It explains why present-day ruminant clines from the north need not reflect ecological gradients, but reflect only the the dispersal history of the species. It explains the correlation between evolutionary advancement and Pleistocene glaciations,as well as the irreversibility of evolutionary advancements. It explains why ungulates invading continents uninhabited by their kind evolved into grotesque giants such as *Bison latifrons*, or the large-tusked elephants (*Mammutus jeffersoni, M. imperator*) that appeared in North America in mid-Pleistocene times. It also explains another mystery, namely why the oldest fossil forms of a genus or species of large mammal in any one locality tend to be the largest representative of that lineage.

*Dispersal and social evolution in tropical environments.* The same process as described above must also take place in the tropics, provided a species evolves which differs ecologically from the parent species. This new species dispersing across the continent and filling a new niche would also experience superabundance of resources during colonization. It, should then respond in the manner described for Ice Age forms. However, it would be subject to an additional form of selection: since the parent species strongly resembles the new species, interbreeding is likely. Selection against hybrids would soon lead to a divergence in the external appearance, courtship and dominance behaviour of the new species from the parent species; since the new ecological species is relatively rare and hence outnumbered by individuals of the parent species, it is the new species which diverges from the old in external appearance and behaviour. Once the new species has colonized the land it will be characterized by individuals of larger body size, improved combat and display organs, and more distinctive colouration in hair coat and skin outgrowths than those of the parent species. Since each new species arising must go through the same process, the result is that the species most specialized ecologically will also be the most specialized socially and have the most bizarre external appearance. A corollary will be that the ecological specialists are more likely to extinction than the generalists and that the latter may survive over far longer periods than the bizarre, advanced forms. Secondly, it is evident that it is the ecological generalist that is most likely to disperse to new habitats while the specialized forms are more likely to remain in the land of their evolutionary origin and have a smaller geographic distribution. While this supports Darlington's (1957) views of dispersal, the previous example, using the periglacial example, supports Matthew's (1915) views of dispersal and evolution of mammals. These apparently contradictory theories are both correct, depending on where dispersal and evolution took place.

*The dispersal theory and the antelopes.* The predictions of this theory appear to be realised fairly well in the 'antelopes', although there are also a few exceptions. An examination of the Reduncinae, Tragelaphinae, Alcelaphinae, Hippotraginae and Antilopinae as described by Walther (1968a, b, c) shows the following. If we examine the obvious ecological specialists in those tribes such as the Sitatunga (*Tragelaphus spekei*), mountain nyala (*T. buxtoni*), eland (*Taurotragus oryx*), the lechwe (*Hydrotragus leche*), or Lady Gray's water buck (*Onototragus megaceros*), we note that they are relatively large-bodied, have heavy or long horns and bizarre, striking colour, hair and skin outgrowths compared to the ecological generalists such as the bushbuck (*Tragelaphus scriptus*) and reed bucks (*Redunca*). In the Alcelaphinae the genus *Alcelaphus* contains the least strikingly coloured species of the tribe. The genus *Damaliscus*, however, which according to Walther (1968b) inhabits habitats either more mesic and forested, i.e. the topi (*D. lunatus*) or more open and treeless, i.e. the blesbok and bontebok (*D. dorcas*), than does the genus *Alcelaphus*, is also more distinctly coloured. The most striking genus, *Connochaetes*, with bizarre hair outgrowths on face, neck and tail, and relatively heavy horns and specialised social behaviour (see Estes, 1969) should be ecologically the most specialised genus. This, however, is up to the specialists to decide.

In the Antelopinae we find the small-bodied gazelles of the subgenus *Gazella* to have the widest geographic distribution. This we expect from the most generalized subgenus. Quite in accordance with theory, members of this subgenus have a relatively small set of horns and a small rump patch. The subgenus *Nanger* contains larger bodied gazelles with large rump patches and long horns; their distribution is contained largely within that of *Gazella*. The subgenus *Nanger* hence would be the higher evolved of the two subgenera according to the theory. The African ecological specialists among the Antilopinae such as *Litocranius, Antidorcas* and *Ammodorcas* differ from the small, generalized subgenus *Gazella* in more striking body shape, large or complex horns, specialized tails, specialized behaviours, larger body size and relatively small or even tiny geographic distribution. In Asia we find the ecological specialists adapted to the cold steppes or mountains differing from the small gazelles in the expected direction. Thus we find the saiga (*Saiga tatarica*) gazelle with an oddly shaped head, which in males becomes particularly grotesque during the rut. Next in relation is the high altitude form, *Panthalops,* larger in horn size than *Saiga* and with a rump patch. In the cold desert of Mongolia we find *Procapra gutturosa,* large-bodied for a gazelle with a 'mouth sack' as yet of unknown function. Moreover, *Procapra gutturosa* males have a swollen 'crop' during the rutting season. This species has a large rump patch and short tail. It can be noted that where data are available, they do follow the predictions that the ecological specialists have more complex or larger social organs than the generalists and are of larger body size.

If the Hippotraginae, in particular the genus *Oryx* and *Addax, are* indeed descendents of the Antilopinae, then the ecological and social adaptations of these desert antelopes are at once comprehensible following the predictions of the dispersal theory. These ecological specialists should be large horned and marked with striking body colouration, which indeed they are. Moreover, the largest oryx, (*O. gazella gazella*) is also the most colourful one. They should also have a social behaviour derived from that of the Antilopinae, but of an advanced form. If this is so, it remains to be discovered.

The dispersal theory does not predict correctly in a number of instances. In the reedbucks, it is not the largest horned and biggest bodied species (*Redunca arundinum*) which has the smallest geographic distribution, but *Redunca fulvorufula,* the smallest bodied and shortest-horned form. Horn size does not invariably enlarge with ecological specialization: thus the dama gazelle (*Gazella dama*) has rather modest horns, as does the saiga, Mongolian gazelle (*Procapra gutterosa*) and the springbok (*Antidorcas marsupialis*). However, each of these species is highly distinct in some other attribute related to social behaviour. Note the striking body colour, the white face and large rump patch of the dama gazelle, the swollen proboscis, large preorbital glands and facial hair outgrowths of the saiga, the 'crop', rump patch, and 'mouth bag' of the Mongolian gazelle, and the facial colour pattern and dorsal display organ of the springbok. Horn size may remain conservative, but other social organs may compensate for horn size in their evolution.

The scarcity of hard ecological and behavioural data for African and Asian antelopes makes it difficult to test the dispersal theory adequately. It is tempting to suggest that *Tragelaphus scriptus, T. imberbis* and *T. strepsiceros* are an evolutionary lineage, leading from the small, primitive, brush-dwelling form to the arid-zone species in which social behaviour specializes with ecological specialization. Although Walther's (1964) work on the ethology of *Tragelaphus* is compatible with this view, there is insufficient ecological data to make a case. Similarly, the Cephalopinae are ill-known, and although the largest-bodied species (*Cephalophus sylvicultor*) is the most strikingly coloured—as anticipated by the dispersal theory—its horn size is similar to that of other duikers, and we know nothing of its ecological differences from other duikers. Although our limited knowledge of the food habits, behaviour and zoogeography of duikers suggests that we are dealing with the most primitive of bovids, the paleontological record is as yet too inconclusive to clinch the argument.

*Accelerated evolution during the Pleistocene.* The acceleration in rate of evolution during the Pleistocene, as compared with pre-Pleistocene times can be explained by noting that frequent minor and major glaciations caused contraction and subsequent expansion of habitats upon melt-off. This would cause frequent dispersal of a species into vacant habitat, and frequent subjection to selection pressures typical of colonizing populations, hence a rapid change of the species towards large body size and sophisticated combat and display behaviour, as well as enlarged horn-like organs.

An association between specialized tooth structure and increased body and horn-like organs in Pleistocene forms can be explained as follows. If large body and horn, tusk, etc. size is strongly selected for, then increasing digestive efficiency is also selected for. Hence males with improved mastication equipment benefit by having slightly more energy, surplus to maintenance, for growth of body and combat organs. Over geologic time one would notice an increase in specialization of masticatory apparatus, horn-like organs and cranial defense mechanisms. Such evolution, however, does not imply ecological specialization, but only increasingly efficient exploitation of forage within any niche.

*Evolutionary stagnation.* Lastly, how does one account for evolutionary stagnation in ungulates? The present theory suggests that this is due to the generalized ecological adaptations of long-lived species and the relative stability of the plant communities inhabited by these forms. Even if such plant communities contract and expand in response the climatic conditions and fragment into geographically distinct units during maximum geographic contractions, the generalized ungulate species would nevertheless fail to find much opportunity to expand into identical habitat not occupied by its own kind. Under circumstances minimizing the opportunity for dispersal into vacant habitat, little or no evolutionary advancement would take place. I have explained evolutionary stagnation in the clines of sheep in detail elsewhere (Geist, 1971a).

## BEHAVIOURAL CONSIDERATIONS

From the foregoing considerations it is evident that behavioural differences between northern ungulates and those from tropical continents can be expected. It has been noted that intense competition for females in the colonizing populations by large, relatively young and vigorous males would select for intense combat. It should not surprise, therefore, if northern species of ungulates are found to be far more damaging in intraspecific combat than African antelope or cervids from South-east Asia, for instance. Our present-day, meagre evidence is in line with this and we can say that severe wounding or killing in intraspecific combat is not uncommon in northern cervids or bovids. I have reviewed the evidence elsewhere (Geist, 1971a).

Secondly, we can anticipate noticeable quantitative differences in the social behaviour of ungulates from stagnant, poor quality populations, and high quality populations with access to adequate forage. It can be predicted that courtship, combat and display will be more frequent and intense in the high quality population. We have evidence to show that this is indeed so, but it is insufficient to demonstrate the point conclusively (see Geist, 1971a).

Thirdly, in a comparison between primitive and advanced races of a species (or species of a genus) the primitive forms should be found to have more generalized combat, a greater likelihood of body rather than weapon displays, and the less neotenous social behaviour. Data to show this exist today only for caprids (Geist, 1971a).

There are other relationships between the ecology of species and their social behaviour, but they were irrelevant to the present theme. I have discussed in detail elsewhere the impact of climax plant communities on the evolution of sheep and that of fluctuating ones on the evolution of moose (Geist, 1967; 1971a, c), as well as the many direct and indirect consequences of ecological adaptations on sheep biology (Geist, 1971a). Mention has also been made of Eisenberg's (1963, 1966, 1967) and Eisenberg and Gould's (1970) contribution to this subject. Of particular significane is Jarman's (1968) theoretical contribution which for the first time plausibly relates bioenergetics and feeding strategy to body size of ruminants, and considers the secondary effects of the anti-predator strategies and social systems of these animals. Recently Crook (1970) edited a volume that deals largely with the relation of ecology and the social behaviour of various mammals and birds. And, finally, of course, a considerable number of other papers in this volume discuss various aspects of the relationship of ecology to social behaviour in ungulates.

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Paper No. 11

# The Influence of Foster Rearing on Adult Social Behavior in Fallow Deer (*Dama dama*)

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## ABSTRACT

Many species of hoofed mammals are known to form strong social bonds to normal or surrogate parents shortly after birth. Despite the similarities of this process to imprinting in birds no study of the effects of early experience on the development of preferences for companions or the long term influences on social behavior has been reported.

In this study fawns were separated from their mothers between one and 48 hours after birth and were foster-reared by goats or bottle-fed either in isolation from other fawns or with fawn companions. When four to seven years old these foster-reared deer were compared with normally-reared deer for attachment to people and to other deer. The deer which were bottle-fed without fawn companions had the highest scores of attachment to people, lowest scores on three indices of gregariousness to deer and the highest scores for aggression toward other deer. In addition, the ranks of these measures of attachment to people and lack of gregariousness to deer were highly correlated with the age during the first 24 hours that the fawns were removed from their mothers. The data indicate that the differences in adult attachment resulted from processes initiated in the fawn's first day of life. Deer reared with other fawns ranked lower than isolate-reared deer in attachment scores to people and in aggression, and ranked higher in measures of gregariousness with deer. The normally-reared young of hand-reared does ranked lowest in attachment to people and in aggression, and highest in gregariousness with deer.

The degree of attachments to people or deer in both foster-reared and normally-reared animals was resistant to change and could be transferred to other individuals of the same species. The data suggest that the degree of attachment depends on social interactions during the first day of life.

Observations on the development of fear of people in the normally-reared fawn are presented. Exposures to people for 8 hours in the fawn's first day resulted in delayed withdrawal response during subsequent approach by people.

The major influence of foster-rearing was in establishing the social companion to which species-typical behavior was directed. The frequency of some behavior patterns was changed, e.g. aggression, but no change in the type of behavior was detected.

## INTRODUCTION

The newborn young of hoofed mammals are characterized by well-developed perceptual and motor capabilities as compared with other orders of mammals such as carnivores and rodents. The neonatal wildebeest (*Connochaetes taurinus*) normally stands and follows its mother within 5 to 10 minutes after birth (Talbot and Talbot, 1963). Deer and antelope, although capable of standing within an hour of birth, remain lying in cover for a number of days (Bubenik, 1965; Walther, 1964). Experiments on visual perception in kids and lambs show that they are able to avoid the deep side of a visual cliff at one day of age (Hinde, 1966). At the other developmental extreme,

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[1] This study was undertaken by the author in the Department of Zoology, Duke University.

dogs do not give a startle response to sound until three weeks of age. Socialization occurs mainly from five to seven weeks of age (Freedman *et al.*, 1961). The behavioral precocity of ungulates suggests that they are ideal subjects for the study of changes in behavior resulting from brief experiences encountered shortly after birth, particularly those considered as 'imprinting'.

Information on the early establishment of preferences for parents of parent surrogates in ungulates has come chiefly from anecdotal reports of zookeepers or wildlife biologists (Thorpe, 1956). Very little comparable to the imprinting studies of birds has been attempted despite the *prima facie* evidence for imprinting in ungulates.

The aim of the present study was to examine the influence of very early experience (through foster-rearing by goats and people) on adult social responses in fallow deer (*Dama dama*). Behavior suggesting attachment to, or independence from wild deer, foster-reared deer or people was emphasized. These social interactions were chosen for study since they seemed most likely to be affected by isolation from conspecifics and attachment to parent surrogates.

Studies of the later effects of early experience have concentrated largely on rodents, cats, dogs and primates (Newton and Levine, 1968). Only in a comparative context are these studies relevant to this work on the behavioral development of deer because (a) the rodents, carnivores and primates have considerably more protracted stages of social and locomotory development; (b) the manipulation of early experiences in these experiments consisted largely of total isolation, electrical shock, handling etc. rather than substitution of a parent of another species (thus isolating the subject from social interaction rather than *particular types of species interaction*);(c) the response measures were not of social behavior nor were they obtained without interference with the established groups.

Most of the subjects of the study were deer that had been hand-reared in preparation for another project. This precluded the specification of independent variables. However, the rigid restriction of stimuli and developmental periods for exposing the fawns would have been premature in this early stage of research. The objective, then, has been to correlate the social characteristics of normally and foster-reared mature deer with the varied types of early rearing experiences to which they had been exposed.

## METHODS

### A. Treatment of Foster-reared Fawns

Newborn fawns were taken from the semi-wild does between one and 48 hours after birth. The details for individual animals are given in Appendix I. Only the classes of treatment will be discussed here. They are ranked in order of increasing early contact with deer as follows:

(a) Four fawns were reared individually in homes and bottle-fed. They received much contact with children and adults. Except for the contact with the mother immediately after birth (in one case as long as 24 hours) none of these fawns contacted other deer until 30 days of age (one case) and the others at 7 weeks of age.

(b) Two fawns were suckled by goats and penned with them after less than 24 hours with their natural mothers. They had considerable contact with people during the establishment of suckling since the goats initially rejected the fawns. These fawns were kept with the goats until at least one year of age.

(c) Two fawns were reared together in the same house with two other fawns (not involved in this study). The first born was by itself for only one day immediately after birth. Subsequently all four were together.

(d) Three fawns were born to hand-reared does and nursed by them in the large enclosure. These fawns received occasional, limited visual contact with people when the caretaker entered the enclosure for feeding. One fawn was born in a small pen on a farm. She saw people frequently through the day as children and adults cared for goats and horses in nearby pens. Although people entered her pen daily she never tolerated physical contact. Her behavior will be discussed separately. Other details of the rearing treatments are discussed in conjunction with the results.

### B. Description of Testing Situations

Observations of the deer were made under two conditions of confinement. The studies of leadership, cohesion and independence were made in the large 75 acre enclosure which contained the semi-wild herd. Two groups of foster-reared deer and one of semi-wild deer were constituted to obtain observations of spatial organization at rest, individual resting locations, flight distance of fawns and aggressive interactions. The assignment of foster-reared deer to the groups was made according to whether they had had previous contacts with the semi-wild deer, a variable which I considered as having a potential effect on later social interactions. Three does and their two fawns which had this exposure were enclosed in a pen approximately 52 yards long and with parallel ends measuring 22 and 30 yards wide. They were maintained alone in this area for the duration of the study. The second group of five foster-reared deer had never been exposed to the semi-wild deer. They were enclosed in an irregularly shaped pen with the longest dimensions 52 and 47 yards. The third experimental group consisted of eight of the semi-wild herd which were trapped in a pen within the large 75 arcre enclosure. This pen was approximately 41 yards long and averaged about 17 yards wide.

The procedures used in collecting data as well as further information on the deer are detailed in the pertinent chapters.

## I. SPATIAL ORGANIZATION AT REST

### A. Birth and Nursing

The preparturient doe leaves the herd to give birth. Thus the first contacts of the newborn fawn are restricted to its mother. Immediately following birth the doe begins a prolonged and intensive licking of the fawn, generally after settling down close beside it. This was observed closely in a hand-reared doe giving birth in the forest of the large 75 acre enclosure. The doe licked continuously at the rate of about 140 licks per minute. Except while eating some pine needles with birth fluids on them the 35 minutes following birth was occupied by licking.

Before being licked, the membrane-draped fawn lay still but as the licking progressed the fawn lifted its head, shook it, sneezed and struggled along the ground toward its mother. The vigorous licking frequently rolled the fawn over. It appeared that the doe stimulated the fawn until it had reacted to a particular extent. This was illustrated by an instance of birth in a pen. A semi-wild doe had been licking her fawn continuously and vigorously for 10 minutes following birth when she began brushing it with her forelegs, then kicked and brushed it yet more vigorously. I intervened and found the fawn to be stillborn. Normally the fawn would have responded to the vigorous licking alone and the doe would not have pawed as well.

### B. Lying Out

In the birth described above the hand-reared doe moved away from the fawn about 55 minutes after birth. This is the beginning of the 'lying out' period for the fawn when it spends the daylight hours lying quietly in one spot, occasionally getting up and turning around and being visited periodically by its mother. The concentration of nursing and care-giving of this herd into the early morning and late evening periods has been described in an earlier paper (Gilbert, 1964).

Even in the relatively small confines of a pen the does consistently rested in a remote location from their fawns. In the 40-yard pen the separation was commonly 30 yards or more. This was observed in the hand-reared deer as well as the semi-wild deer.

The 'lying out' site of fawns was rather consistent for periods of days. Individual fawns were readily located by checking 'their' site to which they returned by themselves after nursing or other activity. No differences were noted between the fawns of hand-reared does and those of the semi-wild deer.

### C. Resting Patterns

1. *Semi-wild group.* The semi-wild group of 8 deer trapped in pen # 1 was observed from 18 June to 9 July 1969, at approximately the same time as the hand-reared groups in pens 2 and 3 (between 8 AM and 5 PM). Since this herd was trapped together at one time it is very likely a stable social group with close kinship ties. In all cases the deer had assumed their resting positions before the observer appeared and they maintained them at least until the end of the observation period. No attempt was made to identify individual deer of this herd when their locations at rest were recorded. The close apprach this would have required would have elicited withdrawal by the group. The location of each deer was marked on scale maps of the deer pen. The diameter of the group was defined as the distance between the furthest pair of deer. This was measured with dividers from the map. The mean diameter of thirty-two groupings was 8. 5 yards. In 75% of these observations the deer were much more clumped together, the groups having a diameter of 10 yards or less (Table 1). The instances of greater dispersal were due usually to one or two does seeking a preferred site on clean hay under the hay rack, thereby separating themselves from the main body of resting animals.

TABLE 1. COMPARISON OF THE RESTING DISTRIBUTION OF FOSTER-REARED DEER WITH SEMI-WILD DEER

Percentage of sample in each resting group size

| | 8 semi-wild | 3 hand-reared 2 doe-reared | 3 hand-reared 2 goat-reared |
|---|---|---|---|
| Number of observations | (32) | (32) | (43) |
| | (%) | (%) | (%) |
| 0-10 yards | 75 | 43.7 | 9.3 |
| 11-20 | 25 | 33.4 | 37.2 |
| 21-30 | 0 | 9.4 | 14.0 |
| 31-40 | 0 | 6.0 | 16.3 |
| 41-50 | 0 | 6.0 | 23.2 |
| Mean maximum diameter (yards) | 8.5 | 15.2 | 28.4 |

The space occupied by the semi-wild herd was never greater than 20 yards. This indicates their relatively tight grouping.

2. *Hand-reared group in area 2.* This group consisted of three hand-reared does and their two male yearlings. Two of the does had been together since they were one month old (for approximately 7 years). The third doe, one year younger, had been in the large enclosure with these two does for five years. All were in the small pen three months before observations began. The resting location of each deer was recorded on scale drawings of their pen. As in the semi-wild group 32 observations were made. The mean diameter of these resting groups was 15.2 yards. The much more dispersed nature of the group is indicated by the fact that in only 43.7% of the observations were the herd diameter 10 yards or less. While none of the semi-wild groups were greater than 20 yards in diameter, these hand-reared deer were that dispersed in 22% of their resting assemblages. Thus the five deer in the hand-reared group were more dispersed than the eight semi-wild deer.

3. *Hand-reared group in area 3.* This was a diversely reared group: 2 were reared alone (bottle-fed), two were suckled by goats in the same pen and the fifth was nursed by its hand-reared doe. All were together 12 months before the observations

began. The same technique of collecting data was employed although the observations began earlier resulting in 43 observations being collected between 7 June and 13 July 1969. The mean diameter of the resting group was 28.4 yards. Table 1 shows that this group has an even smaller percentage of resting groups less than 10 yards in diameter, 9. 3%, and 53. 5% were greater than 20 yards in diameter.

4. *Discussion.* Although the data given in Table 1 show clear differences between the three groups the number of variables involved precludes any simple correlations between rearing experiences and the size of resting groups. Besides the obvious variables of age, sex, kinship and type of foster parent, there are those of length of time the group has been together and variations within the specific fawn-foster parent relationship. The differences in the time of separation of the neonatal fawn from its mother may be very important. Although these differences were less than 24 hours in each case, they may have a significant bearing on gregariousness since so little is known about attachments or the establishment of perceptual preferences at this stage.

The semi-wild herd of eight deer was the most homogeneous. They were probably all members of one herd with life-long familiarity with one another and close kinship ties involving a number of direct filial relationships. Further evidence of close relationships in this group will be described later in the section on aggression. The group provides the control situation for the variations observed in the following two groups.

The five deer in area #2 were more diverse in their rearing environments than the control or semi-wild group as mentioned earlier. The greater dispersion can be seen in Table 1. Eight (22%) of the herd diameters were larger than 20 yards and these can be attributed largely to the one isolate hand-reared doe, Gurri, who rested furthest from the group in seven of the eight instances. This doe was 9½ months old before being introduced to other deer. From then on she roamed in the large enclosure with them for the following five years. (Her solitary existence during this time will be discussed subsequently). The other yearling males of two does, Marena and Kiki, rested close to the adults, but not always beside their respective mothers. Their gregarious behavior was similar to that of the control deer. Responses of individual deer to other individuals is discussed in Chapter III.

The third group in area #3 was seen to be both the most dispersed when resting and most diverse with regard to rearing condition. Two does, Nettla and Meredy, were reared separately on bottles. Nettla's interaction with deer in her first few months was limited to 8-18 hours immediately after her birth in June 1964. Meredy was removed 21 hours after her birth in June 1965. 'Shy' and the buck 'Robbie' were born in June 1966. They were taken from their mothers 6-20 hours and 12-24 hours, respectively and suckled six months by a goat. Nettla and Meredy were introduced into the goat herd after the initial bottle-feeding in a home. The last deer of the group, Faline, was reared by her hand-reared mother. She was not handled when young and would run and hide in her pen when approached. On 30 June 1968, after two years with her mother, she was added to this group.

Table 1 shows the distribution of these five while resting. In group #3, 53% of the observations of the resting herd showed diameters of greater than twenty yards, compared with 22% in group #2 and none in the semi-wild herd of eight. Groups #2 and #3 differed in two major ways. Two of the does in group #2 were accompanied by their own yearlings while none of the deer in group # 3 were with their mothers.

Also, group #2 had only one deer reared in isolation from its own kind compared with four of the five in group #3.

Since the sizes and configurations of the areas are different if might be argued that these factors influenced the spatial organization in the groups. This seems very unlikely because the two experimental groups were dispersed only over a small portion of their areas. The control group of semi-wild deer occupied an even smaller percentage of their area.

The influence of rearing companions on later selection of social partners has been studied in rhesus monkeys. Pratt and Sackett (1967) reared one group without peer-contact, a second with only visual and auditory contact, and a third with normal peer-contact. When tested for preferences, monkeys chose those animals raised under the same conditions as themselves even if the stimulus animals were unfamiliar to them. The greater dispersal in the deer groups likewise appears to be due to the number of isolate-reared deer in the group and the heterogeneity of the group composition.

## II. LEADERSHIP AND COHESION

### A. Development in Undisturbed Fawns

From the moment of birth the fawn is enlarging its experience, primarily with its mother. However, unlike many precocial animals the first few days are marked by an attachment to the site of birth rather than to the mobile mother. Thus even if species recognition is established very early, there is little or no opportunity for its manifestation as a following-response of the type seen in imprinted birds. In the first two days after birth loud noises, rapid movement or approaching people cause the fawn to flatten on the ground or to move to a hiding site nearby. After this two-day period the fawn may withdraw from disturbance with the herd. About ten days after birth the fawns begin lying with the herd.

In the semi-wild herd the initiative in moving is taken by older deer. In groups of hand-reared deer and their normally-reared fawns, leadership and following on approach to people is complicated by. the fawn's fear of humans. Typically the normally reared fawns follow the hand-reared deer when approaching people. The fawns will only come to within a certain distance (depending on their age and experience with people) and then will break away and retreat. This is common in yearlings and older deer as well.

Yearlings that have been reared in the woods race about when approached by people in pens. They withdraw well before the tamer adult deer. The extent of the yearlings' reliance on doe leadership is suggested by the yearlings' disorganized behavior when they are accidently separated from the does. Commonly during the release of deer from pens only the does get through the exit gate. The yearlings run frantically about the pen and charge into the fences while attempting to follow the does. Not only do they fail to recognize the open gate (or fear its newness) and the familiar fences, but they appear to get increasingly frightened. Frequently hours pass before they will leave through the gate.

The phases of normal development in leadership seem to change from independence in the neonate through a long period in youth of strong attachment to the doe to relative independence in the oldest deer. The leader, by definition, is completely independent and follows no other deer. Most of the factors affecting these changes are unknown although the independence which follows hand-rearing may suggest some influences of early experience. One gets the impression from watching the behavior of adult does that the older does wait longer in assessing a situation—they appear very deliberate and decisive in their movements. It would be very interesting to know what causes the older animal to be less reliant on others in decision-making. This is the fundamental trait of the leader.

### B. Leadership and Cohesion in Hand-reared Deer

Observations of three hand-reared does were made from April 1965 to February 1969 in the 75 acre wooded enclosure. Gurri, born in June 1964, was bottle-reared alone and introduced the following March to the semi-wild herd. Marena and Kiki, born in June 1962, were reared together with Ronno and also bottle-fed (except that Kiki was reared alone for 30 days before joining the others). The observations of Ronno with the group are omitted for two reasons. First, the pattern of attachment of males to the does is variable depending on the males' reproductive status and age. In addition Ronno died from an obstructed reticulum during the observation period so comparable data are not available. It was assumed that when Marena and Kiki were seen without Gurri, Gurri was by herself and not with the semi-wild does since the hand-reared deer were vigorously bitten and chased away by semi-wild does when near food. At other times the hand-reared deer displayed no inclination to join the herd.

Thirty-seven observations of some or all members of this group of three were made. In 51% of these Gurri was observed alone or not present with Marena and Kiki. During 33% of the observations when Gurri was present with this pair, all three of the deer were at the feeding station. The proximity of the three could be due to mutual attraction to food rather than to one another. Thus Gurri was moving alone 50-84% of the occasions observed. This is a very large and significant percentage in view of the fact that no wild doe was ever observed alone. Marena and Kiki always moved together, along with their fawns.

No detailed study was made of leadership in the hand-reared group. Each of the four deer (including the male Ronno) was observed to lead others. It was obvious, however, that Gurri had the premature independence seen in leaders but lacked a following (except her fawns—this situation to be dealt with later). Gurri's experience of bottle-feeding alone and passing through the socialization period in the absence of other deer appears to have permanently reduced her gregariousness and may also have made her less attractive to other deer. Scott (1945) found a similar independence of other sheep in lambs reared by humans. Gregariousness in rhesus monkeys is much reduced if they are socially isolated when young (Mason, 1961).

## III. INDIVIDUAL RESPONSES

### A. Resting Distributions of Hand-reared Groups

The location of each member of the two foster-reared groups and their fawns was marked on the scale maps. The sampling periods etc. were described earlier. My expectation was that the places chosen by the deer during daily resting periods would reflect their attraction to other members of the group and the level of gregariousness in general.

From each plot of the individuals' resting locations the following measures were selected: (a) the nearest deer to each of the five deer; (b) the nearest pair of the entire group during that observation; and (c) the farthest pair of the entire group during that observation. In addition, the nearest of the two yearlings to each of their mothers in area 2 was measured.

TABLE 2. RELATIONSHIPS OF DEER AT REST IN AREA 2

Percentage of thirty observations

| Subject | Rearing treatment | Nearest to other deer | Member of nearest pair | Member of farthest pair | Nearest yearling to Marena | Nearest yearling to Gurri |
|---|---|---|---|---|---|---|
| Percentage expected (random) | | 20 | 20 | 20 | 50 | 50 |
| Gurri | bottle-fed singly | 15.7 | 11.7 | 30.0 | – | – |
| Kiki | bottle-fed singly | 17.7 | 16.7 | 26.7 | – | – |
| Marena | bottle-fed with fawns | 17.7 | 13.4 | 21.6 | – | – |
| Marena's yearling | nursed by hand-reared doe | 22.3 | 26.6 | 11.7 | 73.5 | 50.0 |
| Gurri's yearling | nursed by hand-reared doe | 26.6 | 31.6 | 10.0 | 26.5 | 50.0 |

Table 2 contains these frequencies as percentages for thirty observations in area 2. The solitary hand-reared doe, Gurri, was least frequently nearest any other deer (15.7%) while her male yearling was most frequently lying near others (26.6%). This yearling remained closest to other deer as indicated by the high frequency (31.6%) of being one of the members of the nearest pair. Gurri, again, was at the other extreme. The other yearling of the companion-reared doe, Marena, had a high frequency as well. The tendency for tight grouping by the yearlings is indicated in the third column by their very low occurrence as members of the farthest pair of deer in the resting group (11.7% and 10%). These two yearlings were most frequently found resting together of any pair. Gurri, as expected, was most frequently a member of the farthest pair.

The resting relationship of one of the yearlings to the mothers is interesting because the yearling exhibited no preference for either doe. The yearling of the isolate hand-reared doe, Gurri, was just as often the nearest of the two to Marena as it was to its mother. Marena's yearling was the nearest to her almost 75% of the time. Note was taken of those individuals who rested well apart from the main group. Of the thirty observations Gurri was independent seven times, Kiki twice and Marena's yearling once.

TABLE 3 RELATIONSHIPS OF DEER AT REST IN AREA 3

Percentage of forty-five observations

| Subject | Rearing treatment | Nearest to other deer | Member of nearest pair | Member of farthest pair |
|---|---|---|---|---|
| Percentage expected (random) | | 20 | 25 | 25 |
| Nettla | Bottle-fed singly | 18.9 | 16.7 | 26.6 |
| Meredy | bottle-fed singly | 21.8 | 18.9 | 31.1 |
| Shy | nursed by goat | 24.0 | 31.1 | 25.6 |
| Faline | nursed by hand-reared doe | 22.0 | 33.3 | 16.7 |
| Robbie | nursed by goat | 13.3 | – | – |

The comparable figures for the other group are presented in Table 3. A modification in the analysis was made to make the groups more comparable; the columns indicating membership in nearest and farthest pairs does not include Robbie, the two year old, goat-nursed buck. This decision was based on his very high frequency of lying apart from the others (23/45) and because he was an older buck. The first column indicates the relatively low occurrence of his lying nearest to other deer.

The four does showed little preference for resting near particular deer although the two solitary, hand-reared does, Nettla and Meredy, have the lowest percentage as did Gurri, reared similarly, in the other group.

Nettla and Meredy also occur least frequently as members of the nearest pair and are most frequently members of the furthest pair. In contrast, the doe Faline, suckled and reared by her hand-reared mother, is most often a member of the nearest pair (33.3%) and least often a member of the farthest pair (16.7%). Shy, the goat-nursed doe, was a member of nearest and the farthest pairs with about average frequency.

1. *Discussion.* In order to compare both groups of deer relative to their rearing experiences the mean rank of each deer for all three parameters of spatial relationship in Tables 2 and 3 was computed. These are shown in Table 4, the ranks used to compute the means being those from the individual's own group. It should be noted

that the order of ranking in the third column of Tables 2 and 3 is reverse, the *greatest* frequency being given the *lowest* rank. This is consistent with the fact that it is the farthest pair that is under consideration here.

TABLE 4. RELATIONSHIP BETWEEN REARING TREATMENT AND SPATIAL DISTRIBUTION AT REST

| Name | Rearing treatment (time with deer after birth, in hours) | Rank of rearing treatment | Mean rank of three parameters of spatial relationship |
|---|---|---|---|
| Gurri | hand-reared singly (1) | 1 | 1.3 |
| Nettla | hand-reared singly (8-18) | 2 | 1.7 |
| Meredy | hand-reared singly (21) | 3 | 1.7 |
| Kiki | hand-reared singly (24) | 4 | 2.2 |
| Marena | hand-reared with fawns (48) | 5 | 2.5 |
| Shy | nursed by goat | 6 | 3.3 |
| Faline | nursed by hand-reared doe | 7 | 3.7 |
| Marena's fawn | nursed by hand-reared doe | 8.5 | 4.0 |
| Gurri's fawn | nursed by hand-reared doe | 8.5 | 5.0 |

The order of rearing treatments is arranged from the maximum of artificial feeding and human contact, ie. hand-reared singly, to the minimum of human contact encountered in normal rearing. It is clear that the four does reared alone were the farthest from other deer in mean rank of all three parameters. Next is the doe that was bottle-fed with other fawns, followed by Shy who was nursed by a goat. The three does that were reared by their mothers rested most closely to other deer. One of these does, Faline, differed from the others in that her mother was not part of the group. All of the deer in Faline's group (area 3) were strangers to her when she was introduced as a two year old, one year prior to these observations.

The high correlation between the rearing treatment and spatial distributions of the experimental deer suggests that gregariousness of the adult deer varies with the amount of exposure to deer when very young, including the first day of life. Before pursuing this relationship there are other uncontrolled variables which must be examined. Age, for example, might influence spatial relationships. If older deer rest farther apart we would expect Marena and Kiki rather than the three younger, hand-reared does to rank higher. Bottle-feeding as a significant factor by itself can be eliminated since it does not help differentiate the five hand-reared does, although duration of bottle-feeding is obviously correlated with the duration of early experience with people.

The four isolate, hand-reared does had spent varying times with their does during the first day after birth. These differences were used to rank the four deer according to rearing treatment in Table 4. Gurri, the isolate hand-reared doe, ranked lowest in spatial relationship (i.e. she was least gregarious). She, also, had been separated from her mother earliest (one hour after birth). Nettla and Meredy, also isolate-reared does, tied for second place in spatial relationships. Nettla had been separated from her mother 8-18 hours after birth and Meredy at 21 hours of age. Kiki, the most gregarious of the four isolate, hand-reared deer had been separated at 24 hours of age. This correlation suggests that the amount of contact with deer (or inversely, people) in the first *day* of life influenced the gregariousness of these four deer three to six years later.

The next most gregarious doe, Marena, had been separated latest of all the hand-reared deer at 48 hours. In addition, she had been hand-reared with other fawns. Shy, separated 6-20 hours after birth and goat-nursed was ranked next in rearing type because goat-nursing was considered to rank between bottle-feeding and doe-nursing in type of rearing treatment. This rank was relegated prior to determination of her rank in spatial relationship, of course. If this procedure is considered unacceptable her rank can be detected without altering the rank correlation significantly. Faline had been nursed by her hand-reared mother in a pen with much close approach by people. She was tested with strange deer. Thus she might have been expected to rest farther away from the others than the most gregarious deer—the yearlings of Marena and Gurri. Both Marena and Gurri ranked highest in gregariousness, likely due to their continued contact with their mothers throughout life and especially because they were tested in pens with their mothers. They were not threatened and bitten as was Faline, a stranger.

## B. Flight Distance from People

1. *Change from immobility to flight in normally-reared fawns.* The responses of 7 fawns to approaching people and other disturbances were recorded at varying intervals after their birth. The fawns had been born within the confines of the maternity pen. Their times of birth were established within 8 hours in most cases. As noted earlier in the discussion of mother-young behavior the newborn deer responds quickly to tactile stimuli from the mother. Visually guided movements toward her were seen shortly after birth. The particular behavior of interest here is the development of different responses to people, ie. the change from hiding to withdrawal behavior in fawns.

During the fawn's first twenty-four hours it remains lying down and if approached will usually lower its head and remain still. Loud noises, such as water striking a pail from a hose, a passing car, or a snapping stick, elicit flattening of the head to the ground. If fawns are standing when approached, they withdraw or flatten themselves on the ground. A male fawn, born to a hand-reared doe and still moist (likely less than two and not more than eight hours old) moved away from me with its tail raised high in fright. It could not have been getting flight cues from its mother since she was not at all alarmed by my presence. Rapid movements of does and the barking of a dog also caused fawns to run and hide. The upper section of Figure 1 shows the responses of seven fawns when approached while lying down at various times after birth. The transition from flattening on the ground ('freeze' response) to jumping up and running (escape response) is indicated by a horizontal line joining the last instance of the freeze response with the first instance of the escape response. The mean ages for the two responses places the time of transition between 19 and 48 hours for fawns which have had no prior exposure to people. This transition period could no doubt be defined more precisely with a systematic study using standardized approaches: the collection of these data was incidental to other studies. The response to approaching people may be rather variable. One male fawn, aged 27 (±8) hours, jumped up when *first* approached by a person and stood its ground. When I approached him, he lowered his head and charged me, striking my legs with his head. This was repeated about six times. It appeared to be a defensive attack and certainly had no components of play behavior. The particular stimulus configuration eliciting this behavior is unknown: I approached slowly in the usual way.

As early as two hours after birth the fawn of a hand-reared doe flattened its head on the ground when I approached. Other fawns responded similarly when deer ran quickly by. If approached very slowly shortly after birth by people or deer this response is not elicited. It may be that very young fawns respond to intense, general stimuli (rapid movement, loud sounds) and later, when the flight response develops at one or two days of age, are able to discriminate unfamiliar objects (people) from the familiar ones on the basis of more subtle visual patterns. This interpretation accounts

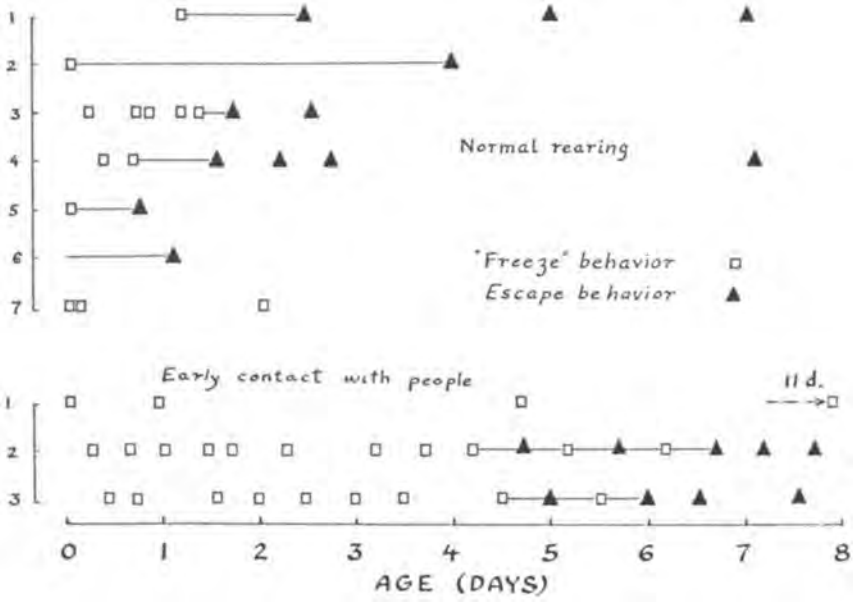

Fig. 1. Change of Fright Response in Newborn Fawns.

for the behavioral changes in newborns of other species of ungulates. Miller (1965) observed a two hour old black-tail deer fawn prostrating himself with his head stretched out on the ground after the doe that was nursing it jumped to her feet and ran away. Similar 'head low' behavior was noted in three pronghorn fawns by Bromely (1967) on the National Bison Range, Montana when approached by men. However, three others were observed to approach men and one followed its captor. All fawns were between 41 and 200 minutes old. This apparent contradiction may be resolved if in fact the fawns are responding to the intensity or quantitative nature of the stimulus rather than the configuration of the object, ie. the approaches of the people may have been different. This is consistent with the observations of fawns dropping down when a twig snaps loudly while its mother walks calmly by. The withdrawal in both instances may be elicited by loud stimuli or stimuli of increasing magnitude (e.g. an approaching person).

Approach behavior in neonates similarly appears to be guided by quantitative differences in stimuli, ie. large receding objects rather than by fine discrimination. This following behavior appears more commonly in the more precocious bovids than in the Cervidae which typically spend the first few days in hiding. Talbot and Talbot (1963) state that a one or two-day-old wildebeest calf (*Connochaeles laurinus*) 'will follow virtually anything that moves, including a Land-Rover or a human.' Buffalo calves were reported to follow hunters on horse-back so closely that they were kicked by the horse (Garretson, 1938). Pinter (1962) found that roe deer fawns that are foster reared when newly born or 'in the very first few days, attach themselves completely to their keeper, dogging his footsteps'. These observations of approach and attachment support the 'approach-fixation' theory of Schneirla (1959).

The rapid change to flight behavior a day or two after birth on the approach of a person likely results from the improvement of perceptual discrimination. The young may still be withdrawing from intense stimuli but now it is the unfamiliar human figure which is providing that stimulation. The change was observed in elk by Murie (1951). The newborn calf allows itself to be handled or lifted from the ground but a calf a few days older is likely to flee when closely approached. White-tailed deer fawns, according to Haugen and Speake (1957), resist handling with increasing vigor after 4 days of age.

In summary, the response to intense stimuli (loud noise or rapid movement) of day-old fawns is to squat if standing and to lower its head and freeze if lying down. Very close approach by people does not elicit jumping up and running, although there is no evidence to assume as Haugen and Speake (1957) have done, that the fawn is relaxed. In subsequent days, fallow deer fawns still hide if standing after the appearance of a person at a distance but jump up on nearer approach and run to the herd.

2. *Change from immobility to flight response in fawns exposed to people.* Various studies with ungulates and my observations made during bottle-rearing suggest that there is a short period early in the fawn's life during which it becomes familiar with nearby objects and to which it later shows no fear. This interval has been referred to as a 'critical period' in birds and mammals if the establishment of a preference occurs during a relatively restricted period of time and not at other times. An experiment was designed to determine the effect of an eight hour exposure to people during the fawn's first 24 hours of life on their subsequent flight response to these same persons. Due to lack of births (one hand-reared male with four does proved infertile) only two fawns were available in the 1969 season for the experimental group. The observations of normally reared fawns from former years (Fig. 1 #15 1-7) were used as controls.

The fawns born in 1969 (Fig. 1 #2 and #3 of the experimental group) received their eight hour exposures to people at different times in the first 24 hours because one was born during the night. One fawn (#2) was born between 8 p.m. 4 June and 10 a.m. 5 June 1969. From 10:40 a.m. until 8 p.m. an assistant and myself alternately sat beside the fawn for a total of 8 hours. We were usually less than five feet from him but he moved occasionally up to about twenty feet away. Fawn #3 was born to a hand-reared doe in the woods outside the pen. I carried it back to the pen for observations. The fawn's mother refused to follow me with the fawn. She persisted in returning to the birth site despite my holding the fawn to her for sniffing as I walked away. Eventually I left her and gave the fawn to Kiki, the hand-reared doe who had given birth to fawn #2 the night before. Kiki licked it immediately and early the next morning was observed nursing it. This continued even though the fawn's own mother entered the pen on her own later that day. Prior to her entry I carried the fawn to its mother and she licked it through the fence. This carrying may have had an effect on the fawn's subsequent reaction to people, as it was the less timid of the two. The time elapsed returning the fawn to the pen is included in the 8 hours we spent with this fawn. The major difference was that this fawn (#3) had one hour's contact beginning one-half hour after its birth.

The third fawn (#1) of the experimental group received rather different attention after its birth on 1 June 1967. Less than one hour post-partum I picked it up and moved it 50 feet so that it could be observed from a hidden site. Twenty-three hours later I sat beside it for ten minutes and carried it from the barn to a pen for observations. It walked into the barn and I carried it out again. This constituted its total contact with people during its first 24 hours.

The response of these three fawns to my approach are shown in the lower half of Figure 1. Fawn #1 did not jump up and run even after eleven days. The mean age of last 'freeze' response of these three is 7.8 days compared with 0.8 days for the seven normally reared fawns (Table 5). The mean age of first 'escape' response was 7.1 days compared with 2. 0 days for the seven normally reared fawns. A conservative assumption was made that fawn #1 would exhibit escape responses after 11 days. Although the different size groups and unequal numbers of tests prevent statistical, analysis, the effects appear striking none-the-less. The long term changes in the behavior of these fawns will be described in Chapter IV.

3. *Flight distance in newborn fawns.* The flight distance of the two fawns which were exposed to people for 8 hours was recorded at the time the responses to approach were observed. The flight distance is the distance between the approaching person and the standing or resting fawns at the time the fawn withdraws. The averages of 3-day periods from birth to 17 days are shown in Figure 2. The trend of increasing flight distance is obvious, although individual scores were highly variable. Especially interesting is the decreasing difference between the resting flight distance and standing flight distance from the 3-5 day period to the 9-11 day period. This was observed

TABLE 5. THE EFFECT OF 8 HOURS OF EXPOSURE TO PEOPLE ON THE APPERANCE OF THE FLIGHT RESPONSE IN FAWNS.

| | No contact with people | Contact with people |
|---|---|---|
| Number of fawns | 7 | 3 |
| Age of last 'freeze' behavior (days) | 0.8 | 7.8 |
| Age of first escape behavior (days) | 2.0 | 7.1 |

in both fawns. The much shorter flight distance for resting fawns in the 3-5 day period suggests that the fawns still had a strong tendency to remain lying down. By the 9-11 day period the distance at which the fawns withdrew from an approaching person was the same whether they were standing or lying down.

The trend for both flight distances to increase would appear to indicate that the sensitivity of the fawns to approaching people was increasing. The fawns are more skittish despite the greater familiarity with people that the fawns obtained during the test approaches. I do not, unfortunately, have similar information for fawns which has no exposure to people after birth.

4. *Flight distance of older fawns.* The flight distances of the two fawns exposed to people were measured on ten occasions between 15 and 18 weeks of age. Both fawns followed the hand-reared doe Kiki since one was her fawn and the other she adopted as noted earlier. The flight distance in this case was the shortest distance the fawns would come to a pan of oats while I sat near it. The modal distance was three feet and the maximum was five feet. On one occasion I was able to touch a fawn on the head. Kiki always led the fawns to the food and it is likely that they were drawn closer to me by her presence.

5. *Discussion.* Even though this experiment is limited by the small number of experimental subjects the paucity of investigations of attachment behavior in ungulates warrants more than cursory discussion. The relatively short exposure to people by the three experimental fawns (Fig. 1) in their first twenty-four hours clearly extended the time period during which they remained immobile on the ground when approached. The oscillation of responses of the two fawns receiving 8-hour exposures may be an artifact of the more frequent testing. There also may have been a greater ambivalence resulting from an increase in the period of transition from one response to the other.

One might be tempted to attribute the transition from the freeze response to flight solely to development of fear in the fawns at about 1½ days of age. This could be based on an increasing ability to discriminate familiar from strange objects. This is unlikely since standing fawns will withdraw from people when approached well before 1½ days of age. If more information were available on the time of first instances of withdrawal while standing we would be better able to judge whether a sensitive period exists for forming attachments and what its temporal limits are.

The increase in flight distance observed up to at least 17 days may be interpreted as a manifestation of increasing fear. The situation is complicated further by observations of month old fawns running to hiding spots such as inside the barn and lying down. In these locations the fawns tolerate much closer approaches than occur in the open.

None of our fawns received prolonged exposure to people immediately after birth. Considering the fawn's hiding response to loud noises and rapidly changing visual stimuli it seems likely that perceptual learning is beginning at this time. This is the period of most intense licking by the doe which may sharpen the fawn's discrimination of visual and olfactory characteristics of deer. Whether attachment processes

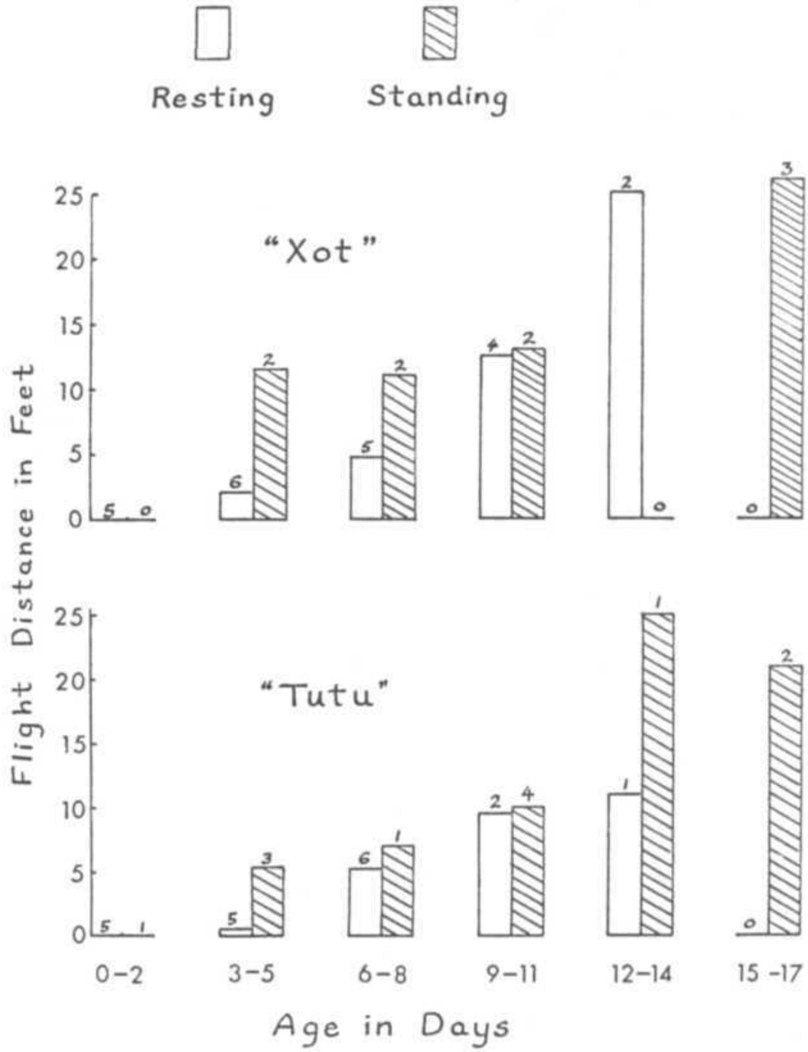

Fig. 2. Flight Distance of Fawns

(Exposed to people 8 hours in their first day)

continue over a longer period of time or only during a short critical period will have to be determined by further experimentation.

The radical reduction of the flight distance of the two exposed fawns at a feeding pan is somewhat difficult to interpret. Their close approach is no doubt affected by their hand-reared mother who approached people and tolerated patting. We do know, however, that fawns born to hand-reared does *in the woods*, thus receiving no close exposure to people and none at all in their first week or so, are still very timid even when their mothers approach people for food. Typically they break away from the does when 100-150 feet away from people and run into the woods. This occurs in spite of their tendency at this age to stay very close to their mother when they are fearful. Much of the change in the approach behavior of the two exposed fawns can be attributed to the eight hours exposure to people but it is also true that the tests for flight distance in their pen gave them an opportunity to become more familiar with people. These two factors can only be separted by testing the later approach behavior of fawns whose experience with people is limited strictly to a period shortly after birth. If they still approach closely then reference to an early 'critical' period would seem warranted.

6. *Flight distance in wild adults.* When the original herd was introduced into the 75 acre enclosure one had to move quietly and rely on binoculars to see them before being seen. Eventually, with more contact, the older deer would approach food placed out for them but the observer still had to withdraw 150 yards or more. When confined to pens the deer were very timid but here again, when very hungry, the older deer would come forward within about 100 feet. These were deer which had been confined in the 41 yard-long pen for a few months and become accustomed to people entering the pen daily to place food. Nevertheless the deer always initially ran to a remote corner.

Young deer, especially yearlings, were noticeably more prone to break away from a captive herd or to get up first from a resting group on the approach of a person.

7. *Flight distance in hand-reared adults.* All but one of the 9 does and 2 bucks reared on bottles were taken from their mothers between 12 and 24 hours after birth. The one exception remained with her mother 48 hours. Since they were handled continuously as young it is not surprising that they had flight distances of zero. This lack of flight response was generalized to strangers. Although the hand-reared deer were skittish if a person held a strange object or wore odd clothes, so were the wild-born fawns when first confronted by an antlered buck.

This tameness did not change detectably over a period of seven years for some hand-reared does. Over a five year period they had opportunities to join the semi-wild herd or remain apart from people in the large enclosure but did neither. One could count on being met by them at dusk at the evening feeding or near the fowl feeders throughout the day.

The hand-reared deer were the most thoroughly tame of all the deer. The subtle differences between those bottle-fed alone and in pairs will be discussed in the next section. This tameness is to be expected since they received much handling in homes from a very early age and also food rewards from people. Thus if there are specific periods for social attachments there were people present to interact with these deer at that time.

The stability of the relationship to people in both wild and hand-reared deer is worth noting. Unlike wild adult members of the genus *Odocoileus* that approach tourists in parks for food our fallow deer remained timid if wild-born.

### C. Maternal Behavior and Fertility

Interference with early social development might be expected to alter the choice of mate and the relationship between the hand-reared or goat-reared deer and their own young. No attempt at a systematic study of these changes was made; however, some incidental observations were striking enough to be worth including.

The semi-wild deer were very fecund. In 7 years the original 10 deer grew to a herd of 43 despite periodic culling. Births among the hand-reared does were common, indicating that the rearing procedures did not prevent mating, in does at least. The ability to rear young was variable, however. Marena and Kiki, who were hand-reared together, nursed and reared fawns successfully. Three of their other fawns were taken from them and hand-reared successfully. In contrast, Gurri, who was hand-reared alone, did not successfully rear either of the two fawns which she bore. The first fawn was found dead two and one-half days after birth. A necropsy by a veterinarian indicated no pathological condition. He speculated that malnutrition was the cause of death. The second fawn born two years later was closely observed. Although Gurri licked it after birth no nursing was observed. When the fawn was strong enough to approach Gurri to nurse, Gurri would walk away when the fawn got near her udder. The fawn may have been weak initially since it was unusually long in moving toward the doe and slow to respond to licking. When 24 hours old the fawn had scrapes in its skin and small, hairless areas of skin which appeared to result from rough pawing by Gurri. Pawing is not uncommon when a fawn fails to rise to her mother's licking at the beginning of a nursing session. Perhaps the fawn had grown tired of attempting to nurse and her mother, not relieved of udder pressure, persisted in trying to raise the fawn. At this same time a large number of blowfly eggs were found matted in the hair around the fawn's anus and adjacent areas of its legs. This infestation and smeared feces were never observed in other fawns and indicated that Gurri was not licking the fawn clean as is usual. Despite cleaning and giving supplemental milk the fawn was discovered moribund when three and one-half days old and was destroyed. No necropsy was performed because death was almost certainly due to malnutrition.

In the fall of 1968 one goat-nursed, and three hand-reared does ranging in age from two and one-half to four years were together with a two and one-half year old buck. This buck, 'Robbie', was suckled by a goat and kept with goats along with 'Shy', the goat-nursed doe noted above. The latter two were suckled by goats for approximately seven months and remained in the goat pen for 16 months. During the rut that fall Robbie displayed the usual agressiveness to the does. Robbie was less aggressive to people than was a hand-reared buck. He thrashed vegetation and fences like other deer. His movements along the fences adjacent to the goat pens indicated he was sexually attracted to female goats. Outside the rut period he was not prone to remain near the fence dividing his pen from that of the goats. Robbie was observed by other people to mount estrous goats and to attempt intromission when he was still in the goat pasture. Mounting was never observed when he was penned with the deer. He did follow does in heat but when he got close behind a doe that stood for him he lowered his antlers and pushed her forcefully from behind. The doe never appeared to be harmed. She moved away after being hit, only to stand again. No mountings were observed. None of the four does became pregnant.

1. *Discussion.* Disturbed maternal behavior in isolate-reared monkeys has been reported by Harlow *et al.* (1963). Scott (1945) separated a lamb from its mother for 9 days immediately following birth. When it bore lambs it showed lessened maternal care and reacted only mildly to frequent separation from them. Like Gurri, it showed a tendency toward independence of its own kind.

An understanding of Gurri's failure to nurse is confounded by two factors likely to contribute to abnormal behavior: (1) her early separation from her mother (at less than one hour of age) and (2) isolation from deer during the following nine and one-half months. The behavior of another hand-reared doe, Kiki, may provide a clue. She was isolated from deer for 30 days following *24 hours* of contact with her mother. Kiki reared fawns successfully. This suggests that the contact with the mother in the first day may be necessary for proper care of young as an adult.

Robbie's preference for goats as mating partners probably resulted from his attachment to them during nursing and later socialization. His failure to mount does cannot be attributed to lack of opportunity to mount fawns during infancy since another fawn was in the goat pen at the time. Mounting of fawns by other fawns is commonly observed in undisturbed deer. Unfortunately no observations of these fawns were made since I had not initiated the present study at that time. We do not know the extent of interaction between the two goat-reared fawns, if any.

Matings between species has been observed in other ungulates, especially in cases of cross-fostering or when the mating pair were reared together. Hediger (1955) relates the conditions of cross-fostering under which alpaca (*Lama pacos*) will cross with vicuna (*Lama vicugna*). Peruvians catch a newborn vicuna and place the skin of a freshly-killed newborn alpaca over it. The vicuna is then accepted by the mother alpaca and reared. It is said that only alpacas with this treatment, similar to our goat-reared deer, will later pair and produce hybrids. Similar crossings are reported by Flowers (1969) by raising the vicuna and alpaca together from infancy. The importance of early experience in producing ninnies (stallion x she-ass) is suggested by Gray (1954). Since the stallion does not readily mate with the she-ass, male foals intended for hinny breeding are kept among asses almost from birth. Other cases are cited, e.g. a young zebu bull brought up in a buffalo (*Bubalus bubalis*) herd mated regularly and frequently with buffalo heifers, and a male eland (*Taurotragus oryx*), reared by a cow, served many cows and heifers. The establishment of preferences for other species must be fairly common in zoos where varieties of species are penned together. The great frequency of hybridization can be appreciated by the check-list and bibliography compiled by Gray (1954).

## IV. INTERACTIONS

### A. Aggressiveness

Aggressive behavior (threats and biting) was very rare among does in the semi-wild herd. Apart from the aggressiveness of males during the rut there were three situations when threats and biting increased in frequency. First, biting among the group increased when preferred food such as oats or corn was placed in one spot. Presumably aggregation around the food caused trespasses upon individual distances. Secondly, does with newborn fawns bit other members of the herd which approached the fawns. Mothers were also intolerant of the fawns of other does: the specificity of this has been analyzed in detail in an earlier study (Gilbert 1964). Finally, the introduction of alien hand-reared deer (one hand-reared group of two female fawns and one male fawn and later one hand-reared fawn) elicited bursts of intense threats, chasing and some biting from the semi-wild deer, all directed at these strangers.

The frequency of biting behavior during feeding was compared in the three groups of penned deer. This method of obtaining information on dominance relationships was chosen because spontaneous biting was so infrequent in the established groups. Thus, while useful for comparing groups or determining the dominance hierarchies it may be of little use for estimating the frequency of aggressive behavior among undisturbed wild animals

All reasonable precautions were taken to ensure similar situations for observations. The observer entered the pen of the semi-wild herd so as to create the least disturbance when placing the grain, then went directly to an elevated site in the nearby deer barn to observe. Observations of the other two groups were made in the open from about twenty feet away. All three groups came to the food shortly after it was set out. Less preferred food (hay and pressed alfalfa) was available *ad libitum.*

Each group was observed for 15 minutes immediately after their food had been set out on twelve different days. A sample of 15 minutes was chosen because the deer almost left the feeding area before the end of this time interval. Often the biting declined precipitously within five minutes.

1. *Between group comparisons of aggression* The total number of bites within each experimental group is given in Table 6. Biting within the control group or semi-wild group (area 1) is omitted in tabular form because it was so rare. Although this group was composed of six deer, only one doe was observed biting and she bit only four times during the total of four hours of observation. The three hand-reared does and the fawn nursed by one of them (in area 2) bit others 96 times. The largest number of bites, 225, occurred among the group in area 3. It consisted of two does, each of which was hand-reared alone, one doe which was foster-reared by a goat and one doe which was nursed by its hand-reared mother in a pen at a distant location.

The original aim in establishing these three groups was to compare the adult social behavior of two groups of hand-reared deer, one of which had considerable subsequent contact with the semi-wild herd. Before the study was completed, the information which has been collected pointed to the conditions of early rearing as being the more significant factor in determining later behavior. Accordingly, the results were analyzed with respect to rearing conditions of individual deer and thus cut across pen groupings. This discussion follows in the next section.

The very low frequency of biting in the semi-wild herd corroborates observations at other times when the deer were less confined. This group was very likely a stable herd in the large enclosure since they were all trapped at the same time. Most of them were probably closely related. Only one of the six deer, an adult doe, was observed biting. In comparing the biting behavior in the groups the most remarkable difference is the high frequency in both of the hand-reared groups.

2. *Between individual comparisons of aggression.* The two groups of mainly foster-reared deer were composed of the following: 3 does (4, 5 and 6 years old) which were

TABLE 6. DOMINANCE RELATIONSHIPS AMONG FOSTER-REARED-DEER

NUMBER OF BITES

AREA 2

| Dominant doe | Age (yrs) | | Subordinate Doe | | | |
|---|---|---|---|---|---|---|
| | | Kiki | Gurri | Marena | M. fawn | Total |
| Kiki | (7) | – | 14 | 13 | 40 | 67 |
| Gurri | (6) | | – | 24 | 3 | 27 |
| Marena | (7) | 1 | 1 | – | 0 | 2 |
| M. fawn | (1) | | | | – | 0 |
| | | | | | | 96 |

AREA 3

| Dominant doe | Age (yrs) | | Subordinate Doe | | | |
|---|---|---|---|---|---|---|
| | | Nettla | Meredy | Shy | Faline | Total |
| Nettla | (5) | – | 50 | 58 | 48 | 156 |
| Meredy | (4) | 5 | – | 21 | 35 | 61 |
| Shy | (3) | | 4 | – | 4 | 8 |
| Faline | (3) | | | | – | 0 |
| | | | | | | 225 |

hand-reared alone: two 7 year old does reared together with three male fawns (except that Kiki, one of the does, did not join the group until she was 31 days old); one 3-year old doe reared by its hand-reared mother; and one 3-year old doe which had been suckled by a goat.

The does in Figure 3, which are classified as hand-reared alone, spent their first thirty days (or more) in houses completely isolated from other deer. The difference in biting frequency of this group is very pronounced. Although these four constituted only one-half of the deer in the two experimental groups they accounted for 97 per cent of the biting. Nettla was the dominant doe in her group with a total of 156 bites which were distributed about equally to the other three deer. Meredy, one year younger than Nettla, bit Nettla five times. This was the greatest frequency of bites by a member lower on the dominance order directed at a more dominant doe.

Among the members of the other group Kiki, a hand-reared doe, was dominant and bit others 67 times. There was a tendency for her to bite the fawn of Marena more often than either Marena or Gurri. Gurri, who spent the least time with deer throughout her early rearing, dominated Marena who was a year older and companion-reared. Unlike Kiki, Gurri tolerated Marena's fawn, biting it only three times. Marena bit each of the two more dominant does once each, giving her a very low total for a 7-year old doe. Faline and Marena's fawn were not observed biting other deer.

3. *Discussion.* Normally-reared deer bit strange deer (introduced hand-reared deer) and the young of others. It seems reasonable that the biting occurred under similar circumstances in the experimental groups. The largest difference separates the four does which were hand-reared from all the others. Since they are as old or older then the others in their respective groups the difference might be attributed largely to age. There is no doubt that older animals are generally dominant over younger animals and this may account for some of the difference. However, the control herd of semi-wild deer had two mature adults, one yearling and three fawns but there were only four instances of biting and those were between one doe and the fawns. Also a hypothesis involving age does not explain why Kiki bit 67 times while another doe,

Marena, of the *same* age and similar rearing (except for her first month) was subordinate in the group and bit other deer 2 times. The difference in the rearing experiences of Kiki and Marena provides a clue to the former's high biting frequency. Kiki was bottle-fed during her first month without contact with other deer whereas Marena was bottle-fed along with three other fawns. Kiki shares this feature with the other three hand-reared deer although they were even older before joining other deer. Thus not only is the high frequency of biting associated with hand-rearing in isolation from other deer but it appears that it results from some lack of social interaction in the first month. This latter conclusion is rather tenuous because only one doe was available for comparison with the four does reared away from other deer.

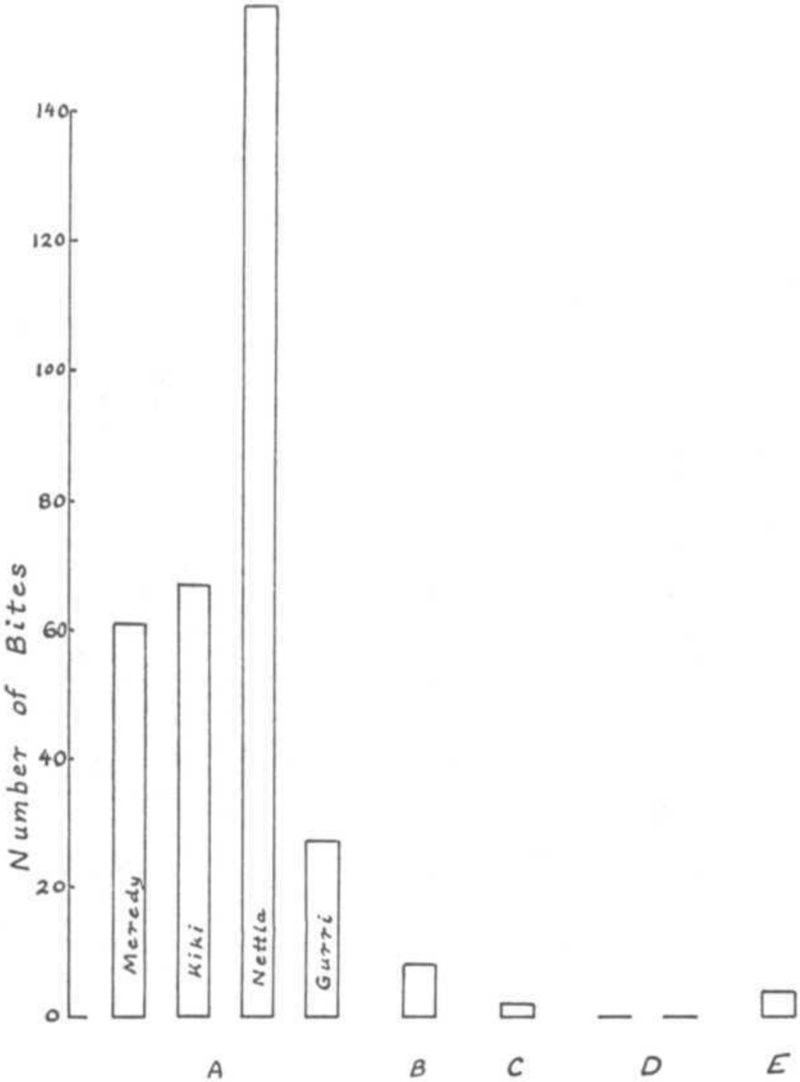

Fig. 3. Number of bites delivered to other deer at the feeding sites (3 groups; 12 trials totalling 4 hours)

(A) isolate-reared
(B) goat-reared
(C) companion reared
(D) tame doe-reared
(E) wild doe-reared

The difference in biting frequency within the class of 'hand-reared alone' does, cannot be explained with certainty. Nettla's rate of biting, which was the highest, might be due to the fact that the deer in her pen were about one year old on the average before being placed together, thus constituting a herd of strangers relative to the deer in the other pen. Thus her very frequent biting may be due more to the fact that all of the deer were one or more years old when brought together rather than just a temperamental difference resulting from rearing in isolation from other deer.

Another possibility is that the difference in aggressiveness between the control and experimental groups resulted *solely* from strangeness, ie. the isolate deer responded in the same way that wild individuals would have if arbitrarily placed together. But some experimental animals *did* bite their life-long companions. And the converse was true, ie. a companion reared deer (Marena) did not bite a stranger (Gurri). Rather Gurri, an isolate-reared doe, clearly dominated Marena. It appears that the frequency of biting was increased greatly by isolate-rearing and further still by placing unfamiliar deer together. It is possible, of course, that isolate-rearing had this effect by enforcing attachment to the foster-parent type during the socialization period, thus ensuring that all other deer would be treated as strangers when first encountered.

## B. Responses to Approach and Contacts with People

One of the major variables in the early experience of the hand-reared deer was contact with people. My experience with these deer under a variety of conditions indicated persistent differences among them in their tolerance of approach and handling. The following tests were devised to investigate these differences. From May 5 to May 20, 1969, each deer in the two experimental groups was tested during ten daily feedings for (i) its tolerance of my rubbing its nose, ears and neck, (ii) the nearest distance which it would approach a food pan with me beside it and (iii) the incidence of solicitation of grooming from me when I sat at a distance from the food pan. To stimulate consistent approach corn or oats was added to the regular food. A positive score for head contact was recorded if the deer did not withdraw its head from near the food pan when scatched gently first on the nose, then ears and neck. Solicitation of grooming consisted of an approach to the observer, who was sitting remote from the food, and holding her head close enough for scratching. Although it was difficult to judge if the animal wanted scratching or more food on first approach, there was never any doubt when I ceased scratching, since the doe would thrust her head sideways and toward me in the species-typical gesture for grooming in a particular spot.

The results for all the deer on ten occasions are shown in Table 7. The three doe-reared deer (Faline and two fawns) allowed no contact with any part of their heads and did not solicit grooming. This was corroboration of all our former casual observations. They were also very consistent in the nearness which they would approach me near their food.

The doe, Shy, and buck, Robbie, which were suckled by goats, would allow head touching in the nose area but Shy allowed her neck touched only once. She never solicited grooming from people. Robbie solicited grooming on five of the ten tests.

The four hand-reared deer (Nettla, Meredy, Kiki and Gurri) who were bottle fed individually in their first month were tolerant of contact on all occasions. Solicitation of grooming was frequent, especially by Gurri who not only had the highest score but was the first to initiate solicitation in her group on eight out of the ten occasions. Marena, the only doe which was hand-reared with companion fawns, did not solicit grooming although she tolerated contact almost as frequently as the others.

1. *Discussion.* The major differences in tolerance of contact with the head are correlated with amount of contact with people when very young. The three intolerant deer remained with their mothers after birth. Faline was born in a small pen where people were frequently walking nearby. This familiarity is evident from the low average approach distance of 2.5 feet. The other two fawns would not approach as close, averaging 11 and 18 feet. Both of them were born in the woods and came in contact with people later, when they were following their mothers a week or more after birth. These short distances were not observed a good deal prior to the test period. It is likely that they became habituated to people while following their unfearing mothers near people.

TABLE 7. TOLERANCE OF DEER TO APPROACH AND CONTACT WITH PEOPLE (10 TRIALS)

GROUP 3

| Name | Rearing treatment | Allows touching | | | Solicits grooming | Nearest approach to a person (ft) |
|---|---|---|---|---|---|---|
| | | Nose | Ears | Neck | | |
| Nettla | bottle-fed singly | 10 | 10 | 10 | 7 | 0 |
| Meredy | bottle-fed singly | 10 | 10 | 10 | 7 | 0 |
| Shy | nursed by goat | 10 | 4 | 1 | 0 | 0 |
| Faline | nursed by hand-reared doe | 0 | 0 | 0 | 0 | 2.5 (0-10) |
| Robbie | nursed by goat | 10 | 10 | 9 | 5 | 0 |
| GROUP 2 | | | | | | |
| Kiki | bottle-fed singly | 10 | 10 | 10 | 5 | 0 |
| Gurri | bottle-fed singly | 10 | 10 | 10 | 9 | 0 |
| Marena | bottle-fed with fawns | 9 | 9 | 9 | 0 | 0 |
| Marena's fawn | nursed by hand-reared doe | 0 | 0 | 0 | 0 | 11 (9-12) |
| Gurri's fawn | nursed by hand-reared doe | 0 | 0 | 0 | 0 | 18 (12-25) |

TABLE 8. RELATIONSHIP BETWEEN TIME OF FAWN'S REMOVAL FROM ITS MOTHER AND ATTACHMENT BEHAVIOR TO PEOPLE

| | Time with doe before removal (hrs) | Rank | Soliciting Grooming | Rank | Contact Grooming and Distance (-) | Rank |
|---|---|---|---|---|---|---|
| Gurri | 1 | 1 | 9 | 1 | 39 | 1 |
| Nettla | 8-18 | 2 | 7 | 2.5 | 37 | 2,5 |
| Meredy | 21 | 3 | 7 | 2.5 | 37 | 2.5 |
| Kiki | 24 | 4 | 5 | 4 | 35 | 4 |
| Marena | 48 | 5 | 0 | 6.5 | 27 | 5 |
| Faline | 100+ | 7 | 0 | 6.5 | –2.5 | 6 |
| Marena's fawn | 100+ | 7 | 0 | 6.5 | –11 | 7 |
| Gurri's fawn | 100+ | 7 | 0 | 6.5 | –18 | 8 |

The deer are ranked in Table 8 according to the number of hours spent with their mothers after birth. (The goat-reared pair are omitted since (a) they developed bonds to goats, not to the deer and people which are of interest here, and (b) the time of removal after birth of one is unknown.) Compared with this are their ranks in solicitation of grooming and an index arrived at by adding all scores of the contact, grooming and nearest approach tests ('nearest approach' was assigned a negative value). These are presented separately since solicitation of grooming is a measure which is independent of the others. A high correlation is present between all ranks. The top four deer constitute a rearing class which were exposed to their mothers less than 24 hours and then individually bottle-fed apart from deer. Within this group note that Gurri was removed from her mother less than one hour after birth and also demonstrated the greatest social bond to people judging from her high rate of solicitation of grooming. Not only was she the first deer to approach for grooming in 8 of the 10 tests but observations throughout her life in the large enclosure indicated a lack of attachment to other deer and a strong bond with people. An instance of Gurri's recognition of classes of people is relevant here. On March 27, 1964, Gurri was moved from the farm of P. H. Klopfer, where she had been reared since birth on June 14, 1963, to the deer enclosure. Gurri had three girls as play companions, ranging in age from 2 to 6 years. Four days after her introduction to the deer enclosure Gurri approached a two year old boy whom she had not seen before, licked him repeatedly on the face and hair and followed him about. She persisted in following him, sometimes beside him, sometimes behind him. This unusual behavior was never observed toward other people or deer. Presumably the boy's short stature elicited the affectionate behavior in Gurri, despite other dissimilarities between him and the long-haired girls.

Of the four does reared in isolation Kiki ranked lowest in the measure of tolerance of people. She solicited grooming on only half of the trials. She also remained the longest of the four with her mother. It is interesting that she was groomed by Marena on a number of occasions in the large deer enclosure, a further sign of her greater bonding to deer than the others

A distinct difference in Marena's relationship to people is indicated by her failure to approach people and be groomed. Her early experience involved late removal from her mother (at 48 hours of age) and subsequent rearing with three other fawns. Although both of these social contacts might be expected to enhance bond development with deer rather than people, I believe the experience with fawns only maintained a preference already determined in the first 48 hours. The evidence supporting this view is present not only in the correlations just discussed for the other four hand-reared deer, but also in the development of flight response discussed in an earlier section (p. 259). Those observations clearly indicate that attachment to people would be unlikely since fawns display withdrawal behavior before they are 48 hours old.

This is not to deny that Marena's fear of people was greatly reduced as can be seen from the data on bodily contacts under discussion. The difference between Marena and the others is that she did not approach people for social contact (grooming). The early and unusual timidity of Marena was noted by another observer when the fawns were about two months old: 'One of the animals (Marena) remained shy and nervous, and could be put to instant flight by an abrupt movement on the part of her human foster parents. The timidity so characteristic of the adults of our herd is apparently not always lost through early handling' (Klopfer, unpublished m.s.). Seven years later a measure of this independence of people is clear from her unwillingness to solicit grooming.

The remaining three doe-reared fawns were clearly different in all the measures from the others, a result of their total lack of physical contact with people any time in their lives. Faline was reared with her mother in a pen for two years. The close approach by people during that time no doubt accounts for the low average approach distance to people of 2.5 feet compared with 11 and 18 feet for the two fawns which were born to hand-rears in the large enclosure. Although these two fawns differ significantly in their approach distances, nothing is known of their early experience with people which might account for the difference. If the small variation in these data is typical of deer the individual specificity is striking.

Although the number of trials for determining willingness to be groomed is small, I believe they reflect reliable differences in the relationship of the deer to people. The data are consistent with my observations over long periods with the individuals and the uniqueness of the acceptance of this type of care-giving behavior. The possibility of bias in the data as a result of knowledge of the time spent with the doe-mother was precluded by delaying inspection of these records until the termination of all experiments. I was aware of the fact that Gurri was raised in isolation of other deer. However, during the many months of contact with the hand-reared deer as yearlings and adults, they had frequent head scratching during approaches for corn tid-bits. Even the most timid of the hand-reared deer would readily tolerate scratching as the price for choice food.

## V. GENERAL DISCUSSION

### A. Preferences in Attachment Behavior

The results of the studies of social interactions clearly indicate that long-term, stable changes have occurred in the selection of companions of the foster-reared deer. The central issue is the role of specific stimuli during 'critical' periods of social development on the structure of this adult behavior. Before examining the evidence it is appropriate to emphasize that while the arguments are suggestive, the many uncontrolled variables made them inconclusive.

The question of the susceptibility of one to two day old fawns to influences affecting selection of later social companions is an important one, in that rearing treatments differed primarily at this age. This leads to a consideration of the factors determining the onset and end of the period of susceptibility or 'sensitive period'. The freeze response with the head lowered to the ground was discussed in Chapter HI. Fawns gave these responses to loud noises and approaching people from 2 hours on. Hebb (1946) emphasized that the avoidance of strange situations implies a background of familiarity against which the strangeness is recognized. Although this may well account for the increasing withdrawal over 17 days observed in the two fawns exposed to people for 8 hours in the first day, some other explanation is needed for younger animals. A general theory has been developed by Schneirla (1959) which states that 'behavior is largely governed in the very early ontogenetic stages of development by stimulus intensity rather than stimulus quality'. One would predict that very slow approach to fawns less than a day old would not elicit the freeze response, and that was the case.

The delay observed in the 'flight' response of the two fawns which were exposed to a person for 8 hours suggests that people were beginning to be included into the class of familiar objects on the subsequent days of testing. Of greater significance is the correlation between the ages when the hand-reared fawns were removed from the mother and the degree of attachment to people as revealed by the various tests. The narrowing of the range of effective stimuli in roe deer fawns has been observed during bottle-feeding by Pinter (1962). He found that fawns up to two days old would accept the bottle without difficulty but older fawns 'almost always refuse the bottle to begin with.' This refusal he attributes to the firm impression of the doe which the fawn has developed. Leuthold (1967) raised Uganda kob fawns (*Adenota kob thomasi*) in captivity and stated that 'the sensitive phase for imprinting appears to be restricted to the first few hours of life.'

The sensitive period for attachment to social companions in fallow deer parallels that for birds in many respects (see Moltz, 1968, for a recent interpretation of imprinting). The evidence from fallow deer further supports this convergence of behavior in the role that fear plays in the termination of the sensitive period. However, unlike experiments with birds, any attempts to expose fawns to people when the 'flight' response has replaced the 'freeze' response would be very difficult because the fawns will not tolerate close approach. Perhaps intervention with tranquilizing drugs would facilitate habituation and prevent the injury which would otherwise result from fawns crashing into the fence. In any case there seems little doubt that fear of even slowly approaching strange objects at one to two days of age is important in preventing further attachments.

It is important to emphasize that the experiments with foster-reared deer involved an extended exchange of social companions, in contrast to the imprinting experiments with birds in which an isolated chick is exposed to the surrogate parent and returned to isolation until the time of testing. The differences observed in the adult social behavior of deer are largely attributable to the differences in the time of removal from the mother and the channeling of social interactions caused by this very early experience in the subsequent days and weeks. The measures of attachment to people of the sub-group of deer which was bottle-fed singly, correlated with the number of hours of exposure to people in the first *24 hours* of life of the fawns. It appears that the attachment (or lack of fear) developed during this short time set the pattern for responses to people which was maintained throughout their life. These individual patterns of very close approach to people and grooming, were regularly reinforced by people with which they came into contact. This process probably simulates the normal social interactions occurring among wild deer throughout their lives. A notable difference between the normal and foster-rearing was the constant companionship of the natural mother following the 'lying out' phase in contrast to the intermittent attention of the human foster mother. It is possible that these separations contributed to the extreme independence of some of the singly-reared does.

It might well be argued that the independence of the hand-reared deer from the semi-wild deer was due to the threats and bites directed at the hand-reared deer following their introduction. This seems unlikely since a normally reared fawn, Faline, consistently rested close to other deer in spite of their threats and bites. Although Faline was a complete stranger when introduced to Area 3 as a two year old, she nevertheless was most frequently a member of the nearest pair in her resting group and least frequently a member of the farthest pair of deer. Paradoxically she occupied the lowest position in the dominance hierarchy and received the largest number of bites. This supports the view that the strength of the attachment remains stable and appears to be resistant to inhibition. Unfortunately the three deer which were hand-reared as a group were introduced to the semi-wild herd together so we have no information on whether a single companion-reared deer could join the herd. They were driven off with threats and bites and thereafter formed a separate herd. A similar tendency of bottle-fed goat kids to stay together and not integrate with the flock was reported by Moore (1968).

## B. Preferences in Sexual and Aggressive Behavior

In addition to the influence of early social environment on the adult social responses already discussed, there were altered preferences for partners in sexual and aggressive behavior which, although involving only one or two animals, may suggest further experiments. Hinde (1966) reviews the evidence for the influence of early experience on adult sexual behavior in birds, which Lorenz (1937) stresses as an important feature of imprinting. In ungulates the importance of early experience in instances of cross-breading was discussed in Chapter HI (Gray, 1954). The goat-reared fallow buck, Robbie, was attracted to goats in heat. He bred none of the four does while he was the only buck enclosed with them. Being reared by a goat also appears to have influenced the objects towards which Robbie directed his aggressive behavior. Although he thrashed fences and vegetation with great vigor he did not approach and threaten people the way the hand-reared buck Ronno did. Hediger (1950) believes that tame roe bucks regard man as a rival of the same sex and so attack him. Records of accidents in zoological gardens suggest that this is common among many species of tamed deer (Lorenz, 1952). However, since bucks in rut are often aggressive towards does as well, these attacks on people may be attributable more to the reduced fear brought about by early contact with people rather than as a result of imprinting and later preference for humans as partners for battle.

When Ronno was first introduced to the semi-wild deer at 8.3 months of age, he ran quickly to the mature buck and butted the large antlers of this buck with his small spikes. Ronno had never seen antlers previously although he was reared with dee fawns of a similar age to him. Ths would seem to be a clearcut instance of a 'releaser' mechanism in the Lorenzian sense of a specific structural configuration eliciting species-typical behavior. While this is an isolated observation the response is quite the opposite of the shy, curious and slow approach which younger fawns of either sex exhibited when freed to mingle with the semi-wild herd. One might have predicted immediate flight response on the part of the young buck since antlers are large unfamiliar objects attached to a very familiar object, the deer's head. When Chimpanzees were shown parts of a Chimpanzee's body they showed signs of autonomic disturbance, aggression and fear (Hebb 1946). The goat-reared buck was never introduced into the large deer enclosure so we have no information on his response. The observation of Ronno's response would seem to indicate that there is still much to be learned about the elicitation of social responses which occur in the absence of experience with the specific releaser.

During five rut seasons Ronno continued to respond aggressively to bucks and people He responded to my approach and my scraping of a tree by going to a nearby branch and whipping it with his antlers. Other responses, which are seen given to a rival, are tense posture and highly stereotyped wiping of the sides of his body with the infra-orbital glands on his face. He thus appeared to give species-typical sexual and aggressive behavior to both deer and people, his companions during infantile and adolescent growth.

## VI. CONCLUSIONS

1. Fallow deer fawns were separated from their mothers between one and 48 hours after birth and bottle-fed either in isolation from deer or with fawn companions. When compared with normally-reared deer for attachment to people and to other deer, from four to seven years after birth, the isolate-reared deer had the highest scores of contact and approach for grooming to people, lowest scores on three indices of gregariousness to deer and the highest scores for aggression toward other deer. The rank of the measures of attachment to people and lack of gregariousness to deer was highly correlated with the age during the first 24 hours that the fawns were removed from their mothers. It was concluded that the differences in adult attachment resulted from processes initiated in the first day of life
2. One doe separated from her mother when 48 hours old and reared with other fawns ranked lower than isolate-reared deer in attachment scores to people and aggression, and ranked higher in the indices of gregariousness with deer.
3. Normally-reared young and hand-reared does ranked lowest in attachment to people and aggression, and highest in gregariousness with deer. The distance of approach to people of these deer was consistent for each individual and was related to the amount of exposures to people when very young.
4. Normally-reared does rested closer to other strange deer than isolate-reared deer did among familiar companions. This strongly suggests that the intense attachments to does which are formed early, are resistant to change and can be transferred to other individuals of the same species. Similar observations were made on the hand-reared deer. They transferred their attachments from the people who reared them to other humans at maturity.
5. All deer reared their fawns successfully except one who failed to nurse two young. This aberrant maternal behavior may have resulted from her early removal from her mother (less than one hour *post partum*), and subsequent rearing in isolation of deer.
6. A buck which was suckled by a goat failed to breed does. He directed his sexual approaches to goats and tended to rest remote from deer.
7. Attachment to companions appears to begin in the first few hours of life. Withdrawal from rapid movement or loud sounds occurs at the same time but withdrawal from slowly approaching, unfamiliar objects develops slightly later during the first day or early in the second day. Normally-reared fawns which were exposed to people for 8 hours in their first day showed more delayed fear responses to subsequent approach than unexposed fawns.
8. The major influence of foster-rearing was in redefining the social object to which species—typical behavior was directed. There was some influence on the frequency of some patterns, e.g. increased aggression, but no change in the type of behavior could be detected.

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## APPENDIX 1

REARING TREATMENTS OF FOSTER-REARED FAWNS

| Name | Rearing treatment | Time with doe after birth, hrs. | Time without fawns, days | Time with fawns after birth, days | Age at first contact with adult deer days |
|---|---|---|---|---|---|
| Gurri | bottle-fed singly | 1 | 50+ | 0 | 288 |
| Nettla | bottle-fed singly | 8-18 | 50+ | 0 | 100+ |
| Meredy | bottle-fed singly | 21 | 50 | 0 | 47 |
| Kiki | bottle-fed singly | 24 | 30 | 0 | 230 |
| Shy | nursed by goat | 6-20 | – | ca. 7 months with goats | 16 months |
| Robbie | nursed by goat | 12-24 | – | ca.7 months with goats | 16 months |
| Ronno | bottle-fed with fawns | 12-24 | – | 63 | 250 |
| Marena | bottle-fed with fawns | 48 | – | 34 | 242 |

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Paper No. 12

# Functional Analysis of Locomotion in Pronghorn Antelope

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## ABSTRACT

An analysis of locomotion in the pronghorn antelope (*Antilocapra americana*) was made by studying 16 mm slow motion movie film (exposed at 80 frames per second) frame by frame through a viewer. Tracings of pronghorn made from successive frames of moving picture sequences arranged in correct spatial relation to one another were used to record the relative positions in space of rapidly moving body structures during the execution of various gaits. Field observations were conducted to collect information on aspects of behavior related to locomotion.

The repertoire of gaits employed by the pronghorn is varied and relatively extensive. The symmetrical gaits consist of the very slow, slow and fast diagonal walks and the slow, moderate and fast running trots (according to Hildebrand's gait graph the corresponding terminology would be very slow, slow and moderate lateral-sequence, single-foot walks and the slow, moderate and fast running trots, respectively). The transverse and rotary canters (lopes) and the rotogallop are the most frequently employed asymmetrical gaits. The rotogallop is the exclusive gait of pronghorn when running at fast speeds (speeds of up to 60 miles per hour have been reported). Although the bound, half-bound and bounding gallop (stotting included) are employed by pronghorn, they are rarely executed in their pure form. Until a fawn is about two weeks old its gait repertoire is limited to a rather awkward rotary canter and gallop and a feeble walk.

In the majority of pronghorn gaits an increase in speed is accomplished by increasing both length and rate of stride. In many fast galloping sequences, however, speed increase is a result of an increase in length of stride but a slight decrease in rate of stride. Total suspension time per stride increases with increased speed in walking and trotting gaits but decreases in cantering gaits. The fast gallop, with its two periods of suspension, has a total suspension time per stride greater than most of the faster cantering gaits. Footfalls spread out and more two and one leg support phases appear in the strides as speed is increased. The galloping gaits of fawns average less suspension per stride than those of mature animals.

A change in either front or rear lead will change the type of gallop or canter employed. The rotogallop is maintained by changing both front and rear leads during the same stride, or more commonly by changing the front lead during one stride and the rear lead in the following stride. When making a sharp turn a pronghorn will employ the rotogallop and lead with the inside forefoot.

Occasionally pronghorn will execute a complete cycle of locomotion with only three of the four feet striking the ground during a change in gait. Apparently holding one front leg during the transitional stride of a gait change is often advantageous to the proper reorientation of legs.

When progressing faster than a walk, pronghorn usually employ the canter or gallop. A considerable degree of synchronization of both lead and type of canter or gallop is apparent in running herds.

Although pronghorn can jump vertical barriers of up to eight feet when pressed, the data collected indicate that they will usually crawl under a fence rather than jump over it if the bottom wire is at least 17 inches from the ground.

## INTRODUCTION

The pronghorn antelope, *Antilocapra americana* (Ord), is the sole living representative of the family Antilocapridae. Although the pronghorn is usually, but erroneously, referred to as an 'antelope', it is not considered by most authorities to be closely related to the true antelopes of the Old World. Simpson (1945) states that the pronghorn evolved during the Pleistocene Epoch and is endemic to North America. Five subspecies of pronghorn are recognized by most authorities: *Antilocapra americana americana* (Ord), *Antilocaptra americana peninsularis* Nelson, *Antilocapra americana sonoriensis* Goldman, *Antilocapra americana oregona* Bailey and *Antilocapra americana mexicana* Merriam. *A. a. americana* is the most widely distributed subspecies in North America and is the one that is the subject of this study.

The pronghorn antelope is reported by many writers as being the swiftest wild quadruped in North America. Much attention has been given to this fast, agile mammal of the American plains in connection with its very rapid locomotion, but most references refer only to speed and do not attempt an analysis of locomotor behavior. It is the purpose of this study, therefore, to analyze the major types of locomotor activity characteristic of this species and to investigate some of the associated adaptations that have occurred as a result of evolution in connection with the pronghorn's specific mode of life. An investigation such as this should give some insight into the adaptations incorporated into an animal exhibiting a cursorial mode of locomotion over a relatively flat, hard prairie or semidesert terrain.

## MATERIALS AND METHODS

The analysis of the locomotor gaits and other related information of pronghorn antelope was made by studying 16 mm slow motion movie film frame by frame with a Zeiss-Ikon Moviscop viewer. A two-times magnifying lens was mounted in front of the viewing window to enlarge the image and thus facilitate analysis. This device was used to obtain information leading to the construction of footfall formulas, gait diagrams and graphs as well as the various gaits employed. To facilitate the study of gaits and the movement of various body structures during locomotion the film was projected on a solid screen using a 35 mm filmstrip projector and the sequences that were being studied were traced in silhouette form from the screen. The projector was placed at varying distances from the screen in order to make all tracings of approximately the same size. This procedure was essential for the analysis of various body members and their relative distance from each other and from the ground. All of the pictures utilized in this study were taken by the author with a Pathe Professional Reflex 16 mm movie camera mounted on a modified rifle stock, using black and white Kodak Plus-X Reversal film exposed at 80 frames per second. This rate of exposure was not completely satisfactory for the most rapid gaits of the pronghorn and caused some blurring of the legs at certain phases of the stride. Where the image was blurred, other sequences were studied to elucidate the analysis. A film speed of about 150 frames/second, as suggested by Hildebrand (1964) for running mammals of moderate to large size, was not possible with the camera available for the study.

Although several different lenses were used in filming, a 300 mm f/1.4 Takumar lens with appropriate adapter proved to the most satisfactory and was used for the majority of the filming. Most film was shot from an angle that would give side-on shots; some sequences, however, were made from directly in front of or behind the moving animal for studying lateral motions of the limbs and body. Over 2000 feet of film were analyzed in studying pronghorn locomotion and 500 feet in connection with the fast gaits of other wild ungulates. Most of the film was shot on the open, native grasslands of southern Alberta. Filming during the early spring (April and May) proved to be most satisfactory for the purpose of determining footfall patterns, because the grass of the previous year is matted down and the new spring growth is just beginning, thus giving a less obstructed view of the feet striking and leaving the ground.

Field observations made of various aspects of behavior related to locomotion were facilitated by the use of binoculars and a spotting scope. Most observations were made from prominent hills which commanded views of large surrounding areas.

Caution was taken to observe animals from a great enough distance (usually about one-half mile or more) to ensure that their locomotor behavior was relatively spontaneous and not induced by fright.

## BACKGROUND TO QUADRUPEDAL GAITS

The various manners in which the movements of the four legs of terrestrial quadrupeds accomplish progression are usually referred to as 'gaits'. Gaits may be divided into many arbitrary categories according to limb sequence (order in which the feet are lifted and advanced), number of feet upon the ground at different times during a cycle of locomotion, time succession of feet striking the ground (rhythm or beat). and the velocity at which the feet strike and leave the ground. Some investigators, therefore, have followed one plan while others have devised their own. However, there is considerable continuity in almost all of the systems as far as the more commonly observed natural gaits such as the walk, trot and gallop are concerned. Regardless of the gait nomenclature used, it is apparent that genetic factors, body structure and conformation, and immediate convenience are in great part responsible for the repertoire of gaits utilized by a particular species of animal.

The advent of photography gave great impetus to the study of vertebrate locomotion. Early workers, such as Stillman (1882) working with the horse and Marey (1895) working with various vertebrates, played a considerable part in the development of cinematography for locomotion studies. However, the most monumental work making use of photographic techniques for the study of locomotion was that of Edward Muybridge, who published most of his results in 1899 under the title 'Animal Locomotion'. Muybridge's classic photographs of about 25 species of mammals and several birds during locomotion were obtained by triggering twelve or twenty four still cameras in sequence at rapid intervals. Using these photographs he determined the succession of footfalls (support patterns) and used this as a basis for delineating and describing the gaits of quadrupeds when progressing upon the ground. He concluded that quadrupeds employ eight different regular systems of progression: walk, amble, trot, rack or pace, canter, transverse gallop, lateral gallop and ricochet. Occasional departures from the eight regular systems were considered to be irregular or abnormal.

Subsequent to the work of Muybridge, Paul Magna de la Croix, a French scientist living in Argentina, attempted a comprehensive analysis of the gaits of vertebrates. Although his approach to locomotion was imaginative, it was also highly theoretical. Therefore, his methods have not been followed and his conclusions are often questioned. Two of his many papers (Magna de la Croix, 1928, 1936) are of interest to this study because they discuss the evolution of gaits in quadrupedal animals. Chubb (1929) was another early author to write on the subject of how animals run.

More recently A. B. Howell employed the slow motion movie camera to carry out comprehensive locomotion studies on terrestrial tetrapods. Many of his findings were published in 'Speed in Animals', dated 1944. Howell distinguidhed thirteen quadrupedal gaits and also recognized irregular gaits and variations. The diagonal walk, lateral walk, running walk (amble) or single-foot, walking trot, trot, walking pace, pace, transverse gallop, lateral gallop, transverse canter or lope, lateral canter or lope, bound and half-bound were listed as regular gaits employed by quadrupeds. He divided quadrupedal gaits into three main groups, two of them symmetrical and one, asymmetrical in rhythm. In symmetrical gaits the intervals between footfalls are evenly spaced and the support pattern of the feet on the ground is repetitively symmetrical. He further subdivided the symmetrical gaits and classified them as two-time, in which two feet are placed on the ground at the same instant (or nearly so) and four-time, in which each foot is placed on the ground at a different instant from the rest. The trot (diagonal support) and pace (lateral support) were treated as examples of two-time symmetrical gaits while the walk was typical of the four-time. The basic characteristic of the symmetrical gaits is the uneven spacing of intervasl between footfalls. The various types of gallops were cited as asymmetrical gaits, the bound and half-bound were considered as symmetrical renditions of the asymmetrical gallop

According to Hildebrand (1966), Muybridge and Howell were much too conservative in recognizing only seven or twelve gaits. A difficulty with the terminologies of Muybridge and Howell that contributed to their limited gait nomenclature is that two animals moving according to the same footfall formulas, can actually be using visibly different gaits because of differences in the relative durations of the various support patterns (Hildebrand, 1963). Therefore, the audible footfalls and the speed of travel might be strikingly different for two animals employing the same footfall formula. To overcome the shortcomings inherent in the footfall formula approach to gaits, Hildebrand (1963) devised a method of analyzing symmetrical gaits (to a lesser extent asymmetrical) which would permit the convenient comparison of many gaits simultaneously and lead the investigator to general concepts of gait analysis.

By studying his films frame by frame in a viewer equipped with a frame counter, Hildebrand was able to prepare 'gait diagrams' which included information on both footfall formulas and the duration of each pattern of support represented. On graph paper he assigned four adjacent horizontal rows of squares to the feet. Vertical rows represented successive moving picture frames and hence equal intervals of time. A square was 'lined in' when its respective foot was in contact with the ground. Although this, type of record included information in addition to that found in footfall formula, it still shared with the footfall formula the difficulty of conveniently comparing different gaits. To overcome this difficulty, Hildebrand (1963) isolated two important variables characteristic of symmetrical gaits and plotted them, one against the other on a simple grid. The variable represented on the abscissa was the percentage of stride, in time, that each foot is on the ground. If the timing of the footfalls of one foot is known in a symmetrical gait, then the timing of the footfalls of its opposite is also known and the relationship of the fore footfalls to the hind footfalls can be expressed. This variable, plotted on the ordinate of the graph, was expressed as the percent of stride interval that the footfall of the forefoot lags behind the strike of the ipsilateral hind foot. Thus, all symmetrical gaits can be expressed by two percentage figures referred to as a 'gait formula' by Hildebrand (1966). The figures are plotted on the graph so that hundreds of gait formulas can be compared simultaneously. By combining the terminologies expressing variation along the two axes of the graph, Hildebrand established gait names which he believes to be descriptive and unambiguous, e.g., a gait formula of 55-18 would be a fast, lateral sequence, lateral couplets walk characteristic of the cheetah.

It is apparent from the early works cited above and from the works of Grogan (1951) and Jacobsen (1960) that the horse has received considerable attention in quadrupedal locomotion studies involving cinematography. Other, quadrupeds, however, have been studied to a lesser extent. Bartholomew and Caswell (1951) clarified some of the details of bipedal and quadrupedal locomotion in kangaroo rats. Later, Bartholomew and Cary (1954) reported on locomotion in pocket mice. Snyder (1949, 1952, 1962) dealt rather extensively with adaptations for bipedal and quadrupedal locomotion in lizards. The galloping gaits of the giraffe were described by Bourdelle (1934), and Dagg (1962) described the role of the neck in giraffe locomotion. Taylor (1970) filled a gap in our knowledge of mammalian locomotion by describing the various gaits of the East African viverrids. Two relatively recent contributions restricted to specific types of quadrupedal gaits were made by Brown (1968), treating walking gaits in general, and Dagg and de Vos (1968) analysing the fast gaits of some pecoran artiodactyls.

In the field of anatomy and mechanics, one of the earliest noteworthy works to appear was a book on the principles of animal mechanics by Haughton (1873). Later, Lull (1904) devoted attention to the adaptations exhibited by mammals toward aquatic, arboreal, fossorial and cursorial habits. Gregory (1912) pursued the problem of adaptations further by reporting on the principles of quadrupedal locomotion in ungulates. His approach was to analyze many skeletal and myological adaptations that had occurred in connection with graviportal and cursorial evolution. Still another extensive study on the mechanics of the tetrapod skeleton was made by Gray (1944). He discussed the mechanics of the tetrapod skeleton while considering all of the locomotory structures (muscles and bones) of the vertebrate body as being part of a complete functional unit. Barclay (1953) reported on some aspects of the mechanics of mammalian locomotion.

Several workers have dealt with anatomical structures as they relate to locomotion from a phylogenetic approach. Howell (1937) and Eaton (1944) studied the modification of the shoulder girdle as related to locomotion in mammals. Camp and Smith (1942) presented a lengthy consideration of the phylogeny and function of the digital ligaments in the horse. Schaeffer (1947) reported on the origin and function of the artiodactyl tarsus. A monumental work by Slijper (1946) dealt with the vertebral column and spinal musculature of mammals. Smith and Savage (1955) discussed some locomotor adaptations in mammals by analyzing post-cranial skeletal characters of several different species. Boonstra (1967) made a study of girdles and limbs of early therapsids to demonstrate the possible evolution of the mammalian quadrupedal walking gait.

Books of a general nature containing chapters on terrestrial locomotion include Gray (1953), Ottaway (1955) and Slijper (1947). A symposium on 'Vertebrate Locomotion' by the Zoological Society of London (edited by Harris, 1961), published in 1961, deals with many aspects of locomotion; a number of the contributors are workers who have been mentioned above.

A few terms used to explain various aspects of locomotion need to be defined before undertaking an analysis of pronghorn gaits: A 'stride' (cycle) is one completed action of all four feet; a 'step' is the complete movement of one foot; a 'stride interval' is the duration of a stride; the 'swing' of any limb is the completed advancement or retardation of a single limb; and a 'phase' is any particular point or instant of motion during a stride.

## SYMMETRICAL GAITS OF PRONGHORN

There appears to be little discrepancy among workers reporting on the symmetrical gaits of pronghorn. However, there is some confusion in the terminology used to describe the various types of walking and trotting gaits. Einarsen (1948) depicts two walking and two trotting gaits by way of illustrations: the sedate walk, the pompous alarmed walk, the leisurely trot and the elegant trot. Bruns (1969) referred to an elegant trot while Gregg (1955) was more explicit and briefly described a slow walk, a normal walk and a trot. Howell (1944) delineates the symmetrical gaits of the pronghorn as consisting of the walk and a rather slow trot which is executed with unusual spirit and action. Some writers (e.g., McLean, 1944 and Throckmorton, 1945) have commented on the stiff, jerky and somewhat awkward appearance of the walking gait of pronghorn. Others have brought attention to the fact that both the walk and the trot can be a rather fast mode of covering distances. It is obvious from the literature, however, that studies involving symmetrical gaits have dealt only with nomenclature and have not approached the subject from an analytical standpoint.

The terminology used in naming the symmetrical gaits of pronghorn antelope is taken from Muybridge (1899) and Howell (1944), with Hildebrand's gait nomenclature being incorporated as a method of further analysis.

### Very Slow Diagonal Walk (Crawl)

The walk is the slowest gait employed by the pronghorn. Of the various types of walks employed, the very slow diagonal walk or crawl is the slowest means of progression. From the viewpoint of support and balance it is also the most stable of all the gaits, having no fewer than three feet on the ground at any time during a complete cycle of locomotion. It is possible, therefore, for the body to stop at any instant during a stride without causing the animal to lose balance. The crawl is a four-time symmetrical gait having eight important phases, one for each of the four footfalls, and one for each period that a foot is suspended. These movements may be best conveyed by a system of notations (diagram) consisting of symbols designating the support patterns of the legs during a complete cycle of locomotion. Such stylized diagrams are usually referred to as 'footfall formulas'. If the left hind foot is arbitrarily chosen as the foot to initiate the locomotor cycle (Fig. 1),then it will always be followed by the left front foot. The next leg to move is the right hind and it is followed by the right front. The three-point support is shifted, with the help of an intermediate four-point support, first laterally (Fig. 1-B), then diagonally (Fig. 1-D), then to the other lateral (Fig. 1-F) and to the other diagonal (Fig. 1-H), completing the cycle of eight different phases.

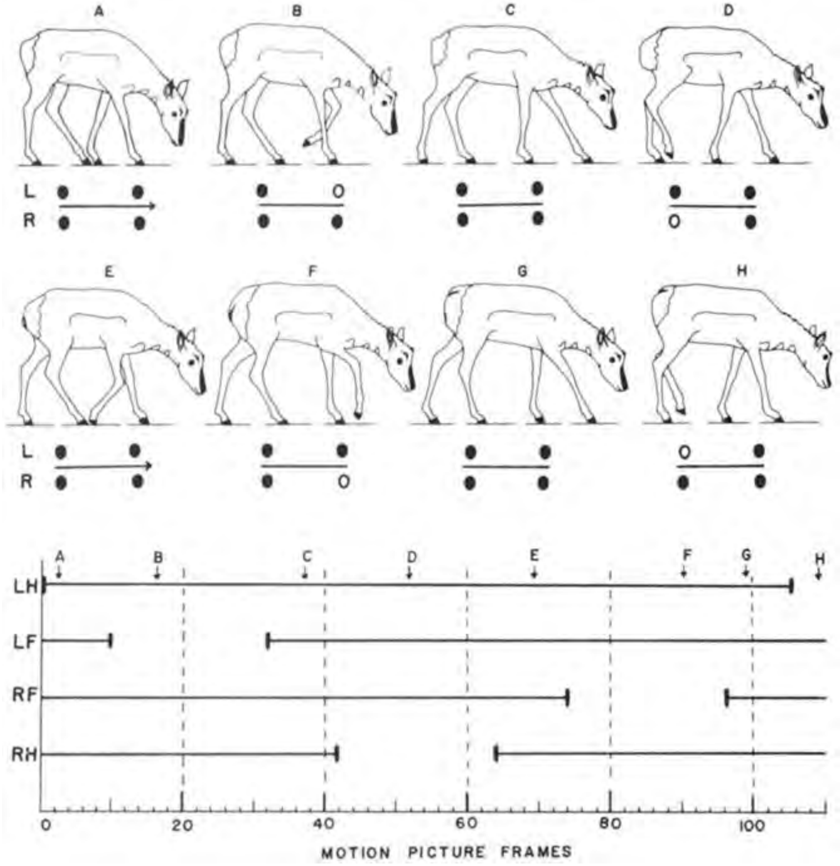


Fig. 1. Pronghorn employing a very slow diagonal walk (crawl). The support patterns of the feet (footfall formula) are represented below the pronghorn silhouettes by circles which are black when the respective foot is on the ground. The gait diagram below indicates the periods of contact of the feet with the ground; time scale is in motion picture frames at 80 frames per second. Initial letters on the left margin of the figure refe to various feet: LH (Left Hind), LF (Left Front), RF (Right Front), RH (Right Hind), L (Left) and R (Right). Pronghorn silhouettes A-H are comparable to stride phases A-H of the gait diagram below.

The support formula (number of feet on the ground at different phases of locomotor cycle) for the sequence of legs is 4-3-4-3-4-3-4-3. Based on the sequence of footfalls, Howell (1944) refers to this type of walking gait as being transverse or diagonal. He arrived at this terminology in a rather arbitrary manner based upon the observation that the second footfall is diagonal to the first footfall when the left front foot is chosen to initiate the locomotor cycle (e.g., LF-RR-RF-LR). Hildebrand (1963), however, refers to such a gait where the hind foot is followed by the footfall of the ipsilateral forefoot as being a lateral sequence gait. He points out that such a sequence is superior for avoiding interference between fore and hind feet, and that all of the various walks employed by the vast majority of ungulates are of this type.

Although the very slow walk is considered to be a symmetrical gait, it is frequently executed in an asymmetrical manner. When progress is extremely slow, the advancement of individual legs may be at uneven intervals of time. This results in a gait with variation in the duration of the three-point support phases even though the actual time interval for the advancement of each of the four feet remains relatively constant.

Pronghorn employ the very slow walk most frequently during feeding activities and when approaching an object that has elicited curiosity. The gait is also used for moving short distances when engaging in various social activities. During this very slow walk the progress is slow because each foot advances only a few inches and a complete stride requires more than a second to be executed. It is not necessary, therefore, to have the hind feet pass lateral to the forefeet as in the case of some fast tempo walks, because the hind feet do not strike the ground in close proximity to their respective ipsilateral forefeet.

### Slow Diagonal Walk

Like the crawl, the slow walk is a combined diagonal- and lateral-support gait with the support alternating between diagonal and lateral limbs but at a faster tempo. The footfalls are all separate and support is by never fewer than two feet, two diagonals being substituted for two of the four-foot supports incorporated in the very slow walk. Accordingly, the support formula for the slow diagonal walk is 4-3-2-3-4-3-2-3. Therefore, this gait is only slightly less stable than the very slow walk and is employed by pronghorn when progression slightly faster than a crawl is warranted. Strides are completed in about one second, with a distance of approximately 31 to 33 inches (79 to 84 cm) being covered during each stride.

### Fast Diagonal Walk

Although 'fast' is a relative term and many gait variations occur between the slow and so-called fast walks (e.g., moderate walks etc.), it is conventient to classify walking gaits in this manner and then indicate various types of transitional support sequences encountered. In many instances, however, the slow walk merges so insensibly into a faster tempo that it is difficult, and somewhat meaningless, to account for all of the intermediate footfall sequences.

The most frequently employed fast walk of the pronghorn (Fig. 2) differs from the slow walk in that the two remaining four-point supports of the slow walk are abandoned and two lateral two-point supports are substituted (Fig. 2 - D and H). This footfall sequence is brought about by an increase in the rate of walking which necessitates each hind foot being lifted off the ground before the contralateral forefoot reaches the ground. Thus the eight phases of each cycle of locomotion are composed of four three-point and four two-point support periods (3-2-3-2-3-2-3-2), the three-point supports alternating between the two-point diagonal and lateral supports. The relative instability of two additional two-point supports appears to be compensated for by increased body momentum due to increased speed, and by each two-point support being followed by a three-point support during which any loss of equilibrium may be corrected.

When the pronghorn is walking at a moderate speed, each front foot leaves the ground just before the ipsilateral hind foot strikes the ground. Therefore, the imprint of the hind foot almost coincides with that of the forefoot. In faster walks, however, the imprint of the hind foot is slightly in front of, and lateral to, the imprint of the ipsilateral front foot. Straddling of the forelimbs by hindlimbs is necessary to prevent interference of lateral legs, while a degree of overstride by hind feet is necessary in order to increase length of stride and hence speed. During a fast walk a pronghorn will move about 38 to 41 inches (97 to 104 cm) with each completed stride; the duration of stride being approximately . 80 second.

Some of the more commonly used support sequences encountered in the various walking gaits of pronghorn are illustrated after the manner of Hildebrand (1965) in Fig. 3. It will be noted in Fig. 3-B (a moderately fast walk) each hind foot is lifted at the same instant contact is made with the contralateral forefoot, and each front foot is lifted at the same instant the ipsilateral hind foot contacts the ground. This results in a shortened support pattern with a support formula of 3-3-3-3. The support pattern illustrated Fig. 3-C is also somewhat shortened due to synchronization of lifting and placing feet. The fast walk (Fig. 3-A), the slow walk (Fig. 3-D) and the crawl (Fig. 3-E) are illustrated for comparative purposes. Individual idiosyncrasies are not reported.

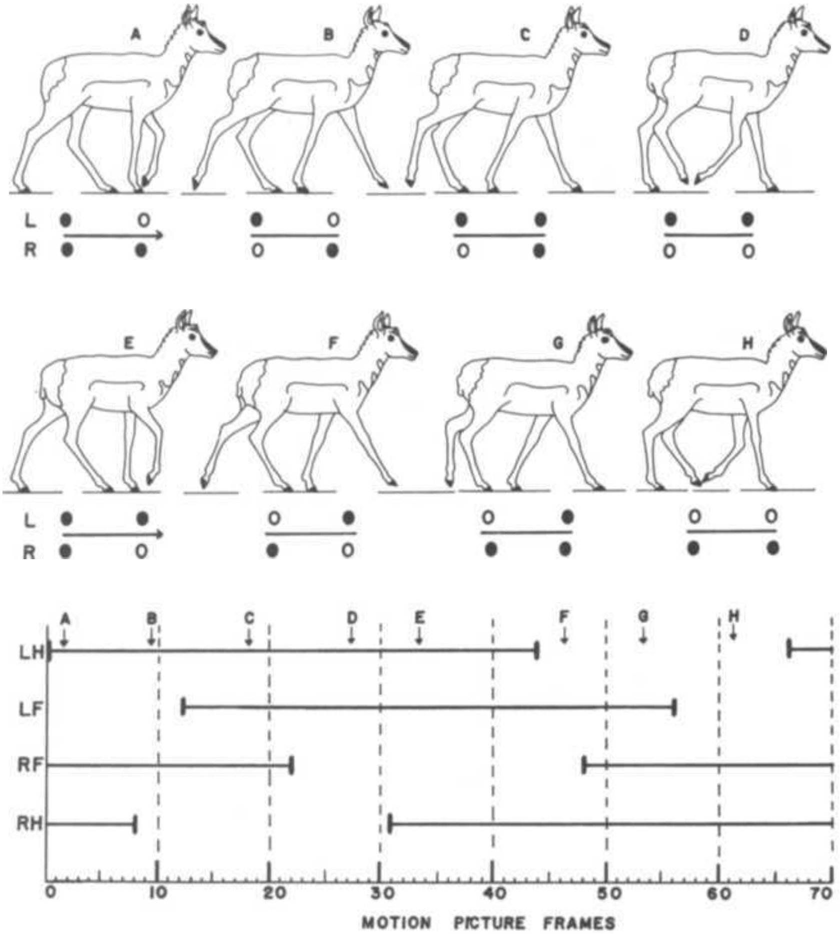


Fig. 2. Footfall formula and gait diagram (compare Fig. 1) of a pronghorn employing a fast diagonal walk. One complete stride is illustrated.

Gait formulas calculated from gait diagrams are plotted on Hildebrand's symmetrical gait graph indicate that the pronghorn employs the very slow, slow, and moderate lateral-sequence, single-foot walks. (Representative gait formulas for the above gaits are: 82-26, 73-26 and 68-26). According to Hildebrand (1966) the lateral sequence, single-foot provides continuity of support and is selected as the walking gait by most large ungulates.

### Trot

The pronghorn employs the so-called 'true trot' (Howell, 1944) or 'running trot' (Hildebrand, 1965) as its gait of medium speed. In this two-timed symmetrical gait, support is furnished by alternation of diagonal pairs of limbs moving in unison, or at least approaching synchronization. It is a sure-footed gait providing good balance because the line of support passes approximately under the animal's center of mass. If the diagonal pairs strike and leave the ground in exact unison (Fig. 4), then the support formula is shortened to four different phases, 2-0-2-0. The body, then, is unsupported twice during each cycle of locomotion (Fig. 4-B and D). This completely synchronized trot is slightly slower in tempo than the more frequently employed footfall sequence of the running trot, and appears to be limited to occasional strides mingled with the

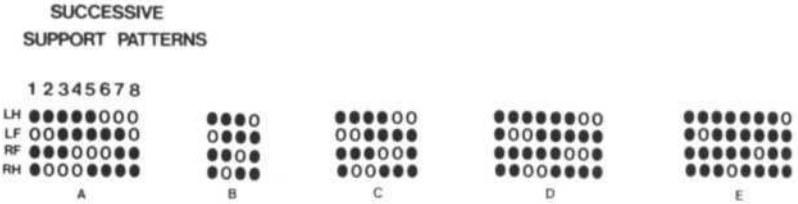


Fig. 3. Five support sequences that might be used by a pronghorn when walking. The initials L, R, F and H stand for left, right, fore and hind feet. Dark circles indicate feet in contact with the ground; open circles, suspended feet. Within each diagram, a vertical column of four circles shows a particular pattern of support. Each sequence starts with the footfall of the LH foot.

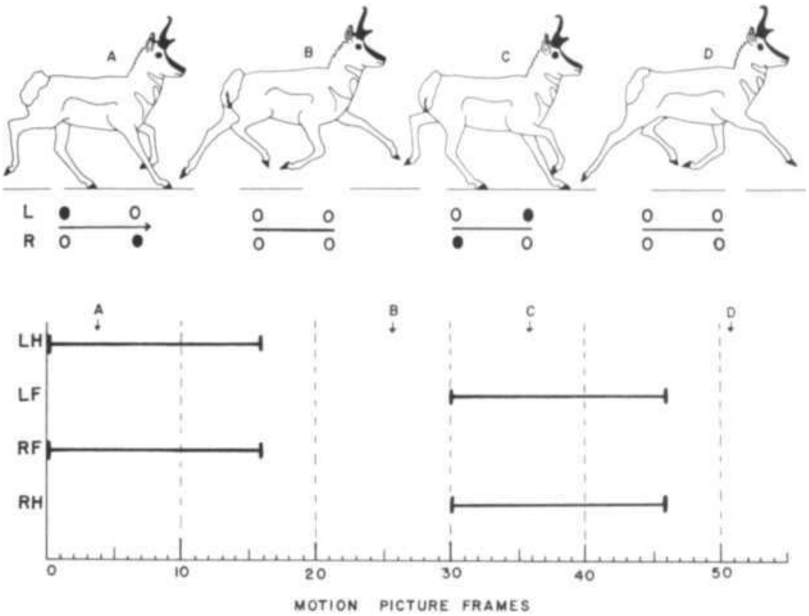


Fig. 4. Footfall formula and gait diagram (compare Fig. 1) of a pronghorn employing a symmetrical and synchronized rendition of the trot.

more normally executed trotting sequences. More commonly, the symmetrical rendition of the trot is accomplished by either the hind foot striking the ground slightly in advance of same, or by the front foot of a pair contacting and leaving the ground prior to the contralateral hind foot. Although in both instances the duration of contact is the same for both feet of a diagonal pair and the trot retains its symmetry, the gait does not consist of synchronized diagonal support. Both of the above footfall sequences are used only occasionally by pronghorn, the sequence in which the front feet contact the ground first is the least employed of the two. The support formula is the same for both footfall sequences: 1-2-1-0-1-2-1-0.

Inasmuch as the front legs of pronghorn antelope are somewhat shorter than the hind legs (Bullock, 1971), a full stride of the hind legs cannot be matched by the front legs when the animal is trotting at high speed. Therefore, the most frequently employed trotting sequences are slightly asymmetrical, i.e. the hind feet are in contact with the ground for a longer period of time (6 to 11%) than the front feet. Of these support sequences, two appear to predominate: one in which the hind foot of a diagonal pair strikes the ground first and then both feet leave the ground at precisely the same instant, and alternately, when both members of a diagonal pair contact the ground simultaneously but the front leg leaves slightly in advance of the hind leg. Occasionally the hind foot of a diagonal pair will contact the ground prior to the contralateral forefoot and leave in advance of it but will be in contact with the ground for a slightly longer period of time. On rare occasions a trotting pronghorn may execute a stride in such a manner that the front foot of a diagonal pair will strike the ground subsequent to the contralateral hind foot and leave in advance of it. It is also possible for a trot to be of such a slow tempo that there are no periods of suspension in the gait whatsoever. This rather anomalous footfall sequence appears to occur only when a pronghorn is going from a slow trot to a walk or vice versa, and is, therefore, probably transitional in nature.

During most of the trotting sequences described above, the hind foot that is being brought forward (flexed) passes lateral to the ipsilateral forefoot during a period of suspension. This is necessary to prevent interference of ipsilateral feet. The straddling maneuver of the hind legs causes slight lateral hip movement which undoubtedly adds somewhat to the length of stride and results in a slight increase in speed.

The spacing of footfalls (total length of stride) and the duration of stride (time required to execute a stride) vary with the speed of the trot and the individual animal performing the gait. Measurements taken from the foot impacts of several trotting pronghorn indicate that the length of stride varies from about seven to nine feet (2.1 to 2. 7 m) and the duration of the various stride lengths from . 57 to . 68 second. As the rate of stride increases (less time required for each stride) the length of stride also increases, resulting in a greater rate of speed.

When gait formulas are calculated and plotted on Hildebrand's symmetrical gait graph, it can be seen that the pronghorn employs the slow (42-52), moderate (38-54) and fast (25-52) running trots. Several of the plots fall near or on the line separating the trot from the diagonal sequence, diagonal couplets gait. It is also apparent from the graph that as the trot gets faster, the periods of support shorten and the periods of suspension lengthen. Therefore, as the rate of stride increases, the animal is suspended without support for a greater interval of time during each stride.

The trotting gait is freqeuntly executed in a very elegant manner with considerable leg action: head held high, chin pulled back, mane raised, rosette (rump-patch) raised and considerable flexion between epipodial and metapodial leg elements. Although it is difficult in most instances to determine the eliciting factor of the elegant rendition of the trot, a pronghorn that has been alarmed will usually employ this type of trot. The trotting gait in general, including the elegant trot, does not demonstrate excessive vertical body movement and is, therefore, a relatively smooth gait.

## ASSYMETRICAL GAITS OF PRONGHORN

As was the case with symmetrical gaits, the literature dealing with the asymmetrical gaits of pronghorn is also fragmentary, superficial and general in nature. There appears to be unaminous opinion, however, among all workers in ascribing the term 'gallop' to the pronghorn's most rapid gait. Howell (1944) was more specific and referred to the pronghorn gallop as being a lateral or rotogallop. A galloping gait at a slow tempo is referred to as a lope (Einarsen, 1948 and Gregg, 1955) or canter (Howell, 1944).

### Transverse (Diagonal) Canter or Lope

The canter or lope is for the most part a slow gallop but because of the exigencies of equilibrium at slow galloping speeds, support looms larger in the picture. In the transverse or diagonal canter the fore and hind feet use the same lead; i.e., the second hind footfall (leading hind foot) and the second front footfall (leading front foot) are unilateral. If a pronghorn initiates a stride with the right hind foot striking the ground (Fig. 5-A),then the next foot to contact the ground is the left hind (Fig. 5-B) followed by the right front (Fig. 5-D) and then by the left front (Fig. 5-E). The left

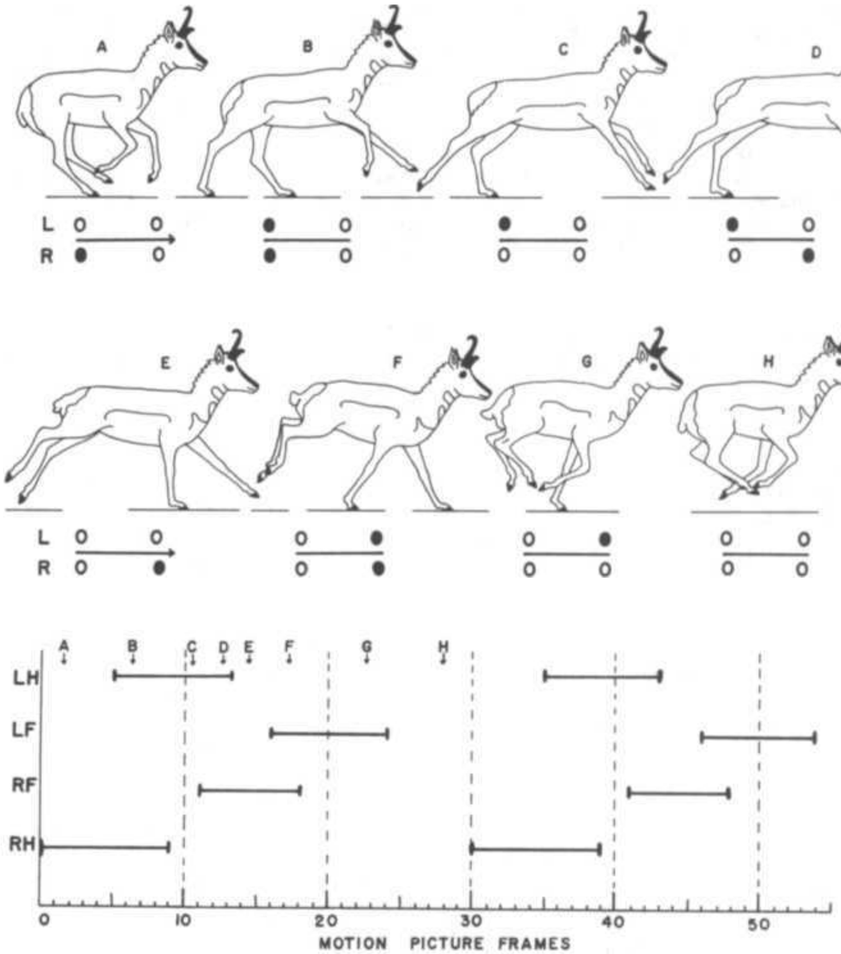


Fig. 5. Footfall formula and gait diagram (compare Fig. 1) of a pronghorn employing a transverse (diagonal) canter or lope.

front foot (leading foot), and to a lesser extent the right front foot (lagging foot), give a powerful upward thrust to the body resulting in a period of suspension with the legs gathered together (Fig. 5-H) in preparation for the next stride. The pronghorn's body appears to go through a rocking or see-saw type action when employing this gait.

The speed at which the canter is executed has a great deal to do with the footfall sequence used. In a slow canter the second rear and first front footfalls may coincide, making a three-time canter instead of the typical four-time canter, or the first front footfall may precede the second hind footfall. The latter is referred to as an 'atypical' canter by Howell (1944). In both of the aforementioned slow canters, as well as in the more normally executed slow canter the leading front foot strikes the ground before the lagging hind foot is lifted, thus resulting in a four-point support phase during the stride. The support formulas for these three slow canters are 1-3-4-3-1-0 for the three-time canter and 1-2-3-4-3-2-1-0 for the two four-time canters. The typical formula for the moderate canter is 1-2-3-2-3-2-1-0, the formula for the fast canter (Fig. 5) being 1-2-1-2-1-2-1-0.

The length and duration of stride vary considerably with the speed of the canter and with the individual animal performing the gait. The length of stride varies from about eight feet (2.4 m) in the slow canter to 14 feet (4. 2 m) in the fast canter, while the duration of stride varies from .31 to .45 second. Although the visual method of evaluating speed is somewhat arbitrary, it appears that in all cases the rate of stride increases as the length of stride increases, thus resulting in a greater rate of speed. Compared to the time interval of a trotting stride (. 60 to . 68 second), it can be seen that the increased rate of stride in the canter accounts for at least some of the greater speed of the canter.

### Lateral (Rotary) Canter or Lope

This gait is essentially the same as the transverse canter except for the sequence of footfalls. In the lateral or rotary canter the fore and hind feet use opposite leads. Therefore, the footfalls succeed each other in a rotary manner, e.g., LH, RH, RF and LF. Straddling of the leading front foot by the lagging hind foot (ipsilateral foot) during the suspension phase of the stride is more pronounced in this sequence of footfalls than it is in the transverse canter. According to the literature this type of canter or 'gallop' is the only one employed by pronghorn. Data from this study, however, show this to be false. Although the rotary canter may be employed more frequently (but only slightly), the transverse canter is a regularly used footfall sequence. This is particularly true for the slow and moderate canters.

As in the transverse canter, there are several different footfall sequences utilized by pronghorn when employing the rotary canter. The support formulas reported for the transverse canter are essentially the same as those found in the rotary canter. Therefore, these footfall sequences will not be elaborated upon. However, one stride of a very slow canter that had no period of suspension was encountered in a film sequence.

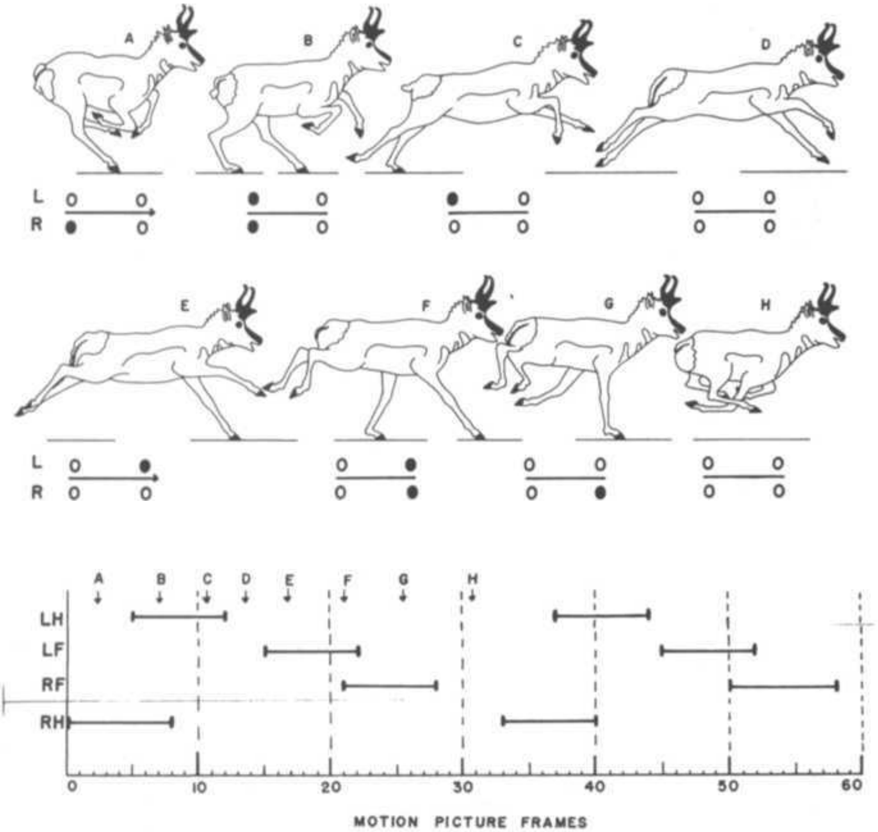


Fig. 6. Footfall formula and gait diagram of a pronghorn employing a lateral (rotary) gallop.

Inasmuch as the stride was executed during the transition from a slow canter to a walk, it can probably be viewed as being transitional in nature and not a frequently employed footfall sequence. This type of stride is probably rare but also encountered in the transverse canter.

### Lateral (Rotary) Gallop

The lateral or rotary gallop (rotogallop) is employed by the pronghorn as its most rapid gait. Typically, at very fast speeds, there are two periods of suspension during a stride: an extension phase where all four feet are extended just prior to the contact of the lagging forefoot (Fig. 6-D) and a flexion phase where all four feet are gathered under the body (Fig. 6-H). Accordingly, the support formula is 1-2-1-0-1-2-1-0. The durations of the flexed and extended suspension phases vary with the speed, terrain, individual animal etc. In the majority of cases the flexed suspension is usually of greater duration. However, the two suspension periods may be of equal duration or, occasionally, the extended suspension period may exceed the flexed one. It also appears that the total suspension time per stride increases, while the total contact time decreases. Therefore, with increased speed the animal is suspended for a greater percentage of time during each stride.

The rocking action characteristic of the canter disappears in the gallop and the animal's back remains low and parallel to the ground. The head is held low, ears laid back and mouth open. The horizontal extent of the leaps or strides is increased to 18 feet (5. 5 m) or more (strides of up to 23 feet (7 m) have been reported to the author by personal communication), but the duration of each stride (about . 34 to . 41 second) remains within the limits reported for the canter. It can be seen, therefore, that although speed is a product of rate and length of stride, the increased stride length accounts for most of the increase in speed. The rotary sequence appears to be the only sequence employed by pronghorn when progressing at very rapid speeds.

### Transverse (Diagonal) Gallop

Transition from a canter to a gallop is gradual. Therefore, it is difficult to discuss canters and gallops without being somewhat arbitrary. If a slow gallop (fast canter) is considered as a true gallop, then this gait (having the same footfall sequence as a transverse canter) is employed by pronghorn. If, on the other hand, only the very fast gallops with two periods of suspension are considered true gallops, then, according to the film viewed in this study, the pronghorn employs the roto-gallop exclusively.

### 'Gallop' of Fawns

A newly born fawn exhibits a very limited repertoire of gaits. Studies of fourteen different fawns moving from one hiding place to another indicate that fawns are only capable of executing a few feeble steps of a slow walk and a rather awkward bound-like gallop. The most commonly observed fast gait was found to be a normal rotary canter with one very short period of flexed suspension (Fig. 7). However, many strides consisted of a normal rotary canter sequence without any period of suspension whatsoever.

Hence, the running fawn always had at least one foot on the ground at all times. This unusual footfall sequence was found to be common among fawns but was only observed on one occasion in a mature animal. A few fawns exhibited a true fast rotogallop sequence but the two periods of suspension were very short and usually of about equal duration. The transverse arrangement of footfalls was not encountered in the film sequences of several different running fawns. No trotting gaits were employed by any fawns studied until they were approximately ten days to two weeks of age and running with their mothers.

The apparent awkwardness with which fawns employ fast gaits could be due in part to the lanky body conformation (legs long in proportion to body), lack of muscular and nervous coordination, and the rough terrain (high grass hummocks etc.) they must traverse in the fawning areas. Perhaps the rotary fashion of footfalls, which necessitates a great deal of straddling to prevent lateral leg interference, is also partially responsible for making the gait appear awkward. In any event, the straddling of the front legs by the hind legs of a galloping fawn (Fig. 8-C and D) is considerably pronounced and exaggerated in comparison to the straddling action of a mature animal (Fig.8-G and H).

### Bound

The true bound is a symmetrical rendition of the asymmetrical gallop. In this gait an animal leaps from both hind legs together and lands upon both front feet together (Howell, 1944). The advantage, and hence purpose, of this gait would appear to be in the synchronized action of the powerful hind legs facilitating a propulsive force to the mass of the body. Although pronghorn were not found to use this method for quick starts or gaining speed rapidly, one doe was observed to use it when bounding up a hill of considerable grade. Only one stride, however was truly symmetrical, the remainder exhibited disparity in the synchronization of leaping hind feet and landing forefeet.

### Half-bound

Howell (1944) describes the half-bound as a gait whereby an animal springs from both hind feet at once and lands first on one front foot and then on the other. One stride of the doe cited above was of this type.

### Bounding 'Gallop' or Leap

Although Howell (1944) does not name this unique 'gallop', he treats it as a gait peculiar to the mule deer. In it all four feet leave the ground in unison, this being followed

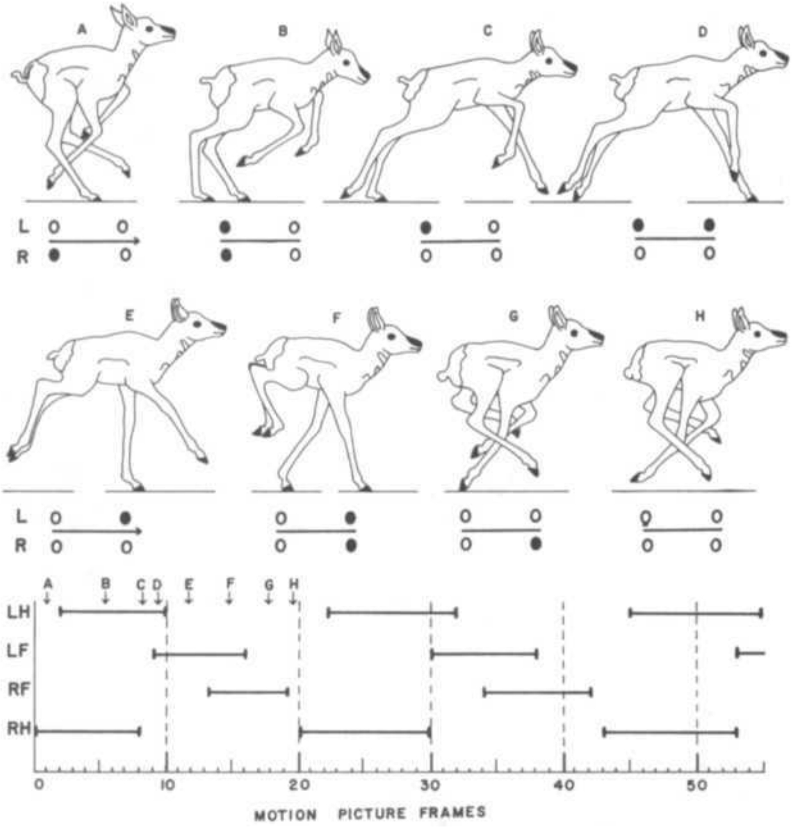


Fig. 7. Footfall formula and gait diagram of a pronghorn fawn employing a rotary canter or gallop.

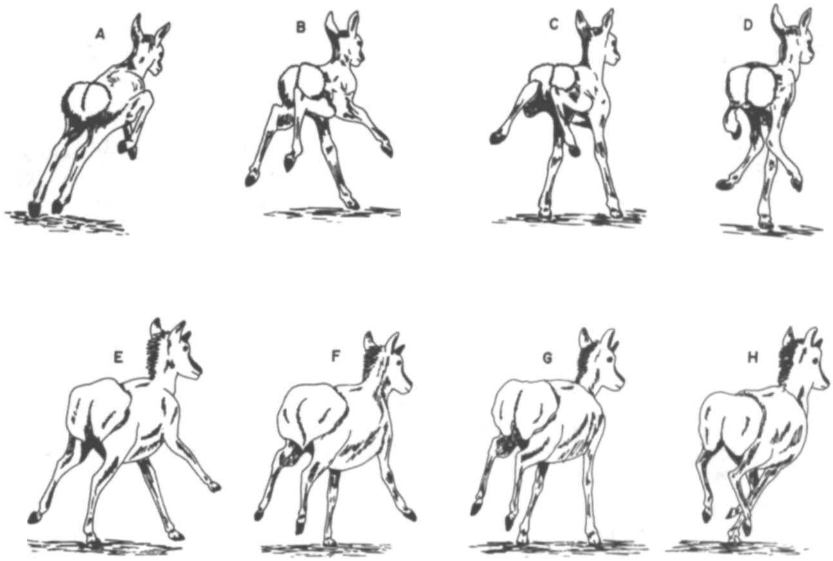


Fig. 8. A comparison of body and leg movements (particularly the straddling of front legs by hind legs) of a galloping fawn (A-D) and an adult pronghorn (E-H).

by a relatively long period of suspension with front and hind legs hanging parallel to each other, and then all four feet contact the ground in unison. Einarsen (1948) refers to this gait, when employed by pronghorn, as the 'sudden bounding leap'. According to my data this gait is most commonly used by pronghorn to initiate a rapid start from a standing position. Here again the powerful musculature of the hind legs work in unison to overcome body inertia.

In most instances, however, the true form of this gait was rarely seen. Usually the symmetry of the gait was broken by the front feet striking the ground at different intervals of time, followed by a gradual separation of the hind footfalls until a true gallop sequence was accomplished.

### Rotting

Stotting consists of a stiff-legged stomping action in which the animal bounds high into the air and lands on all four feet simultaneously. Although the footfall formula is identical to the bounding gallop or leap, there is usually no (or little) horizontal movement accomplished. Couey (1950) states that stotting appears to be a warning gesture and that it has been observed in bighorn, mule deer and elk. In African gazelles stotting (prelljumping) is used to increase speed or to express excitement (Walther, 1968). Bruns (1969) recognized the gait in pronghorn antelope as a form of winter play activity. During the course of this study pronghorn were observed stotting most frequently during the mating season. Stotting was usually accomplished in a very elegant manner with head held high and mane and rosette raised.

## GENERAL GAIT ANALYSIS

### Support Intervals of Fast Gaits

To obtain a better insight into the support phases of the feet during strides of various fast gaits, it is convenient to caculate the percentage of a stride spent on various combinations of supporting legs. This has been done for the trot and bounding gallop (Table 1), and for the canters and gallops of both mature pronghorn and fawns (Tables

TABLE 1. AVERAGE PERCENTAGE TIME OF STRIDE SPENT ON COMBINATIONS OF SUPPORTING LEGS FOR THE TROT AND BOUNDING GALLOP OF MATURE PRONGHORN

| Combinations of supporting legs, not in the order in which they are used. | Moderate Trot | Fast Trot | Bounding Gallop |
|---|---|---|---|
| Lateral legs on ground | 0 | 0 | 0 |
| Diagonal legs on ground | 62 | 48 | 0 |
| Four legs on ground | 0 | 0 | 46 |
| One hind leg on ground | 4 | 6 | 0 |
| One front leg on ground | 1 | 1 | 0 |
| Total suspension | 33 | 45 | 54 |
| No. of strides averaged | 20 | 20 | 2 |

3 and 4). These values tabulate what some individual animals have done, and thereby give some indication and generalizations about what pronghorn usually do when employing various gaits.

From Table 1 it is evident that pronghorn spend most of each trotting stride on diagonal supporting legs. One hind or front leg may, however, give complete support to the body for short periods of time during a stride, the hind leg giving longer intervals of support, particularly at fast speeds. As the speed of the trot increases the total period of suspension also increases, while the total diagonal support phase decreases. Therefore, at a fast trot the body is suspended for a greater portion of the stride than at a slow trot.

Although the pure rendition of the bounding gallop is rarely employed by pronghorn, when it is (Table 1) the period of suspension is usually slightly more than half of the total stride duration. More commonly, however, the hind feet are on the ground for a greater portion of the stride than are the front feet. It is also relatively common for one leg (front or hind) to give sole support to the body momentarily. These latter sequences usually grade into slow canters and are, therefore, difficult to classify and evaluate.

The accurate tabulation of the time intervals of the various support combinations of an 'average' canter or gallop is difficult because of the many variations encountered in these gaits, the idiosyncrasies of individual animals employing the gaits, and because of the problem of determining relative speeds. However, a few trends appear to be significant, especially those between the moderate canter and the fast gallop (Table 2). As speed increases both front and hind footfalls are spaced further apart; the feet of a pair being on the ground together for a shorter period of time. With increased speed the support of the leading hind foot and forefoot is reduced. At all speeds, however, the leading forefoot is on the ground proportionately longer than the leading hind foot. The flexed suspension phase is reduced throughout the canters as speed increases. With the addition of an extended suspension phase, the gallop acquires more suspension time per stride than the faster canters. The flexed suspension phase remains proportionately longer, however, than the extension phase. The three- and four-foot support phases are eventually lost as speed increases. The two-leg support is low in the boundlike and slow canters (legs striking the ground in close proximity to one another), rises sharply in the moderate and fast canters and then tapers off as more one-leg support phases appear in the gallop.

The slow canter is often boundlike in nature and executed with considerable variation in footfall formula. Such variation in the execution of a gait makes it difficult to compare the support combinations of the gait with other gaits. However, the support combinations that are relatvely constant (flexed suspension, four-leg support, three-leg

TABLE 2. AVERAGE PERCENTAGE TIME OF STRIDE SPENT ON COMBINATIONS OF SUPPORTING LEGS FOR THE GALLOP AND VARIOUS CANTERS OF MATURE PRONGHORN.

| Combinations of supporting legs, not in the order in which they are used. | Slow Canter | Moderate Canter | Fast Canter | Gallop |
|---|---|---|---|---|
| First hind leg on ground only | 11 | 17 | 14 | 15 |
| Both hind legs on ground | 24 | 20 | 17 | 13 |
| Lead hind leg on ground only | 12 | 17 | 13 | 11 |
| Extended suspension | 0 | 0 | 0 | 9 |
| First foreleg on ground only | 15 | 17 | 18 | 16 |
| Both forelegs on ground | 17 | 14 | 9 | 6 |
| Lead foreleg on ground only | 17 | 22 | 19 | 16 |
| Flexed suspension | 35 | 19 | 16 | 14 |
| Two legs on ground | 9 | 30 | 33 | 20 |
| Three legs on ground | 25 | 14 | 0 | 0 |
| Four legs on ground | 6 | 0 | 0 | 0 |
| No. of strides averaged | 20 | 20 | 10 | 10 |

TABLE 3. AVERAGE PERCENTAGE TIME OF STRIDE SPENT ON COMBINATIONS OF SUPPORTING LEGS FOR THE RUNNING GAITS OF FAWNS

| Combinations of supporting legs, not in the order in which they are used. | Slow Canter | Moderate Canter | Gallop |
|---|---|---|---|
| First hind leg on ground only | 7 | 9 | 9 |
| Both hind legs on ground | 34 | 30 | 26 |
| Lead hind leg on ground only | 9 | 4 | 4 |
| Extended suspension | 0 | 0 | 4 |
| First foreleg on ground only | 23 | 17 | 13 |
| Both forelegs on ground | 14 | 22 | 17 |
| Lead foreleg on ground only | 23 | 22 | 22 |
| Flexed suspension | 0 | 4 | 4 |
| Two legs on ground | 55 | 52 | 43 |
| Three legs on ground | 5 | 4 | 0 |
| Four legs on ground | 0 | 0 | 0 |
| No. of strides averaged | 10 | 10 | 10 |

support and two-leg support) fit into the general support trends outlined above for the other canters and the gallop.

Support trends of the galloping gaits of fawns are similar to those of the adults but not as pronounced (Table 3). One noticeable exception to the support trends reported for the cantering gaits of adult animals is the increase in the flexed suspension phase of the canter of fawns as speed is increased (there is a decrease in the suspension phase of the canter in adult animals as speed is increased). Table 3 also indicates that fawns have both hind legs on the ground together for a greater portion of the stride, as are both of the front legs, than do adult animals employing the same gait. A large percentage of the fawn's stride is spent on two legs, a very small percentage on three legs and no four-leg support is present. The footfalls of fawns are spread out over the stride in such a manner that they eliminate (slow canter) or at least restrict (moderate canter and gallop) the suspension phases. Therefore, a galloping fawn has at least one leg supporting the body all of the time, or practically all of the time.

## Leads

During a slow canter the lagging hind foot and forefoot are usually on the ground about 92 percent as long as their leading counterparts. However, it is not uncommon for the two front feet to be on the ground for the same length of time. With increased speed the disparity between the contacts of the front feet is increased and the lagging forefoot is only on the ground approximately 83 percent as long as the leading one. The hindfeet, however, reverse the trend at higher speeds and the leading hindfoot is usually on the ground about the same length of time as, or 85 percent as long as the lagging hindfoot. This latter trend is continued in the fast canter and the various gallops.

Perhaps the reason for the leading hindfoot and forefoot being on the ground longer than their lagging counterparts in the slow canter is because the leading feet not only have a larger support function, but also give a more powerful thrust, with a certain amount of 'follow through', before leaving the ground. At faster speeds the leading hind foot apparently spends a smaller proportion of its energy in merely keeping the body from falling and uses more of its energy in executing a quick powerful propulsive thrust.

Film tracings of the paths followed by the leading and lagging feet of both front and rear pairs of feet indicate that individual strides often vary as much as, or more than, do leading and lagging feet. Therefore, it is difficult to determine whether the feet of a pair are doing different things spatially or just utilizing energy in different ways. In any event, due to the difference in duration of support between leading and lagging feet and the disparity in resulting stresses, leads are changed periodically. Howell (1944),Grogan (1951),Hildebrand (1959) and Jacobsen (1960) suggest that one function of lead change is to equalize the work of the leg muscles in order to postpone fatigue. It is also evident, however, that leads are changed in anticipation of turns or gait changes, or in order to maintain balance while traversing rough terrain. The actual lead changes are accomplished during the period (or periods) of suspension when the feet are off the ground and the legs can be reoriented before striking the ground. Figure 9 shows four positions of a cantering pronghorn changing front and rear leads (top), and four positions of a galloping pronghorn changing rear lead (bottom). Trajectories followed by the feet are in correct spatial relationship.

Front and rear leads usually change at about the same frequency. However, at slow speeds the front lead appears to be changed more frequently. Lead changes in general (both front and rear) usually occur most frequently during the fast galloping gaits when the legs are under considerable stress. However, some animals were observed to change leads very frequently while employing a slow canter. This latter phenomenon appeared to have little to do with the fatigue factor involved in lead changes.

A phenomenon that has not been mentioned in the literature (perhaps it has not been applicable to any of the animals studied thus far), but which is very much in evidence in pronghorn locomotion, is the changing of front and rear leads independently. If a pronghorn is employing a rotary canter or gallop and changes the front or hind lead (not both), then the footfall sequence changes to that of a transverse canter or gallop.

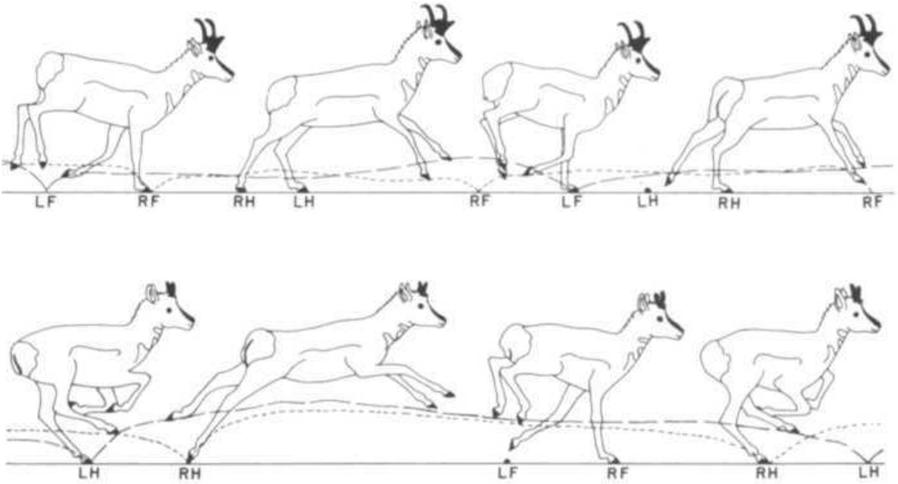


Fig. 9. Four positions of a cantering pronghorn changing front lead (above), and four positions of a galloping pronghorn changing rear lead (below). Trajectories followed by the feet are in correct spatial relationship, long dashes for left feet and short dashes for right feet. Positions of footfalls are indicated below ground line by the initial letters LH, LF, RH and RF.

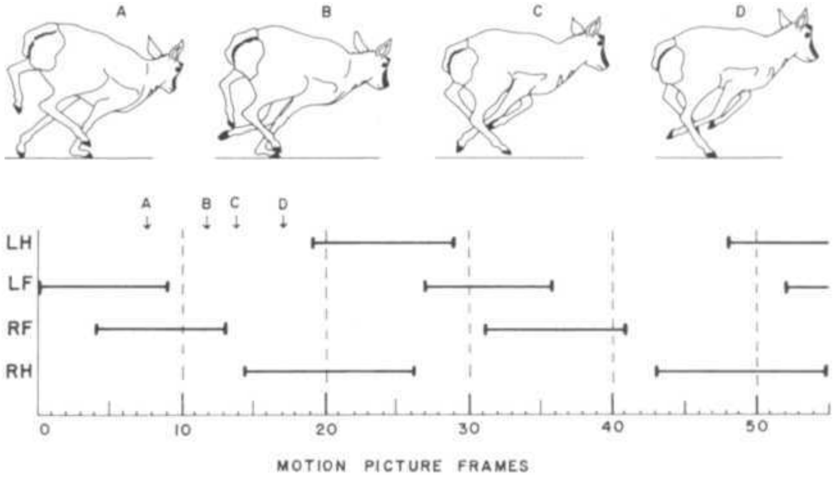


Fig. 10. Gait diagram of a cantering pronghorn executing a sharp turn. Pronghorn silhouettes A-D are comparable to stride phases A-D of the gait diagram below.

The pronghorn must change both front and hind leads simultaneously in order to maintain the same type of canter or gallop. Film sequences analyzed in this study indicate that pronghorn change leads frequently and often independently. Therefore, it is relatively common for a cantering pronghorn to change footfall sequences (and hence type of canter) every few strides and occasionally every other stride.

In order to maintain the rotogallop (the exclusive gait at fast speeds) a pronghorn must change front and rear leads simultaneously. This, however, is seldom the case. More commonly, the front lead is changed during one stride and the rear lead in the following stride. This, of course, results in a stride between front and rear lead changes with the footfall sequence of a transverse gallop. It is apparent, therefore, that although the rotogallop is maintained at fast speeds, a few transverse gallop strides are mingled with it. This order of lead change was the only one encountered in pronghorn employing the rotogallop. It was not uncommon for a pronghorn to change leads every five or six strides during a rotogallop.

## Turning

When making a sharp turn during a canter or gallop a pronghorn will lead with the inside forefoot (Fig. 10). The obvious advantage of this lead is to place the body in a stable trajectory path during the period of flexed suspension. The inside leg is usually the first hind leg to touch the ground in order to keep the body in a proper attitude for executing the turn. It follows, then, that for sharp turns a rotary gallop or canter is preferred, regardless of the considerable amount of straddling and overstride of the inside legs that is necessary (Fig. 10-C). The fetlock joints (pasterns) of the inside legs (particularly the front) are flexed to a considerable degree so as to shorten the inside legs and make proper placement of the outside feet possible (Fig. 10, A and B). Leads are frequently changed a few strides in advance of a turn.

Hildebrand (1959) reports that a galloping cheetah (rotogallop) can turn more sharply by leading with the inside forefoot. The horse also leads with the inside foreleg while executing a turn (Grogan, 1951 and Jacobsen, 1960). The horse employs a transverse gallop and would, therefore, lead into the turn with a different hind foot than the pronghorn.

## Change of Gait

Changes from one gait to another are made very smoothly in pronghorn. It is possible for different animals to change gaits in different ways, and for the same animal to change gaits in different ways at different times. Therefore, the football sequences that can be used in changing from one gait to another are numerous and variable. It is not the purpose of this study to examine the many possible ways in which gait changes can be accomplished by pronghorn, but rather to indicate a few of the more interesting ones encountered.

The section dealing with 'Leads' has already indicated how asymmetrical gaits (canters and gallops) can be changed by a mere change in front or hind lead. When a pronghorn is employing a rotocanter,a change of front lead or rear lead will result in the footfall sequence of a transverse canter. Likewise, a transverse canter can be changed to a rotary canter by changing either the rear lead or front lead. However, when both leads are changed during the same stride (simultaneously), the gallop or canter remains the same and no gait change occurs.

In several film sequences of galloping and cantering pronghorn, complete cycles of locomotion were observed in which only three of the four feet would strike the ground. Although these three-legged strides were rare, they were observed in both bucks and does and on several different occasions. A stride consisting of only three feet striking the ground followed by a period of suspension was observed as a transitional stride between a transverse canter and a trot (Fig. 11) and between a bounding gallop and a trot (Fig. 12-A). In both instances the foreleg being held during the transitional three-legged stride was the foreleg involved in the first trotting stride. The leg was apparently being held so that proper alignment of diagonal pairs could be accomplished and a trotting stride executed. A three-legged stride was also encountered as a transitional stride between a transverse canter and a rotary canter. In this case the foreleg that was being held came down before the leading hind leg, thus resulting in an atypical, slow rotocanter.

One of the most frequently observed gait changes occurred between the trot and canter. Figure 12-B is an example of how one pronghorn went from a trot to a rotary canter, while Fig. 13 illustrates a pronghorn going from a transverse canter to a trot without holding one foreleg during the transitional stride. It should be noted that in both cases the canter is being employed at such a slow tempo that it is atypical: lagging forefoot strikes ground before leading hind foot.

Changes from a walking gait to a trotting gait (and vice versa) are extremely variable in pronghorn and usually occur over several strides. Therefore, it is difficult to

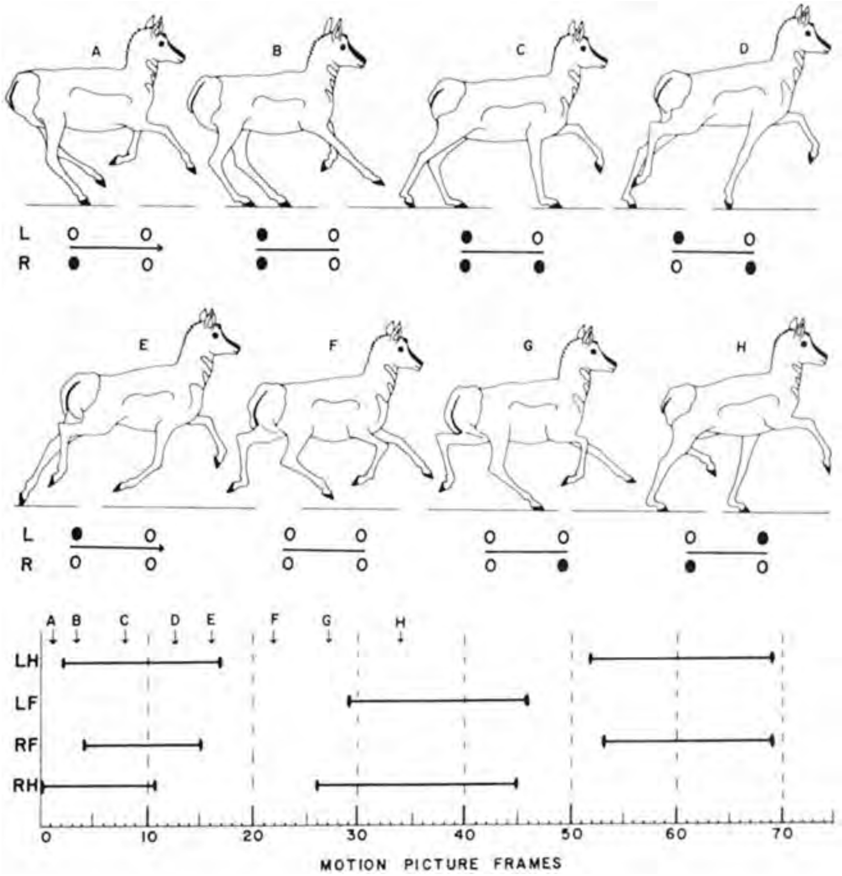


Fig. 11. Footfall formula and gait diagram of a pronghorn changing gaits (transverse canter to trot) with a transitional stride consisting of only three feet striking the ground.

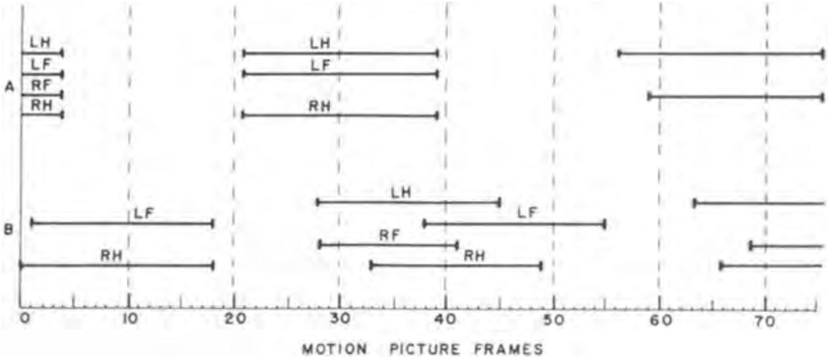


Fig. 12. Gait diagrams of pronghorn changing gaits: A, bounding gallop to trot with three-legged transitional stride; B, trot to rotary canter.

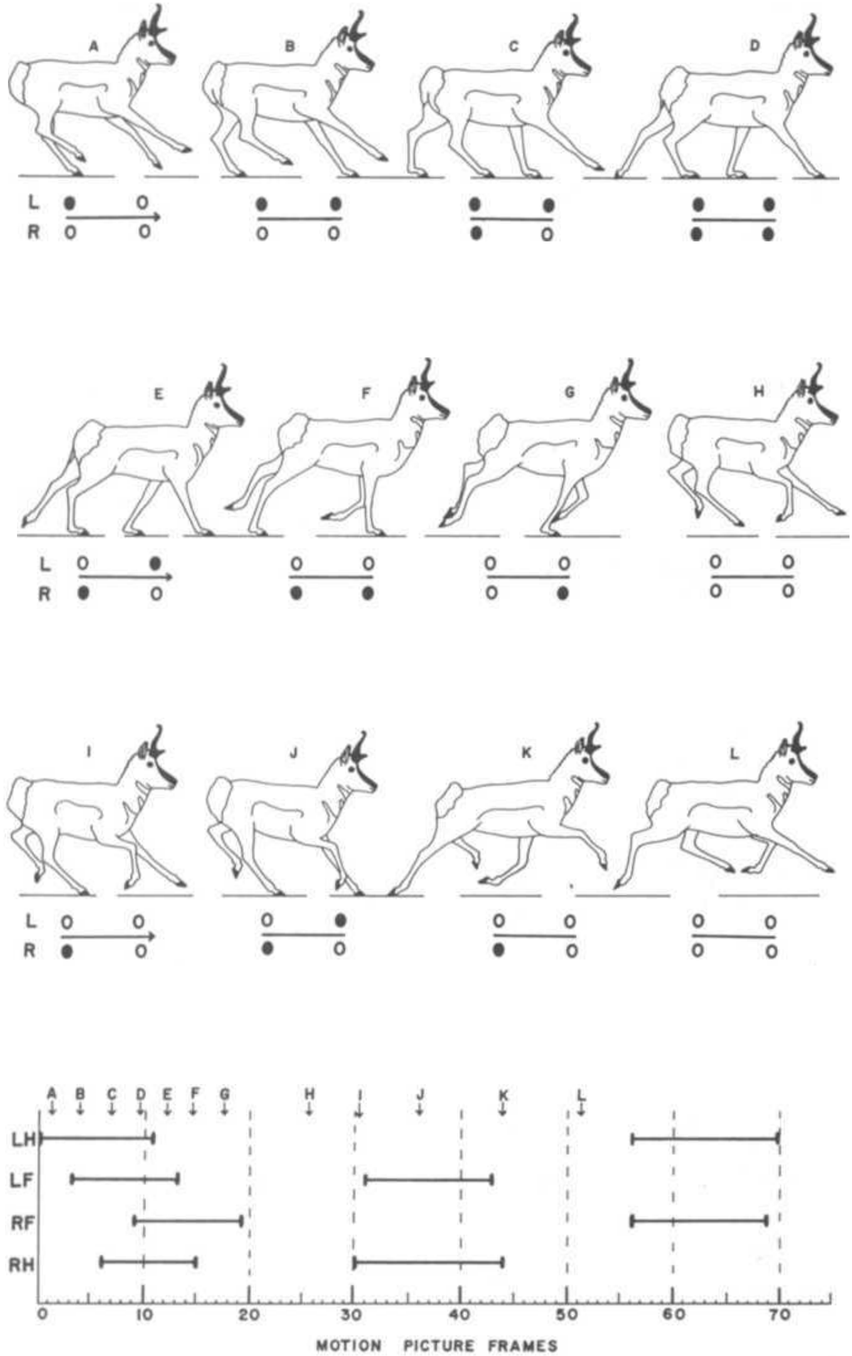


Fig. 13. Footfall formula and gait diagram of a pronghorn going from a transverse canter to a trot.

generalize about these changes except to say that the footfall pattern is gradually arranged to accommodate the new gait. A series of photographs depicting a horse going from a walk to a trot (Muybridge, 1899) is similar to one of the sequences observed in pronghorn. However, his photographs of a horse going from a trot to a gallop are not representative of any of the pronghorn gait changes analyzed in this study.

## Synchronization of Gait and Lead

Howell (1944) asserted that gregarious animals, especially wild ones, exhibit a group synchronization in gaits to the extent that often every individual of a closely bunched herd will be leading with the same foot. Pronghorn, being both gregarious and social, not only exhibit a considerable degree of synchronization in lead but also in the type of canter or gallop employed. During the study 22 herds of running pronghorn were analyzed, 13 of the herds were closely bunched and nine were strung out. The closely bunched herds demonstrated an average of 97 percent synchronization of gait and 92 percent synchronization of lead. The nine herds that were strung out exhibited an average of 79 percent synchronization of gait and 70 percent synchronization of lead All 22 herds combined gave a 90 percent gait and 83 percent lead synchronization. Therefore, it is apparent that closely bunched herds exhibit a greater tendency toward both synchronization of gait and lead, and that the synchronization of gait is greater in both types of herds than is the synchronization of lead. It should be noted at this

TABLE 4. FREQUENCY OF FAST GAIT UTILIZATION IN PRONGHORN FOR VARIOUS SEXES AND AGE CLASSES.

| Age class and sex | No. of observations | % Trot | % Gallop and/or canter |
|---|---|---|---|
| Mature males | 80 | 14 | 86 |
| Mature females | 80 | 16 | 84 |
| Mature animals | 160 | 15 | 85 |
| New born fawns | 14 | 0 | 100 |
| Three week old fawns | 50 | 8 | 92 |
| Six week old fawns | 50 | 13 | 87 |

TABLE 5. METHODS USED BY PRONGHORN IN TRAVERSING BARBED WIRE FENCES (MEASUREMENTS IN INCHES).

| Age class and sex | No. of strands | Approximate distance between strands | Fence height | Height of bottom strand | Method of traversing fence |
|---|---|---|---|---|---|
| Mature female | 4 | 10 | 49 | 19 | Crawled under |
| Mature male | 4 | 11 | 50 | 17 | " " |
| Mature female | 4 | 11 | 51 | 18 | " " |
| Mature male | 2 | 14 | 38 | 24 | " " |
| Mature male | 4 | 10 | 53 | 23 | " " |
| Fawn | 4 | 11 | 50 | 17 | " " |
| Mature male | 4 | 9 | 41 | 15 | Jumped |
| Mature male | 4 | 9 | 34 | 8 | Jumped |

point that individual animals in a herd change lead periodically and that this change of lead is synchronized throughout the herd within a few strides. Therefore, it becomes difficult (and somewhat arbitrary) in some cases to determine the degree of synchronization of lead at any one given time in a herd structure. It should also be pointed out that there does not appear to be any correlation between the leading foot (left or right) and the type of gallop or canter being employed.

### Utilization of Fast Gaits

Results of observations of pronghorn spontaneously employing gaits faster than a walk are tabulated in Table 4. Although more observations might substantiate the frequencies of gaits more accurately, it is apparent from the data presented that pronghorn 'prefer' the asymmetrical canter or gallop when progressing faster than a walk. As the trot is basically used to initiate and/or complete a burst of locomotion, it is employed much less frequently than is the canter or gallop. Usually an animal (adult or juvenile) will go directly into a gallop from a standing position but use the trot sequence to finish the locomotor activity. However, many bursts of locomotion are initiated with a few trotting strides. Occasionally an animal will go a short distance employing the trot exclusively.

Trotting was not observed in fawns until they were about two weeks old and running with their mothers. Fawns appear to acquire the ability or propensity to employ the trot at approximately the same frequency as adults when they are from three to six weeks of age. Gregg (1955) noted that young fawns ten days old are capable of executing all pronghorn gaits.

### Jumping

During the course of this study eight pronghorn were observed traversing barbed wire fences (Table 5). From the data collected it would appear that pronghorn will usually crawl under a fence rather than jump over it if the bottom wire is at least 17 inches (43 cm) from the ground, notwithstanding the fact that the fence may only be 38 inches (97 cm) high. Cole (1956) came to a similar conclusion while working with pronghorn on a food preference study in Montana. When crawling under a low fence wire a pronghorn will drop to its knees, push forward with the hind legs until the front legs are bent back and the chest is on the ground. The back is arched downward to avoid rubbing the wire, and the hind legs are extended out back until recovery is made on the other side of the wire. This crawling procedure can be accomplished at very rapid speeds when the animals are being pressed.

The two instances of jumping were somewhat atypical in that the animals were being moderately pressed and the bottom strand of wire was unusually close to the ground. Several animals were observed to approach fences of moderate height (about 38 inches) with bottom strands close to the ground (less than 17 inches) and walk down them rather than attempting to jump over, or crawl under them. Inasmuch as pronghorn are native to the flat prairie and semidesert terrain and have little need for jumping vertical barriers, it is not surprising that most of them appear to be reluctant to make vertical jumps, and do so only rarely. However, broad jumps of 20 to 25 feet (6.1 to 7. 6 m) to cross horizontal obstacles are relatively common.

Although no pronghorn were observed during this study to cross a fence by going between strands of wire, such observations have been reported by Howell (1944), Throckmorton (1945) and others. According to them, this method of traversing a wire fence can also be accomplished at a very rapid speed.

### Speed

Accurate records of the speeds at which pronghorn employ their various gaits were not obtainable. An approximation of speed was arrived at for each gait by utilizing motion picture tracings and taking into account the speed of exposure and the distance travelled in each stride relative to the length of the pronghorn's body in the picture, and then equating this to the actual length of a pronghorn's body. This method proved helpful in determining relative speed but was not accurate enough to be used for the purpose of indicating absolute speed. Therefore, the literature will be relied upon for this information.

Although the literature to date does not give relative speeds for the various pronghorn gaits, many references have been made to the maximum speed a pronghorn can obtain. Both Einarsen (1948) and Belden (*In* Howell, 1944) concluded that pronghorn can reach speeds of up to 60 miles per hour for relatively short distances. A speed of 53 miles per hour was recorded by McLean (1944) for two bucks over a distance of one-half mile. Speeds in the neighborhood of 40-50 miles per hour have been reported by Cottam and Williams (1943), Chapman (1948), Bridge (1942), Jaegar (1961) and others. Carr (1927) reported pacing a pronghorn with an automobile at 30 miles per hour for seven miles. One or two day old fawns can reach speeds up to 20 miles per hour (Ormond, 1958), while older fawns have been observed maintaining an average speed of 36 miles per hour for 27 miles (Howell, 1944). According to the references cited above, it would appear that speeds of up to 60 miles per hour can be reached on occasion by exceptional individuals under the best of conditions and that they can only maintain such speeds for short distances. Pronghorn can, however, maintain speeds of 30-40 miles per hour for several miles (Hildebrand, 1959).

During the study several pronghorn were paced by automobile. The fastest speed recorded was 45 miles per hour. It became apparent during these occasions that does and young adult animals were fleeter afoot than were older animals, especially older bucks.

It should be noted that if the rate of stride remains relatively constant at very rapid speeds (as indicated by the data), then a pronghorn would have to increase its stride length to approximately 29 feet (8. 9 m) in order to gallop at 60 miles per hour. Such a stride length would appear to be beyond the pronghorn's ability, and would, therefore, suggest that the actual top speed of the pronghorn is somewhat less than 60 miles per hour.

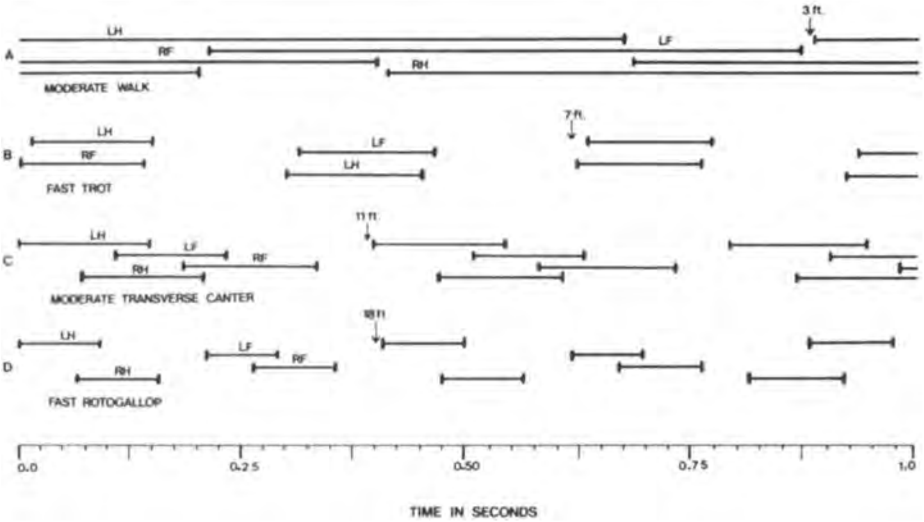
## DISCUSSION

Although the pronghorn, like most quadrupeds, employs the diagonal walk, Gray (1944) asserted that walking quadrupeds can theoretically advance their four feet in six different sequences: (1) RH (right hind), RF (right front), LH (left hind) and LF (left front). (2) RH, LF, LH and RF. (3) RH, LH, RF and LF. (4) RH, LH, LF and RF. (5) RH, RF, LF, and LH. (6) RH, LF, RF and LH. Sequence 1 in which the front foot begins advancing only after the ipsilateral hind foot has done so, appears to be the one that evolution has favored and is the sequence used by the vast majority of quadrupeds. Brown (1968), discussing Gray's six sequences, stated that only in sequence 1 do the feet form the best triangles—the bases of tripods—to support and balance the animal properly. He pointed out that in the five other sequences the feet form triangles that are small and do not lie under the center of gravity and that an increase in speed would bring problems of balance and risk of one foot interfering with another. Gray (1953) maintained that sequence 1 is the only order of stepping which conforms to the requirement that no foot should ever be lifted unless the center of gravity of the body lies over the triangle marked by the other three. Sequence 2, referred to as the lateral walk by Howell (1944), the 'false walk' (Brown, 1968), and as the diagonal sequence, diagonal couplets gait (Hildebrand, 1966), is very rare and is only employed by the kinkajou, the unguligrade giant armadillo, the aardvark, most apes, and all monkeys. Although Einarsen (1948) illustrates this type of walk for pronghorn, the illustrations are obviously in error. It would appear from the evidence of modern forms that the walk was undoubtedly the primitive system of locomotion employed by all terrestrial vertebrates (Muybridge, 1899). Boonstra (1967) and Magna de la Croix (1936) concluded that the walking gait was basic to the evolution of mammalian gaits.

In the walking gaits, as in most pronghorn gaits, speed is a product of rate and length of stride. As a pronghorn increases the tempo of a walk from a very slow walk to a fast walk, the rate of stride increases from 0.7 to 1.2 strides per second, while the length of stride increases from approximately 20 inches to 41 inches (51 to 104 cm). Increased speed and body momentum appear to compensate for the relative instability of the fast walking gaits where there are more phases in a stride consisting of only two legs supporting the body.

The disparity in support time of legs of a diagonal pair in a trotting stride is a result of the front legs of a pronghorn being somewhat shorter than the hind legs and not being able to match the stride of the longer hind legs. This discrepancy in the length of fore and hind legs is not unique to pronghorn, for Howell (1944) has pointed out that this condition is true for most mammals. The disparity in support would be greater, however, if it were not for the anatomical adaptations present in pronghorn and other cursorial mammals for lengthening the functional length of the forelimb. Loss of clavicle associated with the incorporation of the scapula (now free to swing) into the functional length of the forelimb increases length of stride and makes it possible for the front leg to match the stride of the longer hind leg more closely (Eaton, 1944). This allows the length of stride and the timing of fore and hind limb movements to approximate symmetry in walking and trotting gaits. As with the walk, the rate and length of the stride increase as the trotting speed of a pronghorn increases.

Chubb (1929), Howell (1944), Dagg and de Vos (1968), and others have reported that the 'galloping' gait of pronghorn antelope is the rotary gallop. It was found, however, that the transverse system of footfalls is also a natural and frequently employed gait at slower galloping speeds (canters). Such diversity in 'galloping' gaits appears to be lacking in most other mammals. Authors reporting on the natural gaits of horses (Muybridge, 1899; Stillman, 1882; Howell, 1944; Grogan, 1951; and Hildebrand. 1965, to mention a few) have concluded or inferred that the horse employs the transverse gallop or canter exclusively. It has been reported by Chubb (1929) that the members of the Family Equidae, the cow, buffalo, goat, bear and others employ the diagonal (transverse) gallop, while some of the ruminants such as the deer, elk and antelope adhere to the rotatory system of the dog. The cheetah, a member of the cat family, employs the rotary gallop (Hildebrand, 1959). Film shot and analyzed during this study confirms the gaits of the horse, deer, elk and dog as reported above, and suggests that the exclusive galloping gait of the Rocky Mountain Bighorn Sheep (*Ovis canadensis*) and the Rocky Mountain Goat (*Oreamnos americanus*) is the transverse gallop. It would appear from the references cited above and from film analyzed in this study, that there has been a selection for certain types of galloping gaits within phylogenetic groups: transverse for Families Equidae, Bovidae (many genera) and Ursidae, rotary for Families Canidae, Felidae and Cervidae, and both for the Family Antilocapridae at cantering speeds, with a preference for the rotary sequence at fast



Fig, 14. Sequences of footfalls (gait diagrams) of various gaits shown in relation to time in seconds. Letters R, L, H and F, respectively, mean right, left, hind and front feet. Time intervals required to cover specified distances (one complete stride) are indicated.

galloping speeds. Magna de la Croix (1928) noted the evolutionary trend toward the rotogallop in many artiodactyls and the transverse gallop in many perissodactyls.

As previously mentioned, speed is increased in the walking and trotting gaits by increasing both length and rate of stride. This was also found to be the case with canters. In the gallop, however, speed is increased by increasing the length of stride but the rate of stride is actually decreased in many cases. Figure 14 shows comparative stride lengths for various gaits according to time. Hildebrand (1962) noted that, as speed of travel increased, small rodents would decrease stride rate while increasing stride distance, but asserted that ungulates and carnivores increased stride distance considerably but increased stride rate only slightly. His statement holds true for all pronghorn gaits with the exception of some fast galloping strides. The most rapid stride rate recorded for a pronghorn was 2.8 strides per second, the longest stride length being 18 feet (5.5 m). Both the cheetah and horse average about 23 feet (7 m) per stride at a fast gallop but the rate of stride for the cheetah is 3.5 strides per second, whereas it is only 2.5 strides per second for the horse (Hildebrand, 1959). Hildebrand also points out that the stride of the cheetah is 8½ to 11½ times its shoulder height, compared with 4½ to 5 for the horse. The stride of a mature pronghorn is about 6 to 6½ times its shoulder height. Therefore, the length of stride (relative to shoulder height) and rate of stride are greater in pronghorn than in the horse but somewhat less than the cheetah with its flexible back.

McLean (1944) stated that when pronghorn are running most of their power seems to be generated by the hind legs and the forelegs are used mainly for stability. However, the body weight of a pronghorn is carried principally on the larger front feet when running, whereas the rear hooves do not strike the ground as forcefully and the hind legs act merely as supports (Einarsen, 1948). The foregoing statements appear somewhat contradictory, but are in fact dealing with two different phenomena: propulsion and support. Although the propulsive-support ratio of limb function varies in mammals according to body conformation, speed, etc., if both limbs are approximately the same size, the support role is relatively higher in the pair nearest the center of gravity and the propulsive role in the other pair (Howell, 1944). Inasmuch as most mammals, including pronghorn, have the center of gravity near the front quarters, the main propulsive thrust is produced by the hind limbs and the forelimbs act more as struts. Taylor (1970), working with East African viverrids, and Hildebrand (1959) working with the horse and cheetah, reported similar results. An investigation of the walk in the cat (Manter, 1938) resulted in the conclusion that the forelimbs meet the ground with greater retarding action while the hind limbs contribute more forwarding impulse to the body. Gambarian and Oganesian (1970), using a specially designed instrument to measure forces of thrust, conclude that the forelegs of animals adapted to the rebounding jump (gerbils of the genus *Meriones*) work exclusively in the absorption of shocks, whereas the forelegs of small galloping mammals (*Mustela nivalis* and *Ochotona princei*) accomplish an active thrust as well as absorbing the shock of impact. Perhaps further studies involving the galloping gaits of ungulates will demonstrate a greater propulsive role for the front limbs.

Hildebrand (1965) states that his limited data show no significant differences between the gaits of colts and adult horses. Pronghorn, however, were not observed to employ the trot until they were about two weeks old. Although the footfall sequences of cantering and galloping fawns are comparable to those of the adult animals, there was considerably less suspension, or no suspension, during each stride of a fawn's gait. As fawns have longer legs in proportion to their bodies than mature animals and, because of their apparent lack of muscular coordination at a very young age, it would appear that the stability acquired from very short periods of suspension, or lack of such, would be of great value. A considerable maturation of the coordinating mechanism of the body appears to be necessary before fawns can execute the intricate footfall sequences of the symmetrical gaits. The fact that the rotary sequence of footfalls was the only one observed in running fawns, and is the exclusive sequence of mature animals at fast speeds, suggests that perhaps the rotary sequence is more basic or primitive to the species than is the transverse one.

Straddling of the front legs by the hind legs to prevent interference of ipsilateral legs was observed to some extent in all gaits, being most pronounced in the rotogallop, especially the rotogallop of fawns. The manner in which straddling occurs in the pronghorn is widespread among mammals. Chubb (1929) pointed out that even the English bulldog with broad shoulders and narrow hips will execute the stereotyped straddling procedure though it appears very awkward in doing so.

Gregg (1955) maintains that the bound (bounding gallop) is a distinct and isolated gait that does not develop from or into any other gait. It was found, however, that although pronghorn do usually use the bounding gallop to initiate flight, the gait would usually grade into a trot,boundlike canter or normal canter sequence.

Pronghorn spend a greater percentage of each trotting stride on diagonal supporting legs at slower speeds than at faster speeds, 62 percent being the average for the slower trots and 48 percent for the faster trots. These percentages are low when compared to the trotting gaits of the twelve pecoran species reported by Dagg and de Vos (1968). The average percentage times of the trotting strides of these species (relative speed was not indicated) ranged from 72 to 92 percent (e.g. *Alces americana,* 80; *Cervus canadensis,* 75; *Rangifer tarandus,* 83; *Odocoileus hemionus,*86; *Dama dama,* 72; *Odocoileus virginianus,* 77; and *Gazella thomsoni,* 92). As with the pronghorn, most of the twelve species were reported to have short periods of time during the trotting stride when one front and/or one hind leg gave sole support to the body, with the hind leg usually having a greater percentage time than the front leg. However, the total percentage time spent on one leg alone was considerably higher for most of the twelve species than for the pronghorn. A longer one-leg support phase would, of course, result in a shorter total suspension. Whereas in the pronghorn total suspension is from 33 percent (moderate trot) to 45 percent (fast trot) of the total duration of stride and four-point support is very rare, Dagg and de Vos (1968) report that there is no period of suspension in the trotting strides of moose, elk, gazelle, etc. ,a very small percentage (3 to 20%) in other forms, and that several animals, including the moose, elk, caribou and mule deer, have a very short (1 to 4%) period of four-point support. It would appear, therefore, that the trotting stride of the pronghorn is more symmetrical than many other species and that the body is suspended for a greater percentage of the stride.

Hildebrand (1966) asserts that large animals accelerating from a moderate gallop to a fast gallop decrease the duration of those intervals when all feet are off the ground. Although pronghorn are not 'large' animals compared to many ungulate groups, nonetheless the trend is true for the pronghorn if only canters (one period of flexed suspension) are considered. However, when a pronghorn increases speed from a fast canter to a gallop a period of extended suspension is incorporated into the gait, thus increasing the total suspension time per stride for the gallop to more than that of the moderate canter. During the speed increase from slow canter to fast gallop the footfalls are spread out to accommodate the period of extended suspension. Therefore, the percentage of stride time spent on four legs and three legs decreases while the time spent on two-leg and one-leg support is increased. Dagg and de Vos (1968) maintain that theoretically the fastest gait would be one in which two-leg support is completely eliminated in favor of one-leg support.

According to Dagg and de Vos (1968) heavy animals such as moose and elk never have an extended suspension and the period of flexed suspension is often missing, particularly when galloping slowly. They also report that the mule deer has a period of extended suspension but no period of flexed suspension, and that the white-tailed deer has both a flexed and extended period of suspension with the extended period being the larger of the two. Howell (1944) depicted a light horse that had a very brief period of extended suspension. Although the cheetah is quite different from ungulates in many respects, it is interesting to note that it is reported to be the fastest of animals for a short dash and like the pronghorn has two periods of suspension in its gallop (rotogallop). The suspension periods of the cheetah's gallop increase in duration with increased speed, the extended suspension period increasing proportionately more (Hildebrand, 1961).

Limited data indicate that pronghorn change front leads during slow and moderate canters more frequently than rear leads. A possible explanation for this could be that the heavy front quarters with head attached (center of gravity being a few inches behind the shoulders) puts considerable stress on the front legs during the rocking action of canters where the body is thrust vertically into a period of flexed suspension at slow speeds with little body momentum. At a fast gallop the hind legs are required to increase their propulsive force (hence stress), the front legs displace the shoulders less vertically, and the front and hind lead changes approach the same frequency. As pronghorn maintain the rotary sequence of footfalls at fast galloping speeds, front and rear lead changes must occur together, hence leads change at the same frequency.

The changing of front and rear leads independently, resulting in a change from transverse to rotary canter or vice versa, appears to be unique to the pronghorn according to the available literature. The inference from the works of Jacobsen (1960),Grogan (1951) and Howell (1944) is that the horse retains the transverse footfall sequence, although front and rear lead changes occur regularly to postpone fatigue. It follows that front and rear leads must be changed simultaneously during the execution of one stride if the transverse footfall sequence is to be maintained. Reporting on lead changes in the horse and cheetah, Hildebrand (1959) states that lead reversal is usually accomplished by the forelimbs first but that the motion of the hind limbs must be coordinated to avoid the interference that would otherwise follow. Apparently leads are changed simultaneously because the cheetah maintains a rotogallop and the horse a transverse gallop. The pronghorn, however, even when maintaining a fast rotogallop will usually change the front lead during one stride and the rear lead during the following stride. Therefore, a stride consisting of a transverse footfall sequence is often interjected into the stride between front and rear lead changes.

When progressing faster than a walk, adult pronghorn and fawns usually employ the canter or gallop. Lack of heavy antlers and moderate body size are probably two reasons responsible for the selection of the asymmetrical canters and gallops as the most commonly used fast gaits. Dagg and de Vos (1968) point out that animals with heavy antlers or horns use the symmetrical trot more frequently than the gallop since the center of gravity changes less radically than in the gallop, and the heavy head is more easily controlled. They also point out that in a gallop all of the animal's weight must be launched into a period of suspension from one foot. Galloping, therefore, requires relatively less energy for moderate-sized animals than for heavy ones. Inasmuch as the force of contraction of a muscle varies as the square of linear measure while the mass of the body varies as the cube of linear measure, largeness places muscles at a disadvantage. Although skeletal and muscular adaptations can help to reduce the load placed on the muscles of larger animals, size is still important. Pronghorn appear to be in the size range that is best suited for rapid locomotion.

The observation that pronghorn will usually crawl under or occasionally through a fence rather than jump over it has been reported by many writers. Pronghorn have, however, been reported to have jumped a six-foot (1.8 m) trap fence (Buechner, 1950), a 34. 3 inch (87 cm) four-strand barbed wire fence (Bruns, 1969) and barriers up to and over eight feet (2.4 m) high (Spillett *et al.*, 1967). A study on the effects of various livestock fences on pronghorn movement (Spillett *et al.*, 1967) concluded that, with few exceptions, pronghorn appear to be unaware of their ability to jump vertical barriers and rarely jump fences over 32 inches (81 cm) high unless under severe stress or active pursuit.

It is a general consensus that the cheetah is the fastest of animals for a short sprint. Speeds of over 70 miles per hour have been reported for this remarkable cat. The pronghorn with recorded speeds of up to 60 miles per hour appears to be the fastest pecoran (ruminating artiodactyl) species followed by the smaller true antelope, with the cervids being the slowest of these families (Dagg and de Vos, 1968). Speed and endurance are both important factors in cursorial mammals such as the cheetah and pronghorn. The cats are typical short distance sprinters whereas the larger herbivores, particularly the horses and their relatives, are stayers par excellence among mammals (Slijper, 1966). Hildebrand (1959) reports that a horse ran 50 miles at an average speed of 15 miles per hour. Although pronghorn can only maintain extremely rapid speeds for a mile or so, they can run at approximately 30 miles per hour for eight or nine miles. Thus, the pronghorn with its moderate body size would appear to be a good sprinter with a good endurance capacity. Inasmuch as the length of stride varies in direct proportion to leg length, but the intrinsic rate of muscle contraction, and hence rate of stride, varies inversely with linear measure (Hill, 1950), the pronghorn's body may be a successful solution to the problem of maximizing running speed.

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Paper No. 13

# On the Behavior of Punjab Urial (*Ovis orientalis punjabiensis*)

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## ABSTRACT

Urial sheep were studied in the Salt Range of Pakistan for one month during October-November, 1970. About 500 urial inhabited the sanctuary in which the study was made. The adult sex ratio was about 1:1, and there were 75 young and 35 yearlings to 100 adult females. A drop in temperature seemed to precipitate the onset of the rut in late October. The average size of male herds then decreased as rams singly and in small groups made transitory visits to female herds in search of estrous ewes. Rams preferred other rams of the same age for company. Agonistic behavior between rams was common. Of 19 patterns described, 13 were quantified. About 90% of the interactions involved rams of the same age or the next larger or smaller one. Yearling rams seldom interacted whereas the largest rams displayed most patterns over twice as often as expected; a similar difference was noted in the frequency of courtship patterns. The behavior of urial is compared with that of 4 other types of sheep. Most patterns are similar in all types, but some qualitative and quantitative differences exist, differences for which there are as yet no explanations. For example, the Marco Polo sheep and American mountain sheep often rear up before clashing horns, but the urial, Soay sheep, and mouflon do not; and the low-stretch posture is common during agonistic displays of American sheep but rare in urial.

## INTRODUCTION

The detailed behavioral studies on North American mountain sheep (*Ovis canadensis*) by Geist (1968, 1971) stimulated us to obtain some comparative information on the Punjab urial (*Ovis orientalis punjabiensis*). The taxonomy of the mouflons and urials in Europe, Near East, and in South Asia remains unsettled, with, for example, Pfeffer (1967) recognizing them only as three subspecies of *Ovis ammon* and Ellerman and Morrison-Scott (1951) dividing them into three species, O. *musimon, O. laristanica* and *O. orientalis,* the last with 15 subspecies. However, urials (*orientalis* group) differ in appearance from argalis (*ammon* group) and we prefer to use the classification of the last-named authorities in this report. H. H. The Nawab of Kalabagh permitted us to observe the Punjab urial in his private sanctuary which is located in the Salt Range of West Pakistan (see Fig. 1). We spent October 6 to November 9, 1970, in a preliminary study of these animals and the main purpose of this paper is to present some information about their agonistic and courtship behavior.

Harried by poachers when they leave the sanctuary, the urial were quite shy, often fleeing as soon as they sensed us. Running over ridges, down slopes or across open terrain, sometimes for over 0. 5 km, they made no attempt to seek the safety of nearby cliffs, behavior which resembles that of-argalis (Heptner *et al.*, 1966) and constrasts with that of mountain sheep (Geist, 1971). Since animals often stood or rested on some vantage point, they easily detected our movements on the barren slopes. Facing us, some snorted, stamped a forefoot, and occasionally initiated their flight with a loud thumping gait, made by hitting the ground with their four legs in unison, all visual and auditory signals that served to alert other urial in the vicinity. Consequently we

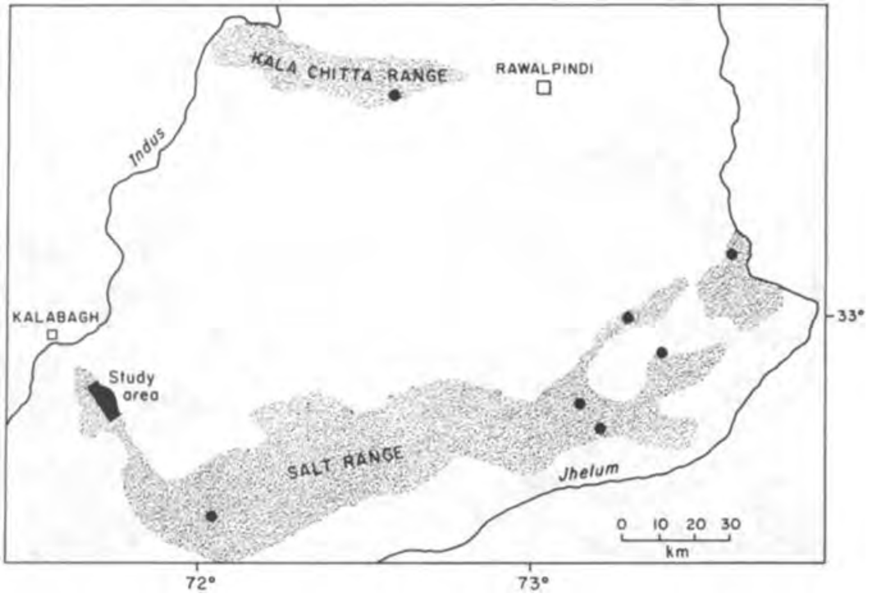

Fig. 1. The Kala Chitta and Salt ranges of north-central West Pakistan in which most of the remaining Punjab urial are found. The ranges are outlines along the 300 m contour line. The black dots represent localities where one of us (Z.B.M.) has encountered urial during the 1960's.

usually observed the animals at distances exceeding 100 m with binoculars and 20x scopes while sitting quietly on some promontory. With daytime shade temperatures reaching 30 to 35°C,the urial usually retreated into deep ravines by 0900 hours and remains there beneath the canopy of trees until the sun disappeared behind a ridge around 1600 and 1700 hours. Most of our 90 hours of observation were thus made in the early morning and late afternoon.

## DESCRIPTION OF STUDY AREA

Punjab urial are confined to West Pakistan, occurring between the Indus and Jhelum rivers below an altitude of 1500 m primarily in the Kala Chitta and Salt ranges (Fig. 1). Urial also inhabit the rugged hills along the west bank of the Indus at that latitude, but we are uncertain if these belong to the *O. o. punjabiensis* or *O. o. cycloceros* (*blanfordi*) race. Excessive hunting has reduced the animals in number or exterminated them in much of their former range (Roberts, 1967), but a sizable population survives in the sanctuary which lies about 30 km south-east of the town of Kalabagh in a small massif that forms the most westerly extension of the Salt Range. The hills rise gently for several kilometers from a flat plain before entering a rugged area of small plateaus, whose edges drop vertically to boulder-strewn streambeds, of sharply tilted beds of rock and of limestone bluffs, before culminating in a series of ridges reaching an altitude of 1000 m (Plate 1). The lower slopes and a few level terraces are partially cultivated, but the rest of the area is too dry and rocky for anything except livestock grazing. With an average annual rainfall of 50 cm or less, most of it falling in July and August, and temperatures of 40°C and above during the hot season, the vegetation consists of an *Acacia* scrub woodland. *Acacia* modesta is the dominant tree and it grows scattered on the slopes and along streambeds often in association with *Snlvadora oleioides, Zizyphus nummularia* and others. Shrubs are sparse, except in some ravines and on the high ridges where *Dodonaea viscosa* is prominent. There were few forbs in October, possibly because no rain had fallen since August 24, and

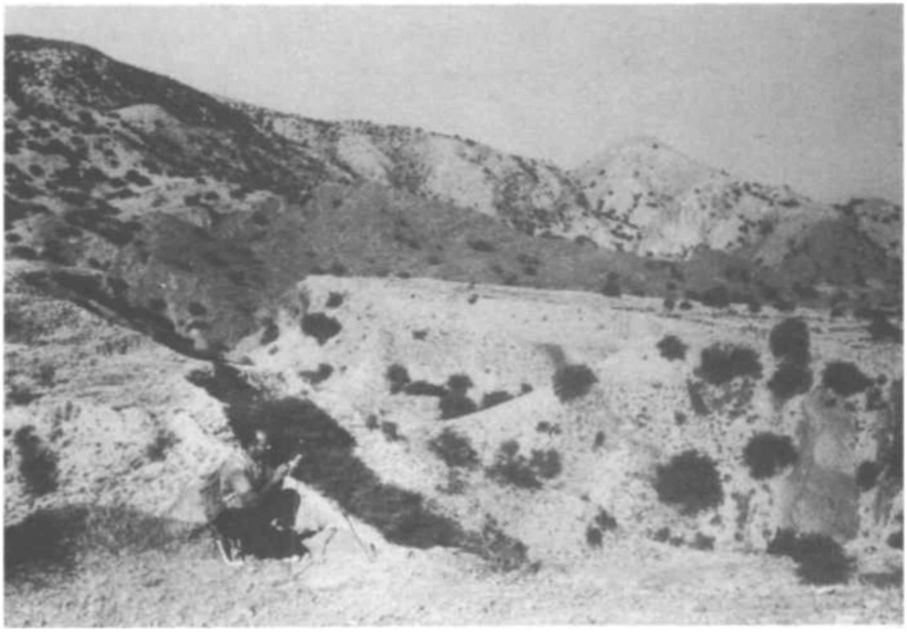

Plate 1. Typical urial habitat in the study area, showing the broken terrain and scattered acacia trees on the lower slopes.

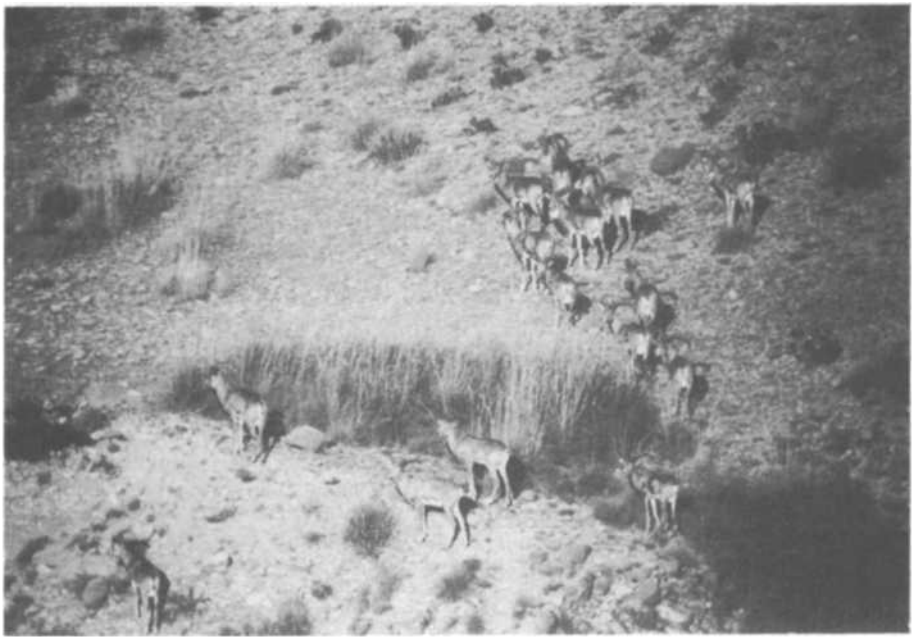

Plate 2. A herd of urial rams.

the predominant ground cover consisted of dry grasses, importantly *Aristida depressa, Cenchrus pennisetiformis, Eleusine flagellifera,* and *Cymbopogon jawarancusa.* To find out what percent of the area was covered by grass, we ran transects through each of four main types of terrain. A 20 × 40 cm rectangle was placed on the ground at 5 m intervals and the vegetation coverage was estimated within it. In a sample of 196 plots, the grass coverage varied from 10% on a steep rocky slope to 24% on a gentle terrace, and the average was 19%. The rest of the ground was bare, yellow, grey and brown in hue, a somber and rather desolate land.

## DESCRIPTION OF ANIMALS

Punjab urial are said to have a more reddish coat, a more conspicuous neck ruff and saddle patch, and a more circular sweep to the horns than the other forms of urial inhabiting this part of the world (Stockley, 1936; Clark, 1964; Prater, 1965). We sexed each urial we saw and placed it into one of several age classes. Those for rams were partly based on horn size and to facilitate comparisons we used the same categories as the ones established by Geist (1968) for mountain sheep. While it is possible to compare the two kinds of sheep on the basis of horn length, the ages of animals older than class I may not be the same.

*Young.* A young is the same color as a female. Its horns are 4-8 cm long, those of males being thicker at the base than those of females. At the time of our visit, most young still accompanied their mother. Kenneth (1953) and Asdell (1964) stated that the gestation period of urial is 6 months. With the peak of the rut in the first half of November and most births occurring in late March and April, according to the sanctuary staff, the gestation period would be 5 months, as it is in mouflon, *Ovis musimon,* (Pfeffer, 1967). Thus the young were 6 to 7 months old at the time of our visit.

*Female.* Adult ewes have a pale reddish-buff pelage which changes to whitish on the belly and insides of the legs and to greyish on the face. A grey wedge of hair extends both upward and downward from the white knee. The horns are thin and roughly as long as the ears. Yearling ewes, 1½ years old, are somewhat smaller and lighter of build than adults.

*Yearling male* (1½ *years*). Yearling rams are slightly smaller than adult ewes, the color of their pelage is more greyish, and their horns are more massive and up to 15 cm long. A thin line of black hair runs down the ventral side of their neck, the first intimation of the ruff.

*Class I male* (2½ *years*). Class I rams are larger than yearlings and they have a broad black line of hair on the neck and a dark, horizontal stripe along the flank. The horns are 20-35 cm in length and curve sharply backward. The scrotum, greyish-white in color, is much larger than that of yearlings.

*Class II male* (3½ *years*). Rams in this class have a pelage richer in hue, more reddish, than young ones, and an actual neck ruff from chin to chest is evident. A few animals have a pale area on the back, the first sign of a 'saddle'. Instead of being grey, the scrotum in this and subsequent classes is strikingly white, a structure as conspicuous as the small white rump patch. The grey pattern on the forelegs, typical of both females and young males, has turned white. The horns sweep outward and down for some 40-60 cm.

*Class III male* (4½ *years*). The pelage of these rams is rusty in color separated from the white belly by a prominent black flank stripe. The saddle consists of a whitish patch with a black vertical slash along its anterior side. However, the pelage of urial is quite variable and the saddle may be prominent in some and not others. The throat ruff is black and large, longest on the upper neck and on the chest, the former sometimes showing a touch of white. The horns sweep in a half-circle and are roughly 70-75 cm long.

*Class IV male* (*fully grown*) (*Plate 3*). Mountain sheep rams reach their full size at the age of 8 to 9 years (Geist, 1971) but urial may do so somewhat earlier (Heptner *et al.*, 1966). Urial rams are handsome, sturdy animals, up to 81 cm high at the shoulder (Lydekker, 1907) and weigh about twice as much as ewes. Their large throat

Plate 3. An adult urial ram (class IV)

ruff may be white at the upper portion and so long at the lower end that it hangs over half-way to the knees. The horns ascribe almost a ¾ circle, with the tips at the level of the neck, and some are 82. 5 to 100 cm long according to Lydekker (1907).

## POPULATION DYNAMICS

We divided the sanctuary into 5 blocks for census purposes and attempted to count all urial in one block each day by walking along ridges and ravines. A total of 410 animals were seen. Some were undoubtedly overlooked and the most westerly portion of the reserve could not be visited, raising the total to an estimated 500, a figure also given by Mountfort (1969) on the basis of information received from the sanctuary staff. This estimate represents a minimum, for local informants told us that urial move into the sanctuary from the surrounding hills during the hot season in order to drink at various pools. These animals use an area of perhaps 40 to 50 sq km.

A total of 1987 urial were classified with respect to their age class and sex, many of them repeatedly in the course of the study. To avoid biasing the population sample we excluded from the computations 904 animals which one of us tallied at a site where rams often lingered but large herds of ewes generally avoided. The composition of the population was as follows: yearling male—5. 2%; class I male—5. 9%; class II male—8. 3%; class III male—8. 5%; class IV male—10. 5%; female—37. 7%; and young—23. 9%. The yearling and adult males total 38. 4% as compared to 37. 7% for the females, a 1 : 1 sex ratio also common to some mountain sheep populations (Buechner, 1960). Yearling males probably comprise closer to 6% than 5% of the population, for all sub-samples except one were around the former percentage. We were unable to separate yearling from adult ewes with precision in many instances, but since the adult sex ratio was equal we assumed that the yearling one was too.

Jerdon (1874) noted the urial 'have generally twins' and Prater (1965) stated that 'one or two young are produced at birth'. Most ewes were accompanied by only one young, suggesting that single births are the rule in the study area. On 6 occasions a ewe had two young at heel, but these may not have been twins in all instances.

Young possibly may follow ewes other than their mother, as described for mountain sheep (Geist, 1971), and lost young may attach themselves to strangers—one tried to do so to a chinkara (*Gazella gazella benetti*). No yearling female was accompanied by a young and this together with the fact that yearlings took part in the rut suggests that urial have their first offspring at the age of two years. There were about 75 young to 100 adult females indicating good reproduction and survival up to an age of 6 months. However, mortality of young may be high after that, for there were only about 35 yearlings to 100 adult females. Assuming similar birth and survival rates in 1969 and 1970, about half of the young disappeared between the ages of 6 and 18 months. It is also possible, however, that survival rates of newborn lambs vary considerably from year to year.

With leopards (*Panthera pardus*) exterminated and protection against poachers vigorously enforced within the sanctuary, predation is not a large factor there, although urial may be shot when they roam into the hills adjoining the reserve. Disease introduced to urial by the several hundred head of livestock that forage in the area during part of the year may be a cause of death, and, according to His Highness, a number of sheep were found dead in January, 1970. (We collected the remains of an old ewe and a three-year-old ram.) He also told us that his domestic sheep suffer from liver flukes and lungworm. The latter parasite is known to cause severe debilitation in mountain sheep (Buechner, 1960). On several occasions an urial dashed around erratically, jerking its head up and down, before halting with its head lowered in a patch of tall grass, behavior which might have been induced by the persistent attention of a warble fly. Parasitism is usually not fatal until linked with malnutrition, and it is possible that the factors combine to produce mortality during the driest time of year. Domestic cattle, sheep, and goats are the urial's sole competitors for the available forage except for a few chinkara. Although urial browse on *Acacia, Zizyphus, Hippophaë rhamnoides* and other trees, sometimes standing on their hindlegs to reach a branch in the manner of mouflon (Pfeffer, 1967), their main food consists of grass, at least at the time we were there. With a ground cover of 19%, grass would seem to be readily available, but 12% of this consists of *Cymbopogon jawarancusa* and *Aristida depressa,* species which urial seem to disdain when dry. Only about 7% of the ground was covered with grasses that urial like, and livestock preferred the same ones. To test for the food preferences of urial we presented 7 species of grass in different piles to 3 captive young which were kept by His Highness in an enclosure at the edge of the sanctuary. Based on the number of visits made by these animals to a pile and the relative amount of time they spent eating, the order of preference of the 3 most preferred species was: *Eleusine flagillifera, Digitaria bicornis,* and *Cenchrus pennisetiformis,* the same grasses eaten extensively by free-living animals.

## HERD SIZE AND COMPOSITION

Herd structure in many hoofed animals changes with the seasons, being particularly influenced by the rut. Punjab urial are said to mate in September (Jerdon, 1874) or in September and October (Prater, 1965). When we arrived on October 6, the animals showed little evidence of being in rut, but a change in their behavior occurred between about October 18 and 22. During that period the minimum night temperatures dropped from around 25°C to 17-20°C and the daytime temperatures seldom strayed above 32°C instead of climbing to 35°C. The drop in temperature seemed to precipitate the onset of the rut and a peak appeared to have been reached in the first half of November. The frequency with which rams sniffed the vulva of ewes provides a rough impression of the intensity of the rut: between October 6 and 22, males sniffed females at the rate of 0. 3 instances per hour of observation, between October 23 and 31 they did so at the rate of 0. 9, and between November 1 and 9 at the rate of 3. 3.

Herds were unstable with animals constantly joining and parting, especially during the rut, and the only lasting associations seemed to consist of a ewe with her young and sometimes a yearling as well. Nevertheless three types of herds could be recognized: female herds comprising solely ewes and young; mixed herds containing one or more rams, ewes and young; and male herds consisting only of rams (Plate 2). Female herds were generally small (Table 1), averaging 3 to 4 individuals, a ewe or two with their young which soon lost their identity when they joined or were joined by others. The average size of mixed herds decreased from 10 to 7 as the rut advanced (Table 1), the disruption caused by courting rams among the ewes possibly initiating the change. As Table 2 shows, mixed herds may contain rams of all classes but percentages differ not only with age but also with the time of rut. Yearling males tended to remain with ewes, fewer than 15% being alone or in male herds; a somewhat higher percentage of class I rams was found in male company, especially early in the rut. In contrast, about two-thirds of class II rams were in male herds prior to the rut, but later most associated with ewes. Adult rams of classes III and IV were primarily in male herds before the rut, then spent an increasing amount of time with the ewes during it. Generally, the older the rams the less time they spent with ewes before as well as during the rut. While this may sound paradoxical in view of the fact that adults probably do most of the mating (see below), the results are explainable on the basis that such rams roam widely in search of estrous ewes, not bothering to tarry in herds that have none available. Geist (1971) noted similar behavior in mountain sheep.

TABLE 1. AVERAGE HERD SIZES OF URIAL DURING DIFFERENT PHASES OF THE RUT

| | Male herd | | | Mixed herd | | | Female herd | | |
|---|---|---|---|---|---|---|---|---|---|
| Date | No. herds | Largest herd | Ave. | No. herds | Largest herd | Ave. | No. herds | Largest herd | Ave. |
| Oct 6-22 | 57 | 30 | 4.6 | 58 | 61* | 10.0 | 52 | 13 | 3.8 |
| Oct 23-31 | 63 | 8 | 2.3 | 73 | 30 | 8.6 | 46 | 10 | 3.4 |
| Nov 1-9 | 93 | 7 | 1.7 | 107 | 35 | 7.3 | 30 | 9 | 3.1 |

* Two herds once joined when disturbed by us to form a herd of 85, including 63 males

TABLE 2. PREFERENCE OF URIAL MALES FOR A SOLITARY EXISTENCE OR FOR THE COMPANY OF OTHER MALES AND FEMALES BEFORE AND DURING THE RUT

| Date | Age class | No. males sampled | Male alone (%) | In male herd (%) | In mixed herd (%) |
|---|---|---|---|---|---|
| Oct. 6-22<br>No rut | Yearl. | 52 | 2 | 13.5 | 84.5 |
| | I | 67 | 3 | 34 | 63 |
| | II | 111 | 4 | 62 | 34 |
| | III | 76 | 8 | 78 | 14 |
| | IV | 94 | 5 | 66 | 29 |
| Oct. 23-31<br>Early rut | Yearl. | 48 | 2 | 0 | 98 |
| | I | 87 | 8 | 12 | 80 |
| | II | 80 | 6 | 28 | 66 |
| | III | 85 | 8 | 52 | 40 |
| | IV | 58 | 8.5 | 65.5 | 26 |
| Nov. 1-9<br>Main rut | Yearl. | 64 | 11 | 3 | 86 |
| | I | 62 | 6 | 10 | 84 |
| | II | 77 | 10 | 21 | 69 |
| | III | 85 | 12 | 28 | 60 |
| | IV | 148 | 18 | 40 | 42 |

TABLE 3. AGE CLASS DIFFERENCE OF PARTNERS IN MALE PAIRS

| Age class difference of partners | 0 | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| No. observations | 32 | 16 | 5 | 1 | 0 |

The average size of male herds decreased by over a half within a few days after the onset of the rut because the large aggregations of up to 30 individuals split up into small units (Table 1), a trend noticeable in Table 2 in which the percent of solitary rams of classes II to IV increased as the rut progressed. While rams of all ages readily associated before and during the rut, a ram preferred another ram of his own age class for company (Table 3).

## AGONISTIC BEHAVIOR

*Agonistic patterns.* Rams often clashed, kicked and, less overtly, displayed to each other, an interaction sometimes consisting of several distinct behavior patterns. In describing these we followed the terminology of Geist (1968, 1971) in most instances. A total of 20 agonistic patterns were recognized and of these we quantified 13. Our discussion is devoted largely to rams because ewes and young seldom interacted.

*Clash.* The clash is the most conspicuous type of behavior in urial as it is in other sheep. A total of 123 clashes were observed. In a clash of low intensity, two rams jerk down their head and either touch horns or bash them together from a distance of half a meter or less, then perhaps push lightly back and forth before separating. Two or more such clashes may follow in rapid succession. At other times, however, one or both males walk some 3 to 10 m, and occasionally as far as 20 m, apart and run at each other, often starting their charge with a slight leap. Just before impact, the ram jerks down his horns holding his head somewhat turned, and occasionally he gives a little jump so that his forelegs are off the ground in contact. During the collision the hindlegs of the combatants may be flung high into the air. Afterwards the animals sometimes face each other for a second, holding their body erect and with head slightly averted, then perhaps clash again. Occasionally only one ram takes an active part in the clash while the other merely waits and catches the charge on his horns, the impact throwing him backwards up to 6 m. Charges may be uphill or downhill, though usually they are on fairly level terrain. A ram sometimes turns aside just at the moment when the other begins his charge, terminating the interaction unless another ram lowers his horns thereby indicating his readiness to receive the blow. In 4 (5%) of the vigorous clashes the animals failed to meet properly, the glancing blow causing them to stumble sideways and in one instance to fall over each other.

*Jump.* On five occasions a ram reared up briefly on his hindlegs in front of another ram, a gesture which Geist (1968) termed the threat-jump.

*Horn-pull.* On two occasions rams stood side by side facing in the same direction, each with a horn hooked into that of the other. Jerking their head sideways, the animals tussled for about a minute before separating.

*Shoulder push.* During one instance of horn-pulling the rams also pushed each other with their shoulders.

*Butt.* One ram bashed his horns into the side or rump of another ram in a dozen instances, usually lightly but sometimes vigorously.

*Jerk.* A ram may jerk his head downward or sideways at an opponent, particularly when several animals are crowded around an estrous female. We noted a total of 34 instances of this pattern. This gesture was termed horn-threat by Geist (1968).

*Poke.* A ram may approach another, occasionally with his mouth open, and poke him with the tip of the muzzle one or more times in the rump, thigh or side. The poke is at times quite forceful, judging by the fact that the nudged animal may jump ahead. Pokes are often given in conjunction with the kick or twist.

*Mount.* One ram mounted another ram on 7 occasions, contact always being brief.

*Low-stretch.* On 3 occasions a ram walked either beside or in front of another ram with his neck held horizontally and with his muzzle pointing forward and raised somewhat.

*Twist.* A twisting ram lowers his head, sometimes stretching neck and head forward so that they are parallel to the ground, and rotates it 90°. Such twisting may be done slowly or with a rapid jerk, and the ram's tongue often flicks in and out of his mouth at that time. Kicking and poking may accompany the gesture as do a series of grunts. A low-stretch occasionally precedes the twist but since we found it difficult to distinguish a low-stretch of low intensity from the dip of the head that normally accompanies the twist, we placed all low-stretch displays terminating in a twist into this category. A twisting male may face his opponent, follow him, approach from the side or walk parallel to him. In the last-named position the ram always twists in such a way that the chin faces his partner. A total of 68 twists were tallied.

*Kick.* The kick is the most common display of rams, with 253 of them having been recorded during the study. A male typically stands by another male and kicks his foreleg up stiffly, often only once, but occasionally 2 to 5 times without lowering it fully to the ground. Several such kicking bouts may follow each other in succession. The kick may hit the opponent between the hindlegs,on the thigh, side, or other parts of the body, but usually it does not touch him. One ram approached another from the front and kicked in about 45% of the encounters, from behind in 36%, and from the side in 16%. In addition, the two animals stood parallel in 2% of the interactions and faced away from each other, kicking the air, in the final 1%. The behavior is often reciprocal, with two rams either kicking in unison or in succession, and 3 rams may also do so briefly. Two rams once kicked each other 44 times in one minute. Other displays, such as the twist or poke, may accompany the kick, and occasionally one ram pushes the other with his chest while kicking. A series of bleating grunts sometimes accompany the display.

*Head-up.* By raising his muzzle and pulling back his head so that the lower neck bulges conspicuously, a ram assumes a posture that makes him look impressive and displays his horns, ruff, and white chin to best advantage. An erect stance and stiff walk further enhance his appearance. Geist (1968) termed this display the 'present'. A ram assumes the head-up in several situations. A quick, upward jerk of the head may precede a clash and a brief display may also follow it. A stiff-legged approach, or a mere erect stance with muzzle raised, may displace another ram. The same posture is sometimes used by rams when joining a herd. The participants in a parallel walk (see below) may also display the head-up.

*Head-down.* On 7 occasions a ram either walked broadside to another one or two rams moved parallel rather stiffly with their neck lowered, their chin tucked in, their tail lifted horizontally, and their back humped.

*Chase.* On a few occasions a ram chased another ram, both animals running steadily for 0. 5 km or more. If the animal in the lead stopped, the one behind occasionally poked or kicked him until he fled once more. Several males may be involved in a chase, stopping at times to clash or huddle.

*Parallel walk.* Two rams sometimes walked or trotted parallel some 0. 5 to 4 m apart, a position they occasionally retained for a distance of more than 20 to 30 m while displaying the head-up or head-down.

*Block.* Endeavoring to halt the advance of a ram, another ram may move in front of him and stand broadside. Blocks were primarily used in two situations. In 4 of the 9 blocks observed a ram cut the access of a second ram to a ewe and in another 4 instances a chase was terminated, or at least temporarily halted, with a block. On one occasion a male left a huddle but another hurried after him, blocked and waited until he returned. The blocked male may turn broadside too, the display ending in a parallel walk.

*Huddle.* On 13 occasions, 3 to 6 adult rams clustered and faced each other with lowered heads while clashing, poking, kicking, nuzzling, rubbing and grunting almost continuously. Occasionally a pair broke away from the huddle in a brief parallel walk and then returned to the others. Huddles may last from 30 seconds to 10 or more minutes. Several huddles represented an interlude during a chase, the animals suddenly resuming their pursuit of some individual.

*Rub.* One ram occasionally rubs its face on the muzzle, horns, or neck of another and he may also lick or nibble those parts, actions which the recipient usually tolerates though he may kick or walk away. Animals probably spread preorbital gland secretions over each other by rubbing. Twenty-one instances of rubbing were seen.

*Horn.* A ram may rub his horns on the head or body of another ram, and at times two animals rub mutually, their mouth open and the tongue flicking in and out. One ram had his penis unsheathed in such a situation. Horning was recorded 32 times.

*Neck-low.* On a few occasions a ram faced or retreated from his opponent with his neck stretched diagonally downward.

*Horning vegetation.* Rams of all ages may belabor a sapling or shrub with their head, either gently rubbing their face and horns on the vegetation or vigorously thrashing it. Such behavior was seen on 10 occasions. One ram kicked a shrub 6 times while horning.

*Agonistic behavior initiated by ewes and young.* Urial ewes seemed remarkably placid, in contrast to markhor (*Capra falconeri*) females which commonly exhibited aggression (Schaller and Mirza, in press). We saw them interact only twice: two jerked their heads at each other and one kicked a neighbor in competition over some forage. One ewe reared up on her hindlegs before a class I ram, clashed with him, and finally kicked him. Twice a ewe jerked her head at a young and once at a class I ram. A ewe once rubbed her horns on a yearling ram. A class I chased a ewe in and out of several ravines until she crouched, neck extended on the ground for 20 minutes in posture reminiscent of the neck-low display. One young reared up briefly and afterwards clashed twice with another young, the only such interaction noted.

*Age classes of rams participating in agonistic behavior.* Rams do not interact randomly. Most (90%) of the interactions involved rams of the same age class or the next larger or smaller one (Table 4). Overt contact patterns—clashing, butting, poking,

TABLE 4. AGE CLASS DIFFERENCES OF PARTNERS INVOLVED IN VARIOUS AGONISTIC PATTERNS

| | Age class difference | | | | |
|---|---|---|---|---|---|
| Behavior | 0 | 1 | 2 | 3 | 4 |
| Clash | 84 | 38 | 1 | 0 | 0 |
| Jump | 0 | 3 | 1 | 1 | 0 |
| Horn-pull | 2 | 0 | 0 | 0 | 0 |
| Butt | 9 | 2 | 0 | 1 | 0 |
| Jerk | 10 | 18 | 3 | 2 | 1 |
| Poke | 19 | 8 | 1 | 2 | 0 |
| Mount | 7 | 0 | 0 | 0 | 0 |
| Low- stretch | 2 | 1 | 0 | 0 | 0 |
| Twist | 24 | 37 | 5 | 1 | 0 |
| Kick | 137 | 90 | 19 | 6 | 1 |
| Head-down | 5 | 2 | 0 | 0 | 0 |
| Rub | 7 | 8 | 3 | 3 | 0 |
| Horn | 17 | 11 | 3 | 0 | 1 |
| Total | 323 (54%) | 218 (36%) | 36 (6%) | 16 (3%) | 3 (1%) |

mounting, kicking—were primarily directed at opponents of equal horn size, whereas threatening gestures such as jerking and twisting were more often than not displayed at opponents of unequal horn size. However, it may be argued that since rams prefer to associate with others of their own size class (see Table 3) it is inevitable that most aggressive encounters would also involve such animals, it being a matter of availability not preference. About 61% of the agonistic contacts (excluding low-stretch, rub, and horn) involved class IV males (see Table 7). To test if these rams preferred to interact with rams of a certain class we tabulated only those contacts in which they had a choice of directing their attention either at another class IV male or at least one male of another size class. Given this choice, class IV males interacted equally often with class III and IV males, relatively little with class II males, and seldom with class I and yearling males (Table 5). That males tend to interact with others of their own size has been reported for a number of species, including *Axis axis deer* (Schaller, 1967), *Capra ibex* goats (Nievergelt, 1967), and mountain sheep (Geist, 1968).

TABLE 5. PREFERENCE OF CLASS IV MALES FOR INTERACTING AGGRESSIVELY WITH MALES OF OTHER CLASSES

| | Age class | | | | |
|---|---|---|---|---|---|
| | Yearl. | I | II | III | IV |
| No. other males present | 30 | 73 | 136 | 185 | 317 |
| % interacted with by class IV male | 3 | 4 | 11 | 23 | 25 |

TABLE 6. FREQUENCY (IN %) WITH WHICH MALES DIRECTED VARIOUS AGONISTIC PATTERNS AT OLDER OR YOUNGER MALES

| Behavior* | No. obs. | Older class agonistic toward younger | Younger class agonistic toward older | Participant in same age class |
|---|---|---|---|---|
| Jump | 5 | 40% | 60% | 0% |
| Butt | 12 | 8 | 17 | 75 |
| Jerk | 34 | 44 | 21 | 35 |
| Poke | 30 | 33.3 | 3.3 | 63.3 |
| Mount | 7 | 0 | 0 | 100 |
| Low- stretch | 3 | 33 | 0 | 67 |
| Twist | 68 | 44 | 19 | 37 |
| Kick | 253 | 36 | 9 | 55 |
| Head-down | 7 | 14.3 | 14.3 | 71.4 |
| Rub | 21 | 5 | 62 | 33 |
| Horn | 32 | 3 | 44 | 53 |

* Clashing and horn-pulling were excluded because it was not possible in most instances to determine which animal initiated the interaction and it required the cooperation of both to conclude successfully.

An animal may establish or reinforce its dominance by behaving aggressively, using either contact patterns or displays depending on the circumstances. For example, the jerk and twist, both horn displays, as well as the kick, are expressions of dominance directed predominantly by older rams at younger ones (Table 6), a situation similar to that found among mountain sheep (Geist, 1971). However, as Espmark (1964) has suggested for reindeer (*Rangifer tarandus*), Geist (1966) for mountain sheep, and Schaller (1967) for axis deer, horns or antlers may serve as rank symbols which help to relegate an animal to a certain status without there being a need for an overt interaction. In this context, it is significant that much aggression occurs between members of the same age class (Table 6). A visual assessment of rank may be difficult when two animals are of the same size with the result that they either try to intimidate each other with a head-up, head-down, parallel walk or other display, or they poke, butt or kick. Clashing rams are usually of similar size too. Geist (1971) noted that among mountain sheep the subordinate individual usually initiates the clash, but, as noted below, we were often unable to determine which of two individuals was dominant. Other types of behavior—chasing, blocking, mounting and huddling—involved primarily class IV males. Differences in horn size are at times evident even when rams are of the same age class, and it is possible that the outcome of some interactions are actually based on small differences in physical features and behaviour which we were unable to detect at a distance. Geist (1968), for example, noted that dominant bighorns mount subordinate ones, whereas Grubb (pers. comm) observed that young Soay rams usually mount adults. The few urial mountings we observed all involved class IV males of approximately equal size, yet a rank order may have existed among them.

We were unable to detect an obvious outcome to most aggressive interactions. A jerk, butt, poke or kick may cause an opponent to move away, but in most instances the participants separated casually. Among mountain sheep, two rams may display mutually until one finally accepts the kicks and other patterns without retaliating, thereby indicating his subordinate position (Geist, 1971). On the basis of this criterion, many interactions between urial rams remained ambiguous, at least to us, even when the two combatants were of different horn size and the animals were presumably aware of their respective rank. Occasionally a small ram kicked, poked or otherwise displayed to a large one without eliciting a response, such inaction on the part of the latter possibly being an expression of dominance too.

Of 19 agonistic patterns described (excluding the huddle), 16 were aggressive and 3 largely submissive. The infrequently displayed neck-low posture appeared to indicate subordination. Rubbing and horning were used primarily by small rams to initiate contact with large ones, as noted also by Geist (1968) for mountain sheep, although animals of equal size occasionally nuzzled each other. The huddle, with its frequent though subdued aggression, appeared to be a means by which rams could test each other's rank informally, so to speak, without precipitating a serious interaction. Geist (1971) felt that huddles help to stabilize rank in mountain sheep.

We quantified various agonistic patterns of rams (Table 7). With few exceptions, every occurrence of a pattern was tallied even if the same one was displayed several times in rapid succession. However, poking, kicking, rubbing and horning were at times difficult to designate as individual acts, the behavior either lacking distinction or being displayed so often that we could not always count it accurately. Instead repeated displays directed at the same opponent were counted only once unless other kinds of behavior interrupted the action. When this happened we counted each separate display or series of displays as one interaction. As noted earlier, a low-stretch preceded by or given in conjunction with a twist was included with the latter. Agonistic behavior in huddles has been excluded from the computations. In tabulating the results we assumed that our observation time on each age class of rams was proportional to the number of animals in that class in the population. As is evident from Table 7, rams of some classes were more agonistic than others. Yearlings seldom interacted, and class I males did so much less often than expected in all categories of behaviour except clashing, butting and rubbing. Ignoring patterns for which the sample is small, class II males participated roughly as often as expected though they jerked surprisingly often and twisted and kicked little. Class III males followed expectations closely, but class IV males displayed most patterns at least twice as often as expected and they were also the main participants in huddles, chases and so forth. Interactions among mountain sheep follow a similar pattern (Geist, 1971).

## COURTSHIP BEHAVIOR

Rams showed little interest in ewes during early October and the only evidence of the approaching rut was an occasional roaming ram. But toward the end of October, after the large male herds had broken up, rams of all ages, particularly those of class III

TABLE 7. FREQUENCY (IN %) WITH WHICH MALES OF DIFFERENT AGE CLASSES EXHIBITED VARIOUS AGONISTIC PATTERNS

| Behavior | No. obs. | Age class | | | | |
|---|---|---|---|---|---|---|
| | | Yearl. | I | II | III | IV |
| Clash* | 246 | 1% | 13% | 16% | 18% | 52% |
| Jump | 5 | 0 | 0 | 20 | 40 | 40 |
| Horn-pull* | 4 | 0 | 0 | 50 | 0 | 50 |
| Butt | 12 | 8 | 17 | 0 | 17 | 58 |
| Jerk | 34 | 3 | 9 | 41 | 21 | 26 |
| Poke | 30 | 0 | 3 | 13 | 17 | 67 |
| Mount | 7 | 0 | 0 | 0 | 29 | 71 |
| Low-stretch | 3 | 0 | 0 | 0 | 33 | 67 |
| Twist | 68 | 0 | 6 | 10 | 20 | 64 |
| Kick | 253 | 0 | 2 | 7 | 20 | 71 |
| Head-down | 7 | 0 | 14 | 29 | 57 | 0 |
| Rub | 21 | 5 | 19 | 28.5 | 19 | 28.5 |
| Horn | 32 | 3 | 3 | 28 | 22 | 44 |
| % males in population sample | | 14 | 19 | 23 | 20 | 24 |

* Both members in an interaction were tabulated because both were active participants

and IV, moved restlessly at a fast walk or trot across the terrain. Many were alone and other traveled in twos and threes. They often halted on ridge tops and seemingly scanned the slopes for ewes. Spotting some, they approached hurriedly and entered the herd. If another ram was already present, the newcomer often interacted with him agonistically. Otherwise, he usually approached a ewe from behind in a low-stretch and sniffed the vicinity of her vulva, occasionally touching the area with his muzzle. She either ignored the gesture, moved away, or squatted and urinated. After sniffing the ground, or on rare occasions placing his nose into the stream of urine, the ram raised his head, sometimes waving it back and forth, with his upper lip raised in a lip-curl or Flehmen. On two occasions an adult ram sniffed a yearling ram in a cursory manner as if he had made a mistake in sex identification. Sniffing urine and lip-curling apparently help a ram to determine whether or not a ewe is in estrus. Other behavior, such as the poke, kick, and twist may also be directed at a ewe and stimulate her to urinate. If one ram pays attention to a ewe, one or more other rams may trot up and attempt to approach her too. If a ewe is not in heat, the ram then often checks another one and perhaps a third. Finding none, he may leave the herd immediately or tarry with it during the midday rest period before resuming his wandering. Such behavior closely resembles that of mountain sheep (Geist, 1971). Pfeffer (1967) noted that some mouflon rams confined themselves to a limited area during the rut, showing behavior reminiscent of territorialism, a pattern not observed in urial or other sheep so far.

We saw little overt sexual behavior. While rams showed more than passing interest in some ewes, standing beside them in head-up for several minutes or running after them when they fled, persistent tending as described by, for example, Grubb (in press) for Soay sheep and Geist (1971) for mountain sheep, was seen only once for 20 minutes.

A class HI male lies about 6 m from a grazing ewe. When she moves off he follows stiffly in a head-up display, making no attempt to approach her more closely than 5 m. Suddenly she flees for 0. 3 km, he close behind her, before she resumes her foraging. Two class II males trot up and the adult ram jerks his head at one of them and kicks. The ewe runs off once more, again with the adult ram at her heels, and both disappear into a ravine.

We are unable to explain why we saw so little tending. Estrus in domestic ewes is on the average 26 hours long and most mating is at dusk and dawn (Fraser, 1968). Urial are perhaps sexually active for only a few hours mainly at night. It is also possible that the animals reached their rutting peak shortly after our study terminated.

TABLE 8. FREQUENCY (IN %) WITH WHICH MALES OF DIFFERENT AGE CLASSES EXHIBITED VARIOUS COURTSHIP PATTERNS, BASED ON 209 INTERACTIONS

| | | Age class | | | | |
|---|---|---|---|---|---|---|
| Behavior | No. obs. | Yearl. | I | II | III | IV |
| Low-stretch | 39 | 0 | 17 | 20 | 17 | 46 |
| Twist | 43 | 0 | 19 | 23 | 5 | 53 |
| Kick | 26 | 4 | 27 | 19 | 4 | 46 |
| Poke | 6 | 33 | 17 | 0 | 17 | 33 |
| Sniff vulva | 137 | 2 | 22 | 22 | 16 | 38 |
| Lip-curl | 88 | 3 | 22 | 19 | 16 | 40 |
| Place chin on rump | 2 | 50 | 0 | 0 | 0 | 50 |
| Mount | 2 | 50 | 0 | 0 | 0 | 50 |
| Chase | 7 | 0 | 14 | 43 | 14 | 29 |
| % males in population sample | | 14 | 19 | 23 | 20 | 24 |
| Total number patterns | 350 | 10 (3%) | 75 (21%) | 73 (21%) | 45 (13%) | 147 (42%) |

Rams were seen to show interest in ewes on 209 occasions displaying a total of 350 behavior patterns of the kind we quantified (Table 8). The agonistic patterns were tallied in the same way as we described earlier, and the others were recorded once per interaction even though on a few occasions a ram twice sniffed, for example, the vulva of the same ewe. Rams of all classes participated in the rut (Table 8). Yearlings showed less than the expected amount of interest in ewes, but rams of classes I and II were sexually quite active, displaying to ewes and testing them in the expected proportion in spite of their youthfulness. On the other hand, class III males were less active than those of class I and II, and class IV males exhibited almost twice the expected number of courtship patterns. The low frequency of activity of class HI males was perhaps due to the fact that class IV males were often in the same herd. Being larger, such rams take precedence if an estrous ewe is present and they may interfere with a class HI male if he takes the initiative, thereby possibly inhibiting the expression of his sexual interests. Young rams spend more time than adult ones with the ewes, being often with them when no rams of classes III and IV are present, and this gives them the opportunity to evince interest in ewes. Since copulation probably terminates a lengthy tending period, subadult rams may have little opportunity to mate, being displaced by an adult before the ewe reaches her peak of receptivity. Ewes may respond to any ram who solicits them. For example, ewes often urinate when sniffed by a ram. Of 137 instances of sniffing tallied, a ewe failed to urinate in 66 (48%) of them, adult rams being ignored proportionately as often as subadults.

Urial rams use some of the same patterns toward ewes in courtship as they do toward males during aggression, a point also noted by Walther (1961), Geist (1971) and Grubb (in press) with respect to the sheep they studied. However, the frequency of some of these patterns differed in the two contexts among urial. A low-stretch not terminated by a twist was rare during aggression between rams, whereas it was a prominent way of approaching ewes; and a kick was common during encounters between rams but not during the preliminary phases of courtship.

## COMPARISONS OF AGONISTIC BEHAVIOR IN SEVERAL KINDS OF OVIS.

Geist's (1971) detailed description of agonistic behavior in mountain sheep provide a basis for some broad comparisons with the display patterns of urial. In addition, Grubb (in press) published data on the behavior of free-ranging Soay sheep, Walther (1961) on captive Marco Polo sheep (*Ovis ammon poli*) and Afghan urial (*O. o. cycloceros*), and Pfeffer (1967) on a wild population of mouflon. While information on the behavioral repertoire of all sheep, except that of mountain sheep, is incomplete, some preliminary comparisons are possible and these show that both quantitative and qualitative differences exist. In discussing mountain sheep we refer specifically to the bighorn race (O. *c. canadensis*), for, as Geist (1971) has shown, the various subspecies may differ in the frequency with which they display such patterns as the kick. Table 9 summarizes the presence or absence of various displays in 5 kinds of *Ovis*. The few notes on Afghan urial by Walther (1961) have not been included in this table because they were based on only one ram whose behavioral repertoire, as far as it was observed, resembled that of Punjab urial except for head-shaking.

Urial run at each other on all fours before clashing, sometimes leaping just prior to impact so that their forelegs may be slightly off the ground, behavior which is similar to that described for domestic sheep, Afghan urial and mouflon. Several clashes may follow in quick succession, as is, for instance, also the case in mouflon. In contrast, mountain sheep and Marco Polo sheep may rear up and race at each other on their hindlegs before lunging downward to clash. Just prior to a charge, one of the urial combatants may turn aside, terminating the interaction. Geist (pers. comm.) also observed such behavior in mouflon but not in mountain sheep. Mountain sheep rams may stand face to face after a clash for as long as a minute in a head-up display, much longer than do urial which halt only a second or so, if at all. The jump is a moderately common form of threat in mountain sheep and Marco Polo sheep but seems to be rare in urial. Grubb (pers. comm.) saw a Soay ram rear up only once, seemingly in a playful manner. Jumping is thus most prevalent in those sheep which rear up before clashing and this tends to support Geist's (1968) interpretation that the behavior represents an intention movement to clash. Horn-pulling was rare in both urial and mountain sheep. Shoulder-pushing was seen only once in urial whereas the pattern is quite prominent in mouflon, Soay sheep and mountain sheep.

A Soay ram may approach an opponent in a low-stretch, all the while grunting and flicking his tongue, before twisting and then kicking, a combination of patterns which Grubb (in press) lumped under the general term 'nudging.' The urial we studied behaved similarly as did the captives observed by Walther (1961). Mountain sheep, too, display these patterns in roughly that sequence. There is, however, a striking difference in the frequency of low-stretching between bighorn sheep and urial. The low-stretch not followed by a twist is rare in agonistic encounters between urial rams, whereas between mountain sheep rams it is one of the most prevalent displays. Geist (1969) noted the frequency with which bighorn rams used various displays. Considering only those 10 displays which we also quantified in urial, he recorded 1602 behavior patterns of which 29. 2% were the low-stretch. We tallied 669 patterns, only 0. 4% being the low-stretch. Although our method of collecting data was not comparable to Geist's in every respect, the magnitude of the difference is great enough to be significant. Geist (1968) interpreted the low-stretch as a display of horns. We doubt that it has such a function in urial, unless the pattern is given in conjunction with the twist. With respect to the poke, Geist wrote me: 'I cannot remember seeing a distinct nudge (= poke) without a twist, although it would be conceivable if the opponents stood at right angles.' Urial, on the other hand, readily poke without the twist. Kicking is prevalent in all sheep that have been studied and twisting is too.

TABLE 9. SOME AGONISTIC PATTERNS IN SEVERAL KINDS OF OVIS[1]

| Behavior | Punjab urial (this study) | Mountain sheep (Geist, 1971) | Soay sheep Grubb, (in press and pers. comm.) | Marco Polo sheep (Walther, 1961) | Mouflon (Pfeffer, 1967; Bubenik, pers. comm.) |
|---|---|---|---|---|---|
| Clash | + | + | + | + | + |
| Jump | + | + | (+)? | + | + |
| Horn-pull | (+) | (+) |  |  | + |
| Shoulder-push | (+) | + | + |  | + |
| Butt | + | + | + | + |  |
| Jerk | + | + | + | + | + |
| Poke | + | + |  |  |  |
| Mount | + | + | + |  | + [3] |
| Low-stretch | + | + | + | + | + |
| Twist | + | + | + | + | + |
| Kick | + | + | + | + [2] | + [2] |
| Head-up | + | + | + | + | + |
| Head-down | + |  | + ? | +? |  |
| Parallel walk | + |  | + |  | + |
| Block | + | + |  |  |  |
| Huddle | + | + | +? |  | + |
| Neck-fight |  | (+) | (+)? |  | + |
| Head-shake |  | + |  | + | + |
| Paw |  | + |  | + | + |
| Head-to-tail |  | + | + |  |  |
| Rub | + | + | + |  | + |
| Horn | + | + | + |  |  |
| Neck-low | + |  | + |  | + |

[1] + = pattern present; (+) = pattern present but very seldom exhibited; blank space = pattern not observed or recorded.

[2] Recorded only in sexual context

[3] Recorded by Bubenik only in lambs.

A head-up display has been observed in all sheep that are listed in Table 9. The head-down display of urial has not been described in the other forms, although Walther (1961) noted that Marco Polo sheep may tuck in their chin and lower their head, and Grubb (in press) described Soay rams standing head-to-tail with their head lowered almost to the ground, both gestures which may contain components of the head-down. Marco Polo sheep and mountain sheep may paw while lowering their head. Pawing was not seen in urial, except before lying down. The parallel walk occurs in urial and also in mouflon and Soay sheep which often push each other vigorously with their shoulder while moving. Blocking occurs in both urial and mountain sheep and the huddle does too. Grubb (in press) noted that Soay rams may congregate rather casually and then rub, kick and twist, behavior which possibly represents a huddle of low intensity.

Rubbing and horning as sociable gestures appear to be similar in urial, mountain sheep and Soay sheep. The neck-low, a submissive posture, is found in urial and Soay sheep, as well as in mouflon where the subordinate individual may not only lower its neck but also kneel (Pfeffer, 1967); no such appeasement gesture occurs in mountain sheep.

Several patterns have been reported in sheep which we did not see in Punjab urial. Walther (1961) observed that an Afghan urial ram shook his head sideways during agonistic encounters. Similar behavior has been noted in mountain sheep. Further observation may well reveal this gesture in Punjab urial. Mountain sheep occasionally place their chin over the withers of their opponent, a vestigial form of neck-fighting (Geist, 1971) that also occurs in mouflon (Pfeffer, 1967). Grubb (pers. comm.) noted on several occasions a Soay ram kicked while resting his head sideways on his opponent's back in a posture reminiscent of neck-fighting. Only this particular ram behaved in such a manner, indicating that personal idiosyncrasies may need to be taken into account when evaluating behavioral repertoires. Aoudad (*Ammotragus lervia*), animals which in their appearance and behavior are intermediate between sheep and goats, commonly neck-fight with one individual placing its neck over that of the other and pushing downward (Haas, 1958). Grubb (in press) described a pattern among Soay sheep which we here shall term 'head-to-tail.' 'In one characteristic position, contestants stood head-to-tail and parallel with each other. They grazed, nudged, butted each other in the flanks or circled...' Mountain sheep behave similarly but only during serious combat.

The evolutionary history of the sheep is complex and there is so far little agreement concerning it. On the basis of distribution and structure, Geist (1971), for example, suggested that sheep represent two different lineages, one comprising the American sheep, including the snow sheep (*Ovis nivicola*) of Siberia, and the other consisting of the mouflons, urials and argalis. He further suggested that similarities in the appearance and behavior of these lineages evolved convergently. Nadler (1971) noted that the diploid chromosome number of Central Asian sheep is 58 or 60 whereas that of both the mouflon and western-most urial and the snow and American sheep is 54. From this he hypothesized that some ancestral Asian stock dispersed both eastward and westward losing chromosomes along the way. Behavior has been used to clarify evolutionary relationships in some groups of animals and it can perhaps be applied to sheep as well. Ignoring quantitative differences, which may occur even between races of the same species, the displays of Soay sheep, mouflon, urial, Marco Polo sheep and mountain sheep are in most respects similar (Table 9). Even the fact that a pattern has been reported in one sheep but not another may have little significance at this stage of our knowledge, for, as Walther pointed out to me, some forms of behavior are either very rare or are only exhibited by the juveniles of a species. Marco Polo sheep, and most likely all argalis, rear up before clashing, contrasting in this respect with other Eurasian forms but resembling the American sheep. Mountain sheep lack a submissive posture whereas Eurasian sheep have one. On the basis of available data, no clear behavioral demarcation between American and Eurasian members of the genus *Ovis* is evident.

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Paper No. 14

# A Comparison of Rutting Behaviour and Grouping in the Ethiopian and Alpine Ibex

by

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## ABSTRACT

The reproductive cycle and grouping behaviour of Walia ibex were studied in comparison with Alpine ibex. The habitat of Walia ibex is steep slopes usually below the timberline in the Afroalpine climate; the Alpine ibex lives above the timberline in the temperate zone. Walia ibex show rutting behaviour throughout the entire year with a significant rutting peak in March to May whereas the Alpine ibex has a distinct rutting season in December/January. It was shown that the frequency of male-female groups as a measure of rutting is relatively higher for Walia ibex than for Alpine ibex outside the rutting peak but lower in the rutting period. Older Walia ibexes, male and female, have a significantly more pronounced rutting peak than younger animals. Older males of Walia ibex associate with females mainly during the rutting period, whereas the association pattern of younger males is far less pronounced. Females of Walia ibex associate with other females less than would be expected in a random pattern of association, particularly from December to May. The frequency of fighting in female groups is also highest at this time.

Walia ibex males, like the Alpine ibex males, do not associate at random. The average age difference among grouped males is greater in groups where females are present, particularly during the mating peak. A positive correlation was found between the frequency of rutting and the age difference among males, and a negative correlation between frequency of fighting and frequency of rutting. Fights among males usually occur among animals of similar age.

Comparisons of average group size in Walia ibex and Alpine ibex indicate a similar pattern for male-female groups in both species, but larger all-female and all-male groups in Alpine ibex than in Walia ibex outside the rutting period. For both species there is a relatively high number of solitary males at the onset of the mating season. The frequency of solitary females during the rut is low for Alpine ibex but high for Walia ibex. During parturition there is a relatively high number of solitary females of Alpine ibex, a pattern similar to that of other species, but this number is low for Walia ibex females. This was interpreted as an adaptation of Walia ibex to the overall presence of birds of prey.

## INTRODUCTION

The Walia ibex (*Capra walie* Ruppell 1835), which lives only in the Semien Mountains of Ethiopia in a relatively small area approximately 150 km northeast of Gondar, is one of the most endangered mammals of the world. In 1968 I estimated its population to be around 150 animals; this alarming situation has been noted by Brown (1965), Blower (1966, 1968, 1970), Nievergelt (1969a, b; 1970a, b), Vollmar (1969), Boswall (1970) and others.

The Alpine ibex (*Capra ibex* L.) was chosen for comparison. Colonies of Alpine ibex referred to in this paper are those of the Safiental colony in Switzerland, an estimated 70 animals; the Swiss National Park, 250 animals; Piz Albris, 600; Wetterhorn, 60; and the Augstmatthorn, 230 (1964 population estimates). Detailed descriptions of these colonies can be found in Bätchier (1919, 1935), Rauch (1937), Couturier (1962) and Nievergelt (1966a; 1968).

A comparison of these two species (or subspecies) should reveal different adaptations to ecological conditions, one Afroalpine and the other temperate, particularly in the reproductive cycle and related grouping patterns. In this paper the grouping behaviour of the Walia ibex is analysed in particular, with comparisons drawn from the Alpine ibex when necessary. Emphasis is given to behaviour patterns as adaptations to ecological and reproductive conditions.

Ungulates of tropical habitats demonstrate a great variety in reproductive cycles: some show almost no preference for a certain season, while others have a distinct reproductive cycle. In Ethiopian ibex, rutting behaviour as well as newly born kids were observed throughout the entire year, with a significant rutting peak from March to May and a birth peak in September/October (Nievergelt, 1970b). Birth peaks or seasons of the various species living in one area often occur simultaneously, but not necessarily so (Schaller, 1967). The birth season is often co-ordinated with the availability of fresh food. The Afroalpine climate, as in the Semien Mountains, has a stable mean temperature throughout the year—the diurnal variations in temperature far exceed the seasonal changes. Seasons are determined by the amount of precipitation (Hedberg, 1964; Coe, 1967). The rainy season, often called 'winter' in Ethiopia, occurs from June to August, but its effects can be observed as late as October. There is not winter per se. Numerous streams outlast the dry season, and newly grown plants are available throughout the entire year. Still, the time following the heavy rains does seem to be best suited for birth, since meadows are definitely greener and numerous flowers create the impression of spring.

The Alpine ibex has its rutting season in December/January, its birth period in June. This pattern of a distinct annual reproductive cycle is typical of ungulates living in temperate latitudes, where winter dictates that spring be the season of birth.

## METHODS

All data on the Walia ibex are based upon observations carried out in November/December, 1966, during a short survey, and from February, 1968, to February, 1969, when I was living with my wife in the Semien Mountains. The data on the Alpine ibex were collected from 1961 to 1964.

Observation methods for Walia ibex were divided to give priority to ecological questions such as density, distribution, habitat preferences, food habits, and competitors. I observed from certain fixed observation points which were visited regularly (Nievergelt, 1971). Data on observed groups of Walia ibex were recorded in the following sequence: (1) grouping pattern with estimated distances between individuals, (2) activity, (3) age class and sex of each animal, and (4) ecological site and location on aerial photograph. I then concentrated either on the feeding behaviour of certain individuals or on further groups. Social behaviour and its intensity was recorded, but I did not distinguish whether or not an animal showed a certain behaviour just once or several times: that is, the amount of rutting and fighting was calculated in proportion to the total frequency of observed class members or class-associations, not in proportion to the recorded observation time.

Groups visible for a long time were sometimes recorded several times. In those cases no individual or group was counted more than twice an hour and more than three times a day. This was done with the Alpine ibex material as well.

In Semien I observed from various lookout points 204 times with an average observation time of 1 hour and 45 minutes. The number of animals seen from one observation point per observation time averaged 7.9; the mean group size was 3.1 animals.

Body size, body proportions, horn shape, horn length, presence and size of beard, and colour of hair were used as criteria to distinguish the sex and age of a Walia ibex. When the horn was seen distinctly, especially of a male, a close estimate of the age was possible. For this study, the following classes were distinguished:

1. Males, over 4 years old
2. Males, 3 to 4 years old

3. Males, less than 3 years old
4. Females, old; approximately 6 years old and older
5. Females medium; approximately 4 to 5 years old
6. Females, young; less than 4 years old
7. Kids, up to one year old

In some calculations classes 4 and 5 were grouped together as adult females. In data of Tables 4 and 5, one-year-old males, when not yet recognized as males, were classified as young together with females less than 4 years old.

In statistical calculations on age-differences among grouped males (Table 6), the following criteria were applied: (1) only males of at least 2½ years old were considered; and (2) each year of a male 2½ years to 6 years old was calculated as one age class, and from 6 to 9 years old as 0.5 age classes; all males over 9 years old were considered as 0.5 age classes older than 9 years. Using these age classes instead of the proper age in years, the fact is taken into account that the absolute and relative annual growth of the animal's body and horns decreases with increasing age (see Nievergelt, 1967).

A major part of this study deals with association among ibexes. The density for the Walia ibex is low and groups are widely scattered; therefore almost any group definition leads to the same group counts. For this paper, an animal was said to be associated with a group if it was within 100 meters of its nearest neighbour. Three types of groups were distinguished: (1) all-male groups, composed of males only regardless of age; (2) all female groups, composed of females and/or kids, and/or young (including males less than 3 years old); and (3) mixed (male-female) groups (male at least 3 years old).

In this study rutting is defined according to behavioural criteria. Ibex rutting behaviour has been described by Hediger (1951), Hainard (1953), Steinhauf (1960), Walther (1962, 1966) and Aeschbacher (in prep.). A male was considered to be in rut when the neck was held straightened, the snout raised and turned towards the female, the horn tips low, and the tail up. This well-known pattern is similar in Alpine ibex and Walia ibex with one exception. The tail of the Walia male is often just slightly raised above its normal position, whereas in Alpine ibex the tail is turned upwards almost permanently, particularly at the onset of rut. Figure 1 shows a rutting Walia male with its tail fairly well raised.

Fig. 1. Mixed group of Walia ibex, observed at 12.15 h on June 6, 1968: drawn after a photograph. The group includes, from right to left: male, 1 year old; male, 5 years; male 9 years (estimated ages); female; female. Not shown in the drawing, to the left, were two more females with kids. The rutting 9-year old male holds its tail raised (rutting Walia males turn their tails up more rarely and less prominently than Alpine ibex males).

In order to compare data on Walia ibex and Alpine ibex more easily, the physiologically corresponding seasons (rutting, parturition) have been diagrammatically juxtaposed in Figs. 2, 4, and 5.

To analyse whether or not the monthly averages in Figures 2 and 3 are randomly scattered, which is the Null-hypothesis, a test proposed by Dr. E.Batschelet, Zürich, was applied. This test is valid for ascertaining a peak and a trough in a time series. It was calculated that the case in which 12 randomly scattered values in a time series are divided by the median into runs of 6, occurs with a probability of 1/77 or 0.013. This is therefore the probability of error with which we can conclude that two phases actually exist in the case of runs of 6. In the case of one disruption, a run of 5 only, the probability of error has increased to 9/77.

## SOME PECULIARITIES IN THE HABITATS OF THE COMPARED SPECIES

Three ecological parameters have been selected to demonstrate differences in the habitat preferences of the two species: altitude in comparison with the altitude of the timberline, cover, and slope (Table 1). Two facts emerge from these data: Walia ibexes generally live in more forested areas and, on the average, in even more inaccessible areas, as indicated by the definite preference for steep slopes.

TABLE 1. ECOLOGICAL PREFERENCES OF THE WALIA IBEX AND ALPINE IBEX

| | average altitude of ibexes observed (meters) | timber line at (meters) | number of ibexes observed | | | number of ibexes observed on slopes of | | |
|---|---|---|---|---|---|---|---|---|
| | | | in forest or savanna | near single shrubs or trees | in open areas | <30° | 30-40° | >45° |
| *Caprawalie:* | | | | | | | | |
| Semien Mountains National Park | 3390 | 3600 | 724 | 840 | 532 | 191 | 517 | 1281 |
| *Capraibex:* | | | | | | | | |
| Safiental | 2400 | 1800 | – | 10 | 2181 | 425 | 937 | 694 |
| Swiss National Park | 2590 | 2200 | 4 | 280 | 1821 | 225 | 1425 | 391 |
| Wetterhorn | 1880 | 1600 | 22 | 290 | 635 | 8 | 279 | 644 |
| Piz Albris | 2390 | 2200 | 80 | 512 | 1377 | 433 | 1254 | 378 |
| Augstmatthorn | 1880 | 1600 | 25 | 743 | 677 | 45 | 498 | 823 |

Other factors besides topography and vegetation which influence ibex grouping patterns are those of natural predators and man. The adult ibex in Switzerland has no real predators, though it might be possible for a red fox (*Vulpes vulpes*) or golden eagle (*Aquila chrysaetos*) to snatch an ungarded kid. Since ibex hunting is prohibited today, the only hazard for the Alpine ibex in Switzerland is winter with its avalanches and slippery ice.

There are several predators of the Ethiopian ibex, but not all are real threats: the leopard (*Panthera pardus*) and the serval (*Leptailurus serval*) are heavily hunted and therefore not numerous, the golden jackal (*Canis aureus*) and Semien fox (*Simenia simensis*) are not effective as enemies, and the spotted hyena (*Crocuta crocuta*) most likely does not range in preferred, inaccessible ibex terrain. Birds of prey, however, are present everywhere, so that females with young always have to be on guard for vultures and various eagle species.

Hunting of the Walia ibex in the Semien Mountains National Park is no longer permitted. When I was in Semien observing ibex, however, there was still strong evidence of poaching. We hope that the I.E.G. Wildlife Conservation Organization is successful soon in implementing adequate protection.

## REPRODUCTIVE CYCLE AND GENERAL GROUPING PATTERN

Ibex form all-female or all-male groups except during the rutting period when they join together in mixed groups. The proportion of mixed groups and the frequency of individuals observed in mixed groups should therefore reflect the amount of rutting behaviour in each month: a discrete rutting season for the Alpine ibex and just a pronounced peak for the Walia ibex. Data for the two species are presented in Fig. 2 in such a way that the rutting season and peak, respectively, are juxtaposed. The Alpine ibex is represented by the Safiental colony in which, as in Semien, the ranges of males and females outside the rutting period are not completely separated. According to the test for time series proposed by Dr. E. Batschelet (see last para. of the Introduction), the number of mixed groups in both species, as well as the frequency of Alpine ibex living in such groups, show a significant change over time ($P<0.02$). There is a run of six values above and below the median.

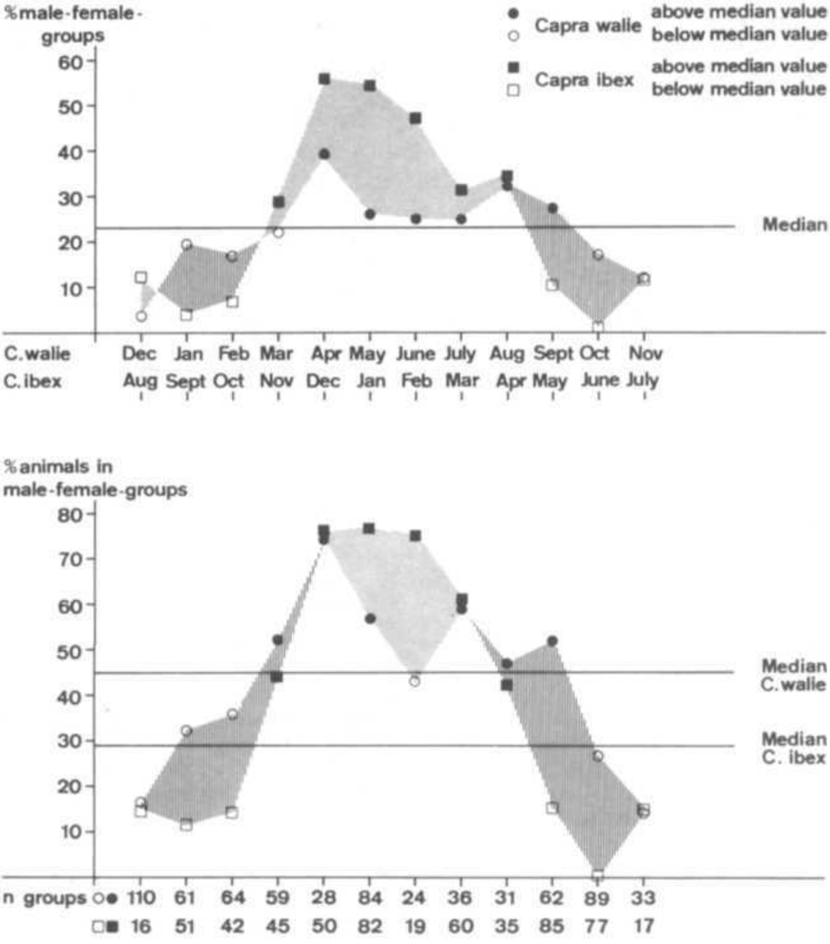

Fig. 2. Percentage of male-female groups (above) and percentage of animals in male-female groups (below) in Walia ibex and Alpine ibex (Safiental colony). The physiologically corresponding seasons of the two species were juxtaposed for easier comparison. Shadowed areas indicate that rutting period values for Alpine ibex tend to exceed those of Walia ibex in certain months and vice versa. (n = number of groups)

A quick comparison indicates that during the rutting peak, values for the Alpine ibex are higher than those of the Walia ibex (see shadowed area in Fig. 2). In contrast, Walia ibex show consistently higher values outside the rutting peak, corresponding to the fact of an 'unlimited rutting period'.

When for both species the frequency of mixed groups is taken as an indicator of the population's rutting tendency, it must be mentioned that in some groups males show rutting tendencies as indicated by a lifted tail, but in other groups there is no evidence of rutting activity at all. For Walia ibex the percentage of male-female groups in which at least one male was rutting was as follows: December to February, 56%, March to May, 54%, June to August, 48%, September to November, 39%, These figures show the seasonal variation to be small; therefore, in Semien the proportion of mixed groups at any particular time can indeed serve as a rough measure of the population's overall rutting tendency at that time. This is not applicable to the Alpine ibex, where in the rutting season, particularly at the onset, almost every male has its tail continuously turned upwards and is clearly recognized as being in rut. On the other hand, the mixed groups observed from April until the end of September are apparently not formed out of sexual motivation. A group of 13 males and 2 females or 21 and 4, for instance, as has been recorded in the Safiental colony in summer, does not fit at all into the pattern of a mixed group (see Fig. 4). Nevertheless apparently accidentally formed groups occur throughout the year and in both species.

## REPRODUCTIVE CYCLE OF THE WALIA IBEX IN RELATION TO AGE OF MALES AND FEMALES

It has already been reported (Nievergelt, 1970b) that Walia ibex of different age-classes are not synchronous in their reproductive cycle. Table 2 contains data of the frequency of rutting during the four seasons for males over 4 years old, from 3 to 4 years old, and less than three years old.

The Chi-square test carried out for each class separately was used to show whether or not the observed frequency of rutting was the same throughout the year. Data show that the oldest males have a relatively sharp and significant rutting peak from March to May, that males of 3 to 4 years of age have a preference for this season (though the peak is wide and therefore less significant), and that the youngest males do not seem to show a preference for any particular season. To determine whether or not females of different age-classes differ in the timing of estrus, the same test was carried out for females. A female was recorded to be in estrus when a male in rut-regardless of its age—followed the female closely. Data presented in Table 3 show that among females the seasonal frequency of estrous individuals varies significantly only for the oldest females. Hence, as in males, the older animals show a more pronounced rutting peak.

For younger females, the rutting peak (underlined in both tables) is retarded, similar to that of the young males (Table 2). This corresponds to the phenomenon in other species of young animals being late with their reproductive cycle (Cheatum and Morton, 1946; Nievergelt, 1966b).

I expected these age-differences in the reproductive cycle to influence the grouping pattern. The kind of questions of interest which arise are: Which sex- and age-classes of Walia ibex prefer to associate with females throughout the year? More specifically, do males of different ages differ in their association pattern with females?

For each season the frequency with which all classes (males over 4, males between 3 and 4, males under 3, young, kids and females) associated with females in groups, and the frequency of being the nearest neighbours within these groups were calculated. These data are given in Table 4 for group association, and in Table 5 for nearest neighbours within these groups. The frequencies of kids, young,and females will be discussed later. In comparing the 3 age-classes of Walia males in their frequency of association with females, the peak of association of class 1 males is mainly from March to May and far more pronounced than that of the younger males. The pattern, which is even more obvious if just the nearest neighbour is considered (see Table 5), corresponds with the recorded rutting frequency of the ? classes (Tables 2 and 3). The fact

TABLE 2. FREQUENCIES PER SEASON OF RUTTING MALES OF WALIA IBEX AT DIFFERENT AGES

(N = number of class-members observed, n = number of rutting males observed, p = proportion of males in rut).

| Class | | Dec.-Feb. | March-May | June-Aug. | Sept.-Nov. | $\chi^2$ |
|---|---|---|---|---|---|---|
| ♂ > 4 years | N | 39 | 80 | 63 | 87 | |
| | n | 2 | 24 | 8 | 9 | 17.69 |
| | p | 0.05 | 0.30 | 0.13 | 0.10 | $P<0.01$ |
| ♂ 3-4 years | N | 71 | 50 | 37 | 49 | |
| | n | 13 | 16 | 6 | 4 | 9.50 |
| | p | 0.18 | 0.32 | 0.16 | 0.08 | $P<0.05$ |
| ♂ < 3 years | N | 56 | 45 | 18 | 45 | |
| | n | 5 | 3 | 3 | 4 | 1.56 |
| | p | 0.09 | 0.07 | 0.17 | 0.09 | – |

TABLE 3. FREQUENCIES PER SEASON OF FEMALES OF WALIA IBEX AT DIFFERENT AGES CLOSELY FOLLOWED BY RUTTING MALES

(N = number of class-members observed, n = number of females in estrus, p = proportion of females in estrus).

| Class | | Dec.-Feb. | March-May | June-Aug. | Sept.-Nov. | $\chi^2$ |
|---|---|---|---|---|---|---|
| ♀ old appr. 6 years and older | N | 88 | 44 | 27 | 75 | |
| | n | 3 | 7 | 1 | 0 | 16.4 |
| | p | 0.03 | 0.16 | 0.04 | 0 | $P<0.01$ |
| ♀ med. appro.4-5 years | N | 63 | 30 | 21 | 40 | |
| | n | 8 | 4 | 4 | | 0.56 |
| | p | 0.13 | 0.13 | 0.19 | 0.15 | – |
| ♀ young less 4 years | N | 250 | 119 | 59 | 153 | |
| | n | 9 | 6 | 6 | 5 | 5.53 |
| | p | 0.04 | 0.05 | 0.10 | 0.03 | – |

that older Walia, male and female, obviously have a much more synchronous cycle than younger animals led to my earlier hypothesis (Nievergelt, 1970b) that young growing ibexes, males and females, can reach the onset of rutting behaviour at any time of the year, the time being determined by age, physical condition and external stimuli, and that the older the ibex the more sensitive it is to these stimuli. The above fact indicates that young animals of Walia ibex are more adaptable in their reproductive cycles, whereas older animals are probably no longer, or at least less, adaptable.[1]

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[1] For a discussion of this maturation phenomenon in *Ovis canadensis*, see Geist (1971). *Mountain sheep.* University of Chicago Press, p. 172.

TABLE 4. FREQUENCY PER SEASON OF DIFFERENT CLASSES OF WALIA IBEX ASSOCIATING WITH FEMALES IN GROUPS

(for the expectancy figure the average frequency of associations with females was calculated).

| | Frequency of association with females per season | | | |
|---|---|---|---|---|
| classes | December-February | March-May | June-August | September-November |
| ♂ > 4 years | 0.17 | 0.32 | 0.20 | 0.20 |
| ♂ 3-4 years | 0.29 | 0.30 | 0.28 | 0.29 |
| ♂ <3 years | 0.36 | 0.32 | 0.39 | 0.30 |
| young | 0.37 | 0.37 | 0.23 | 0.38 |
| kids | 0.44 | 0.38 | 0.43 | 0.47 |
| females | 0.32 | 0.24 | 0.26 | 0.30 |
| expectancy (random) | 0.36 | 0.31 | 0.28 | 0.34 |
| total number of associations with females | 1379 | 677 | 272 | 703 |

TABLE 5. FREQUENCY PER SEASON OF DIFFERENT CLASSES OF WALIA IBEX BEING NEAREST NEIGHBOURS OF FEMALES

(for the expectancy figure the average frequency of being nearest neighbour of females was calculated)

| | Frequency of being nearest neighbours per season | | | |
|---|---|---|---|---|
| classes | December-February | March-May | June-August | September-November |
| ♂ > 4 years | 0.08 | 0.31 | 0.11 | 0.12 |
| ♂ 3-4 years | 0.10 | 0.24 | 0.21 | 0.12 |
| ♂ <3 years | 0.26 | 0.33 | 0.24 | 0.18 |
| young | 0.24 | 0.34 | 0.16 | 0.29 |
| kids | 0.77 | 0.82 | 0.75 | 0.71 |
| females | 0.08 | 0.04 | 0.24 | 0.24 |
| expectancy (random) | 0.30 | 0.30 | 0.26 | 0.29 |
| total number of ibexes being nearest neighbour of females | 181 | 134 | 66 | 149 |

When discussing the long rutting period of Walia ibex their small population size has to be considered. It is certainly possible that the poorly synchronized reproductive cycle is a result of this situation. Mutual stimulation might be sufficient only if the density does not fall below a certain critical level. This explanation also seems plausible since a non-social change, moulting, is highly synchronized for both young and adults. Moulting animals were observed only between October and January (7 adult females, 1 adult male and 14 juveniles).

## GROUPING AND FREQUENCY OF FIGHTS IN RELATION TO AGE DIFFERENCES IN MALES

It has been shown for Alpine ibex that males of various ages do not group randomly. Males of similar age have a slight tendency to associate in summer but are usually found in different groups during the rutting season in winter (Nievergelt, 1967). This pattern is thought to reflect increased competition among males of the same age during the rutting season.

To ascertain if this is true for the Walia ibex, the frequency of fights between males of different ages was used as a measure of competition. The median of age differences among all male combinations was 1.25 age-classes. Five fights have been recorded between males with a greater age difference, and 26 between males with a smaller age difference. If fights among males, irrespective of their age difference, would occur in proportion to the frequency of association, a 1 : 1 relationship could be expected. This Null-hypothesis can be rejected with $P < 0.01$. Therefore, as with the Alpine ibex, social competition among males is directed primarily towards partners of similar age. This information should be considered when interpreting data on grouping in relation to age differences of males. The age difference among all associated males was calculated for male-female groups and all-male groups in each month, i.e., the arithmetic mean of the differences in age-class of each dyad-combination within the groups. These data appear in the first two lines of Table 6. Values were given only if at least 5 dyad-combinations were counted. The third line in Table 6 represents the average of all groups, regardless of whether or not females were present (value for January based on 3 pairs only).

With the Wilcoxon-rank-test it was ascertained that the age difference of the males is greater in mixed groups of Walia than in all-male groups ($P < 0.01$ in both cases, whether all values were considered or just of those months in which values for both group types appeared).

These results indicate that mixed groups do not originate by fusion of all-male and all-female groups. Because of the presence of females and/or rutting behaviour, males of the same age show a tendency to avoid each other, regardless of the season.

Apart from this difference between male-female and all-male groups, data in lines 1 and 3 of Table 6 seem to show that age difference is greatest during the rutting peak. Line 1 indicates a tendency for high values from March to June, for low values from July to February. A correlation was calculated between mean difference in age-class among males in groups regardless of the presence of females (line 3, without January) and the frequency of rutting behaviour ($Y = -6.63 + 13.98x$; $r = 0.68$, $t = 2.76$, $P < 0.03$). The correlation shows that grouping of males reflects the reproductive cycle.

For comparison, I calculated the mean difference in age-class among males in four Alpine ibex colonies. The first value stands for December/January, the rutting season with the usual mixed groups; the second value stands for May to October with almost exclusively all-male groups:

| | |
|---|---|
| Safiental | 2.6/1.7 |
| Swiss National Park | 2.4/1.2 |
| Piz Albris | 2.0/1.1 |
| Wetterhorn | 2.4/1.0 |

These values conform well to the discrete rutting season of the Alpine ibex in that the values for this period exceed the corresponding values of the Walia ibex (in Table 6, March to May, in lines 1 and 3).

In Semien, play-fights among males were more rarely observed than in any colony of the Alpine ibex. It also seemed that they were carried out less persistently. During an entire year I observed only 34 play-fights. The correlation was calculated between the monthly frequencies of rutting behavior and of fights. The negative correlation ($Y = 0.02 - 0.29x$; $r = 0.61$, $t = 2.38$, $P < 0.05$) indicates that in months with much rutting, fighting frequency is low and vice versa. It is therefore understandable that for this species, which shows rutting behaviour throughout the year, play-fights are observed more rarely. In the Alps play-fights usually take place in the relatively

TABLE 6. MEAN DIFFERENCE IN AGE CLASS AMONG MALES IN MALE-FEMALE AND ALL-MALE OF WALIA IBEX;

(age-classes see page 659).

|  |  |  |  | rutting-peak |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | Dec. | Jan. | Feb. | March | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. |
| Mean differences in age class among males in-male-female groups |  |  | 1.2 | 1.8 | 2.1 | 1.9 | 2.9 | 1.6 |  | 1.3 | 1.7 |  |
| all-male groups | 1.4 |  | 0.5 |  |  |  | 1.0 | 1.1 | 1.7 | 0.9 | 1.1 | 1.6 |
| All groups | 1.2 | (0.7) | 0.9 | 1.7 | 2.1 | 1.8 | 1.8 | 1.4 | 1.6 | 1.2 | 1.3 | 1.6 |
| number of observed dyad-combinations | 22 | 3 | 10 | 21 | 9 | 44 | 14 | 29 | 26 | 28 | 25 | 29 |

large male groups outside the rutting season, primarily in summer. However, if more males of similar age would meet in the rut, the percentage of fighting would presumably be higher and the manner of fighting probably more vigorous, as indicated by the Alpine ibex in a colony of high density (Nievergelt, 1967). For the Walia ibex I can imagine that if density increased there would be a better synchronization of the reproductive cycle with no rutting behaviour in one season; much fighting would occur as well. It is conceivable that such a period with no rutting behaviour actually existed in the earlier years of higher population density.

## ASSOCIATION IN WALIA OF KIDS, YOUNG AND FEMALES WITH FEMALES

Tables 4 and 5 give the frequencies of association of all the various classes with females. In what follows, the data concerning kids, young and other females are now discussed. The frequency values for kids are high, indicating the expected close association. Those for young are considerably lower and close to the average (i.e. the random expectancy quoted in the penultimate line), but they are still mostly above the frequencies of males. The observed percentages of kids being suckled indicate that towards the end of their first year kids become more independent: September-November, 2. 7; December-February, 3.0; March to May, 1.2; June to August, 0 (altogether 14 observations only).

It was surprising, on the other hand, that females rarely associated with each other. Frequencies in both tables (4 and 5) are consistently below average, although with different percentages. The two low frequencies from December to February and from March to May in Table 5 are particularly noteworthy.

To determine whether or not there was an annual cycle in the frequency of female-female associations, I compared the recorded values per month with the expected values which were calculated on the hypothesis that females would associate to the same extent as did all classes on the average.

TABLE 7. DATA ON WHICH CALCULATIONS BASE LEADING TO FIG. 3.

Separately for whole groups and nearest neighbour only, there are listed: b: the recorded number of female-female associations, n: number of associations of various class-members with females, N: total number of recorded associations. e (expectancy for female-female associations) = $n^2/N$

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | whole group | | | | | | | | | | | |
| b | 100 | 64 | 86 | 38 | 38 | 12 | 26 | 34 | 86 | 116 | 10 | 276 |
| n | 293 | 214 | 318 | 128 | 231 | 53 | 123 | 96 | 319 | 323 | 61 | 872 |
| N | 768 | 566 | 934 | 346 | 906 | 176 | 468 | 330 | 940 | 892 | 262 | 2466 |
| | nearest neighbour | | | | | | | | | | | |
| b | 3 | 7 | 2 | 4 | 0 | 1 | 7 | 8 | 18 | 17 | 1 | 4 |
| n | 49 | 52 | 52 | 26 | 56 | 13 | 27 | 26 | 65 | 66 | 18 | 80 |
| N | 160 | 160 | 167 | 82 | 193 | 56 | 106 | 96 | 206 | 216 | 88 | 274 |

To measure deviation I used the square of the difference divided by the expected values (as is done in a Chi-square test). The results are illustrated in Fig. 3, in which column lengths indicate the deviation upwards and downwards from the expected value, both for the frequency of association in groups (Table 4) and for the frequency of nearest neighbours (Table 5). The pattern is obvious. The values for female-female associations are below expectancy in nearly every month. In the period from about June to November females join each other rather frequently, and in August even slightly more than expected. From December to May females seem to avoid

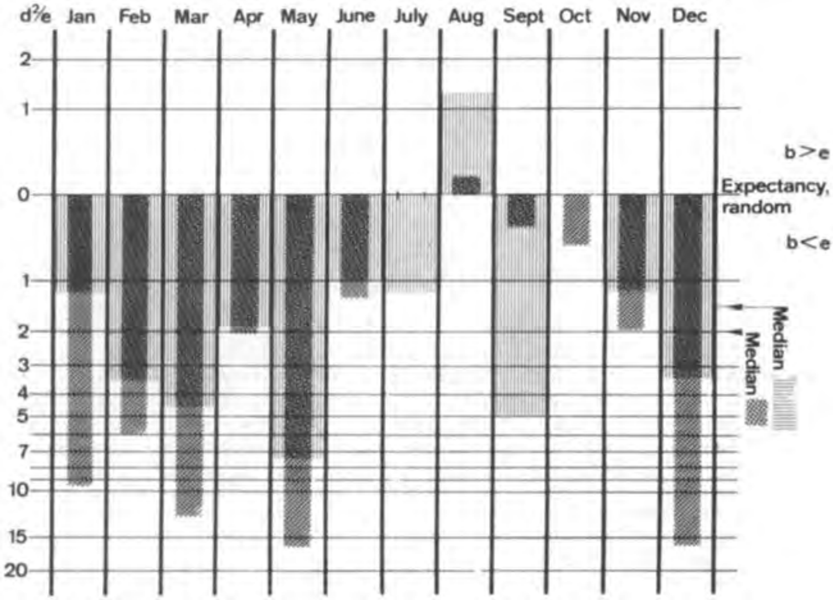

Fig. 3. Comparison of the recorded female-female associations of Walia ibex over the year with random expectancy.

(b: recorded number of female-female associations, e: expected value, b — e = d). $d^2/e$ is taken as measure for deviation from expectancy, columns are drawn upwards if $b > e$, downwards if $b < e$. For the data on which calculations are based see Table 7. The lightly shadowed columns show values for associations calculated on the basis of the whole group (as in Table 4). The smaller, darkly shadowed columns are based upon nearest neighbours only (as in Table 5). The columns are drawn on a logarithmic scale.

each other. The pattern for the values based on nearest neighbours can be interpreted with the test for time series proposed by Dr. E. Batschelet. There is a run of 6 above the median (June to November) and another below (December to May): the level of significance therefore is $P < 0.02$.

This indication of a seasonally fluctuating level of intolerance among females is also confirmed by the frequency of recorded fights. I saw a total of 6 fights between females, all of them occurring from December to May when the degree of female-female association is lowest. Although females do not fight much, there are many fights or play-fights within the female-young groups, mainly by young. Table 8 lists

TABLE 8. FREQUENCY OF FIGHTS IN FEMALE-YOUNG GROUPS IN FOUR SEASONS

| | Dec.-Feb. | March-May | June-Aug. | Sept.-Nov. | $\chi^2$ |
|---|---|---|---|---|---|
| number of observed animals | 1266 | 386 | 183 | 573 | |
| number of fights | 31 | 9 | 8 | 2 | |
| e | 24.7 | 7.5 | 3.6 | 11.2 | |
| $d^2/e$ | 1.6 | 0.29 | 0.57 | 7.54 | 10.0<br>$P < 0.05$ |

the recorded data of the fights in four seasons. With Chi-square it was tested whether or not fighting was evenly distributed throughout the year. The test indicates heterogeneity. Probably the few fights from September to November, the season of most births, is the reason for this pattern.

Fighting among males usually occurs when potential fighting-partners are in the same group; for there are probably different reasons for fighting. Presumably males have to fight in order to ascertain their rank, whereas females fight in order to space out.

## GROUP SIZE AND NUMBER OF SINGLE ANIMALS

I was under the impression that group size in Walia ibex was smaller than in Alpine ibex. To test this, I plotted (Fig. 4) the arithmetic mean with standard deviations for each month for the following groups of Walia ibex and Alpine ibex (Safiental-colony): males in mixed (male-female) groups, females in mixed groups, males in all-male groups, and females in all female groups. The figure reveals that both males and females in male-female groups average about the same size throughout the year and that there is little or no difference between the two species.

Distinct differences between the two species are shown by the patterns of the all-male and all-female groups. Outside the rutting season, mainly from May to October, males of the Alpine ibex join in much larger groups than do Walia ibex. In the Safiental colony, groups of up to 30 individuals were recorded, that is, nearly all the adult males of the colony. The deviations indicate that there is a wide range in male group size. Groups of Walia males do not significantly increase in size outside the rutting period.

In all-female groups there is a similar tendency for both species, but in each month the values are higher for the Alpine ibex. From April to October all-female groups of the Alpine ibex are on the average about twice as large as those of the Walia in the corresponding months. This is true except during the season of parturition, when the continuous increase towards the summer-pattern is disrupted.

Several explanations are possible for the behaviour shown by the Walia ibex:

1. Due to sexual activity year-round, the tendency to associate in larger male or female groups is reduced. In males this is due to social competition; and for the females it is possibly due to the fact that the presence of young of various ages in a mixed group might cause social disturbances. Some females have young, others have older kids, others are in estrus and attract males.

2. Due to low population density there simply are not enough animals of the same class in one area. It has been shown above for both species that groups outside the rutting period are composed of males of similar age.

3. It is possible that large, more-or-less stable herds are broken up by predators and by man.

4. The Walia ibex lives in a more forested habitat than the Alpine ibex (see Table 1). From other mammals it is known that there is a tendency to form larger groups in open areas. Nevertheless, this factor is probably of little influence: average group size of Walia in forest and in open area does not differ in Semien, and bare mountainous areas are not really comparable to open lowland, since cliffs, rocks, and valleys might serve as visual barriers as do trees.

Since the arithmetic mean of group size is influenced to a large extent by the changing number of single animals, data on single animals must be considered as well. The frequency of solitary males and females is given in Fig. 5. These data indicate that the number of single male Walia ibex is, in 10 months, considerably higher than for Alpine ibex, and that the frequency of solitary animals of both species seems to be at its peak just before or at the onset of the rutting period. When males of similar age begin to avoid each other, attraction is overruled by aggression; groups tend to break up and the number of solitary animals is high. This social reason provides a credible interpretation particularly for the Alpine ibex. To round up the cycle for this species: the lowest number of single animals is found during the months when

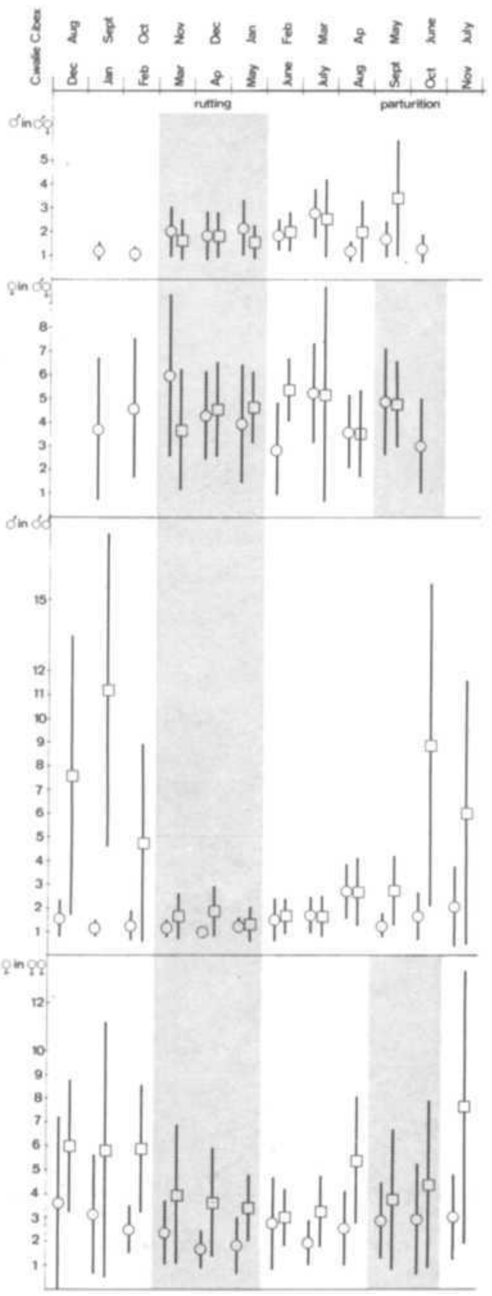

Fig. 4 Group size of Walia ibex (○) and Alpine ibex, Safiental colony, (□). Arithmetic mean and standard deviation of males in mixed groups (♂ in ♂♀) females in mixed groups (♀ in ♂♀), males in all-male groups (♂ in ♂♂), and females in all-female groups (♀ in ♀♀).

The number of groups on which the values base are for the two species Walia ibex/Alpine ibex and for each month from January to December as follows (if this number was below 5, no calculations were carried out).

Mixed groups:
12/45, 11/9, 13A9, U/12, 22/9, 6/(1), 9/(2), 10/(2), 17/(2), 15/(3), (4)/13,(4)/28;

all-male groups:
15/20, 18/6, 13/24, 8/13, 19/29, 10/33, 10/7, 10/9, 17/22,25/29,11/17,27/14;

all-female groups:
34/17, 35/(4), 33/17, 9/10, 43/47, 8/43, 17/8, 11/5, 28/27,49/10,18/15,79/8.

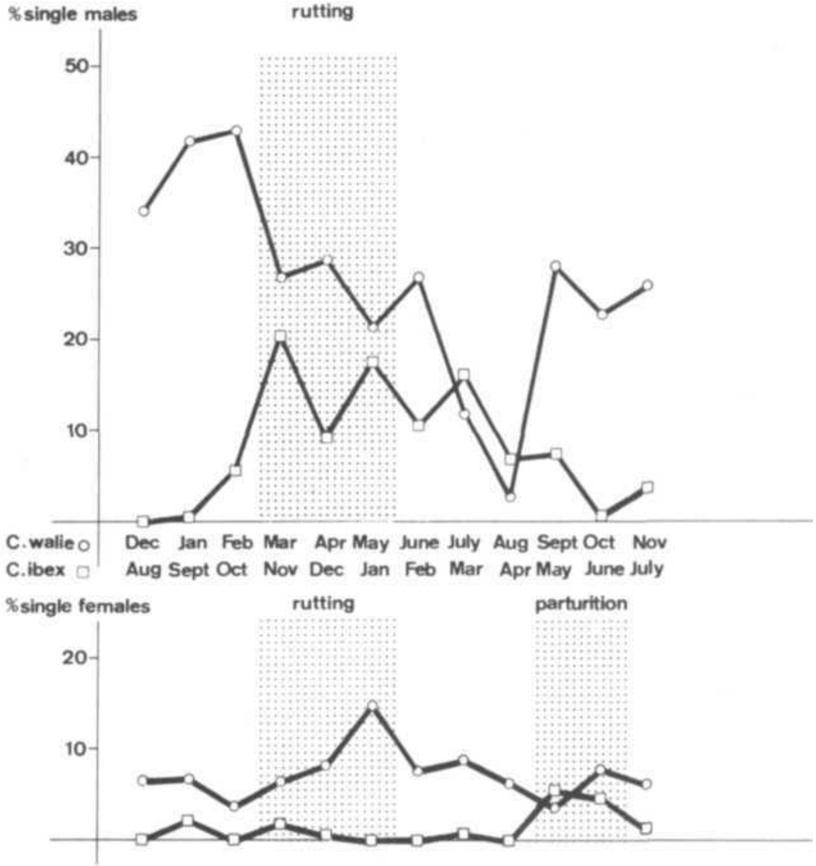

Fig. 5. Percentage of single animals per month of Walia ibex (○) and Alpine ibex, Safiental Colony, (□).

The total number of observed animals is for the two species Walia ibex/Alpine ibex and for each month from January to December as follows:

males:
31/97, 35/28, 41/87, 28/59, 70/110, 26/294, 42/56, 39/70, 50/275, 62/143, 27/49, 50/77;

females:
150/265, 138/60, 156/152, 62/96, 164/220, 39/192, 80/65, 64/45, 164/181, 190/85, 64/106, 341/155.

the animals live in large groups in their summer range—the period when attraction dominates aggression (Nievergelt, 1967). In the Walia ibex, there is obviously less correlation with the reproductive cycle. An explanation involving climate seems more plausible for this species. In Semien the rainy season lasts from the middle of June to August, the period with the last number of solitary animals. The Spearman-rank-test validates the correlation of monthly rainfall with the number of single animals ($P < 0.02$). A possible interpretation for this fact could be that more-or-less stable male groups are formed more readily in the rainy season because bad weather might stimulate grouping.

Important differences between the compared species are indicated in the lower part of Fig. 5, which shows the frequency of single females. During the rutting period the frequency of single Walia ibex is high, but at a minimum for Alpine ibex. For the Walia ibex this peak can be explained as follows: the rutting cycle of the Walia ibex is less synchronized and the females seem to avoid each other during the rut. It is therefore possible that a number of females are left solitary due to the many estrous females who have attracted males and now live in mixed groups.

The second astonishing difference is the fact that there are many single Alpine ibex but few single Walia ibex during the period of parturition. The pattern of the Alpine ibex is common among ungulates—females leave the group to give birth and remain alone for some time. This has been described for other species such as mountain goats (Klein, 1953), chamois (Schroder, 1971), and reedbuck (Jungius, 1971).

There certainly is no lack of suitable, protected places for parturition in the Semien Mountains. As a possible explanation, the pattern shown by the Walia ibex could be viewed as an adaptation to the numerous birds of prey. Kids may be safer from terrestrial carnivores if kept in protected places, since the females resistance against a leopard, for example, would be futile. But the numerous exposed rocks offer shelter which may be inaccessible to leopards. Against birds of prey, however, kids can be defended by their mothers. I presume that guarding and defence of kids are more effective if several females co-operate. We observed many times eagles and vultures flying closely around sites with females and kids, but never saw an actual attack. Further data are needed to substantiate this hypothesis.

If we compare the monthly frequencies of Walia kids, we can see that the proportion of kids starts to increase at the beginning of the main parturition period in September and reaches a high in January, after which time values decrease. The following figures are monthly quotients of kids to females (after Nievergelt, 1971):

| Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.9 | 0.6 | 0.5 | 0.3 | 0.4 | 0.4 | 0.4 | 0.3 | 0.5 | 0.6 | 0.7 | 0.8 |

The period of decrease corresponds with the second part of the dry season. In this period the animals tend to leave the inaccessible places, which are then dry and without fresh food. However, I have no direct evidence that the seasonal increase in kid-mortality in February is caused by ground predators. It is possible that kids born outside the main kidding season spend their first period of life in areas less well protected against carnivores, namely in the open areas away from the crags. This would make ground predators an additional selective force favouring a synchronized reproductive cycle.

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**Paper No. 15**

# The Social System of the White Rhinoceros

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## ABSTRACT

Results of behavioural study carried out on the white rhinoceros in Zululand, South Africa, between 1966 and 1971 are summarized. Cohesive social groups included cow-calf pairs, adolescent groups, cow-adolescent groups, cow-cow groups and adult male singletons; the largest group numbered six. Adult males occupy territories of about 2 km$^2$ for periods of several years. Olfactory marking is carried out by dung-scattering and urine spraying. There are subordinate adult bulls which coinhabit certain territories, but do not perform territory marking. Cows have overlapping basic home ranges covering about 10-12 km$^2$ but at times they may wander further afield. Some adolescents are resident, others semi-nomadic. There are ritualised encounters between neighbouring territorial bulls, while subordinate bulls adopt a defensive threat posture when approached. A deposed territorial bull is not driven out of his territory but becomes a subordinate bull. Territoriality is characterised as a spatially localised dominance. Reproduction is year-round with seasonal peaks. A consort period of 5-20 days precedes mating. A bull manoeuvres to confine the oestrous cow to his territory. Courtship approaches last 15-20 hours and copulation 20-30 mins. Subordinate bulls do not mate with cows. Gestation is 16 months.

The new-born calf remains shaky for 2-3 days. When alarmed it runs off ahead of the cow. Weaning commences at 2 months, but nursing continues to well over a year. The older calf is driven away upon the birth of a new calf. It then bonds onto another adolescent or a cow without a calf. Females have their first calf at 6½-7 years, but a male is probably over 12 years before he can claim a territory and mate.

The well-ordered social system has probably contributed to the success of the species. Large bulk with consequent low predation and year-round reproduction have favoured a territorial organisation. Territoriality regulates reproductive competition but not population growth. For management purposes it is recommended that population expansion be controlled without major social disruption by confining removals to certain 'vacuum' zones.

## INTRODUCTION

The white or square-lipped rhinoceros *Ceratotherium simum* holds special interest in relation to the evolution of ungulate social systems. It is a species which has persisted with little anatomic modification since at least the early Pleistocene, and might therefore also retain 'primitive' features in its behavioural patterns. With adult male weights of about 2300 kgms, it is perhaps the largest entirely grass-feeding animal ever to have evolved. However, apart from the short term observations of Backhaus (1964) on the northern subspecies *C. s. cottoni,* no previous behavioural study has been carried out.

My own investigation was aimed at elucidating the basic features of the ecology and behaviour of the southern subspecies C. s. *simum* in the Umfolozi-Corridor-Hluhluwe game reserve complex in Zululand, South Africa. Because of the unusually favourable conditions for a study of this nature, particular emphasis was placed on social behaviour. Field observations were commenced in January 1966, for a six month period, and were then resumed in November 1968 and continued without further interruption to September 1971. The main study area of about 20 km$^2$ was located in the western section of the Umfolozi Game Reserve, where relatively high white rhino population densities (about 5/km$^2$) occur. Comparative observations were made in four supplementary study areas. The basic technique was to maintain a watch on the activities and interactions of particular individuals or groups for periods of up to twelve hours. Observations were carried out on foot, which method was facilitated by the relatively poor eyesight of the species. Notebook and pencil recording were supplemented by photographic documentation on still and movie film. Individual recognition of all adults was possible using particularly variations in horn shape. Thirty ear-tags were inserted to assist identification mainly of subadults, and ten radio transmitters were placed to follow the movements of cows and subadults.

The background history of this population has been described by Player and Feely (1960) and its continuing rapid growth was reviewed by Vincent (1969). The 1971 helicopter census figure was 2002 white rhinos in the 900 $km^2$ of the Umfolozi-Corridor Hluhluwe unit. The reserve supports large numbers of a wide variety of other large herbivores, and habitat deterioration is causing serious concern.

At the time of writing, field work has only just been concluded and a detailed analysis of data has yet to be undertaken. This contribution will thus merely summarise the essential features of social structure and dynamics; a full treatment of results will be published at a later date. A brief consideration of white rhino territoriality has already appeared elsewhere (Owen-Smith, 1971; also in press).

## A. BASIC ECOLOGY

The white rhinoceros is entirely a grass-feeder, with a preference for short grass. Grazing and resting occur in alternate spells of a few hours throughout the night and during the cooler part of the day. This pattern is broken by a longer rest period through the heat of midday, particularly during summer. For this the animals tend to aggregate under shady trees at certain favoured rest places, usually on the crests of low ridges. Mud wallowing is performed more frequently during summer, but may occur at any time of the day or night. Drinking can occur twice daily while water is abundant. Towards the end of the dry season, when water availability becomes restricted to a few sources, journeys to water are made at 2-4 day intervals. Though lions, leopards, cheetahs and hyenas occur in the area, predation has not been recorded.

## B. SOCIAL STRUCTURE

### 1. Groupings

Cohesive social groups consist mostly of twos, with a few larger groups which may number up to six individuals. The following basic units occur:-

(a) *Cow-calf pairs.* Most adult females are accompanied only by their most recent offspring. In rare instances the previous calf may remain, associated with its mother after the birth of a new calf.

(b) *Adolescent groups.* Animals which have separated from their mothers, but which have not yet reached social maturity, usually team up with one or more companions of similar age. Though groupings of this type numbering up to five and occasionally more animals have been encountered, persistent individual bonds are apparently not formed between more than two adolescents. Both homosexual and heterosexual groups occur, with the former more prevalent.

(c) *Cow adolescent groups.* A cow which has lost her calf through mortality or, more commonly, as a result of rhino capture operations, will readily accept the company of one or more adolescents. Stable groups numbering between two and six individuals have been observed, each adolescent apparently bonding independently to the cow. Transient attachments between adolescents and cow-calf units also occur.

(d) *Cow-cow groups.* Two adult cows, both lacking calves, may also join together. They are likely to be accompanied additionally by one or more adolescents. In some cases one of the two cows is clearly a younger animal, and the possibility of a mother-offspring relationship exists. Because of the readiness with which they will accept the company of others, solitary females are not commonly observed.

(e) *Adult male singletons.* All mature males are basically solitary. They do however attach themselves for short periods to female groups. A bull-cow association persisting over several days is indication that the female is coming into oestrus.

## 2. Spatial patterns

(a) *Adult male territories.* Space utilisation patterns are based on the division of all suitable habitat into a mosaic of adult male territories, typically each about 2 $km^2$ in area. The territories are occupied by individual bulls for periods of several years, and a territorial bull normally restricts all his activities to within his territory, which is thus also equivalent to the home range. The only exception occurs during the dry season, when many bulls are forced to make an excursion to water every few days. Borders are narrow zones which are patrolled and marked by both neighbouring bulls.

Defecation and urination have become ritualised in territorial bulls, and apparently function in olfactory marking of the territories. Defecation is almost always carried out at one of the numerous (20-30) dungheaps which are scattered throughout a territory. Backwardly directed kicking movements are made both before and after defecation, so that the dung is broken up and scattered over the heap. Elements in the urination ritual include wiping the anterior horn over a low bush or the ground, scraping the legs along the ground past this site, then ejecting the urine in the form of a fine spray in 3-5 spasmodic bursts (Plate I). Urination in this manner may occur anywhere in the territory. It is, however, carried out repeatedly whenever the bull patrols a boundary, so that the density of urination sites is highest in a border region. There are also certain large, well hollowed-out dungheaps in the border region attesting to frequent visitation by the territorial bull

About one third of the adult males are not territory owners. Each of these subordinate (or subsidiary) bulls coinhabits the territory of one of the territorial bulls. In some territories only the territorial bull is resident, in others two or three other bulls may share the territory with the territory owner. Unlike the territorial bulls, these subordinate bulls may occasionally wander outside their home territory. They use the same dungheaps as the territorial bull, but neither scatter their dung nor spray their urine, defecating and urinating without embellishment like females and subadults.

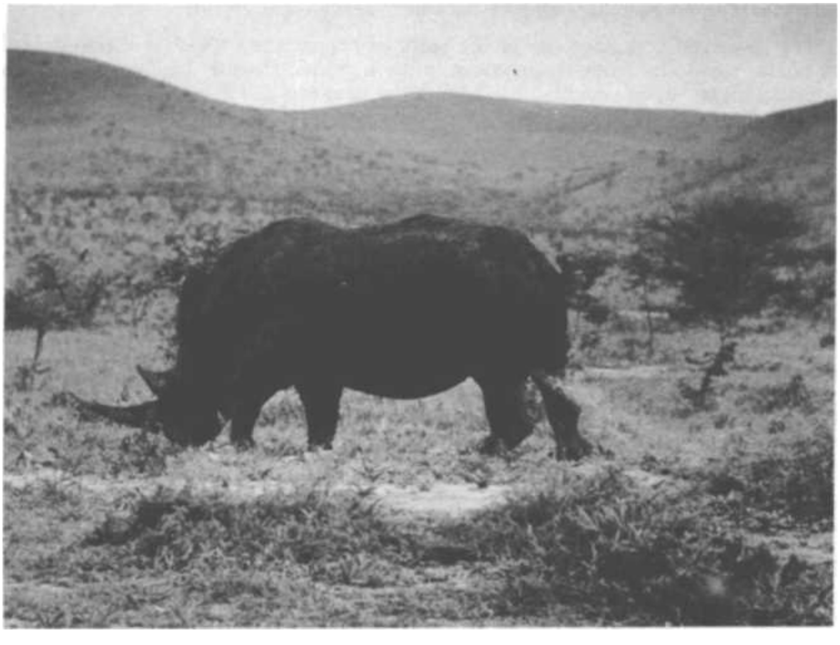

Plate I. Spray urination by a territorial bull

(b) *Home ranges of cows and adolescents.* Adult cows have a basic home range covering about 10-12 km$^2$ and encompassing 6-7 male territories, to which they restrict their movements while good quality food and water are plentifully available. Wandering movements outside their basic range may occur during drying periods or after rains, apparently in search of the best grazing; while drinking excursions become forced during the dry season. The basic home range then becomes extended by corridors leading to long-lasting water supplies, so that the total annual range traversed may encompass 25 km$^2$ or more. However, the cows tend to return to the basic home range in between such journeys. There are no core areas within the basic home range, different sections being favoured during different period's.

The home ranges of individual cows are independent, but overlap extensively with the ranges of other cows. Implications of exclusiveness art thus absent.

Some adolescent groups remain within home ranges of 4-10 km$^2$. Others appear to be semi-nomadic, appearing in a study area, remaining for several months, then disappearing again.

## C. SOCIAL DYNAMICS

### 1. Interactions between bulls

Interactions between males are ordered within the framework of the territorial structure. The course of an encounter is dependent both on the status of the bulls concerned and on the location of their meeting.

Meetings between neighbouring territorial bulls are usually restricted to a border region, and are of infrequent occurrence. One bull may make a lowered head rush at the other, but this is usually checked just before contact. The two bulls come together to stare at each other horn against horn with raised heads (Plate II), then back apart to wipe the anterior horn vigorously over the ground. A sequence of repeated advances to touch horns, then retreats to rub the horn on the ground, usually laots for only a few minutes, but may occasionally continue for over an hour. There may be momentary clashes of horns with lowered heads, but attack is not driven through further than this. Both males remain silent. Eventually the two bulls back, turn away hesitantly, then move apart. One or both may scrape and urinate.

In three observed instances one of the bulls has penetrated 100-200 m into the territory of the other. In these circumstances the intruder steadily backed away during the engagement. Upon reaching his border, he scraped and urinated sprays, and the two animals then separated.

A subordinate bull responds to the approach of a territorial bull by standing his ground, uttering loud roars or snarls with head thrust forward, ears laid back and tail curled upwards (Plate HI). He may make a few quick paces towards the territorial bull. Despite their seemingly intimidatory nature, these gestures are interpreted as defensive threats. The same *snarl-threat* is employed by cows and adolescents against an approach by a bull, among subadults usually by the smaller animal. The territorial bull may approach to stare silently horn to horn, or may clash horns briefly. Such a horn clash is fended off by the subordinate bull to the accompaniment of trumpeting shrieks. Engagements between a territorial bull and a subordinate bull which is resident within his territory, however, are usually very brief, and the territorial bull soon walks away, leaving the other bull standing. Quite often the territorial bull simply wanders on past as if oblivious of the other bull's presence, despite nervous snorts and grunts from the latter. The two bulls can be observed grazing or resting together peacefully only 20-30 m apart.

Should a territorial bull encounter a subordinate bull which is a trespasser from another territory, the basic actions of both animals are the same, but the engagement is likely to be more prolonged (sometimes over an hour), with more frequent horn clashes. The territorial bull may circle away, then approach again, several times. Again the engagement is terminated by the territorial bull wandering off. In one observed instance a fight developed, with the territory owner attacking the trespasser with horn to body blows which the latter was unable to fend off.

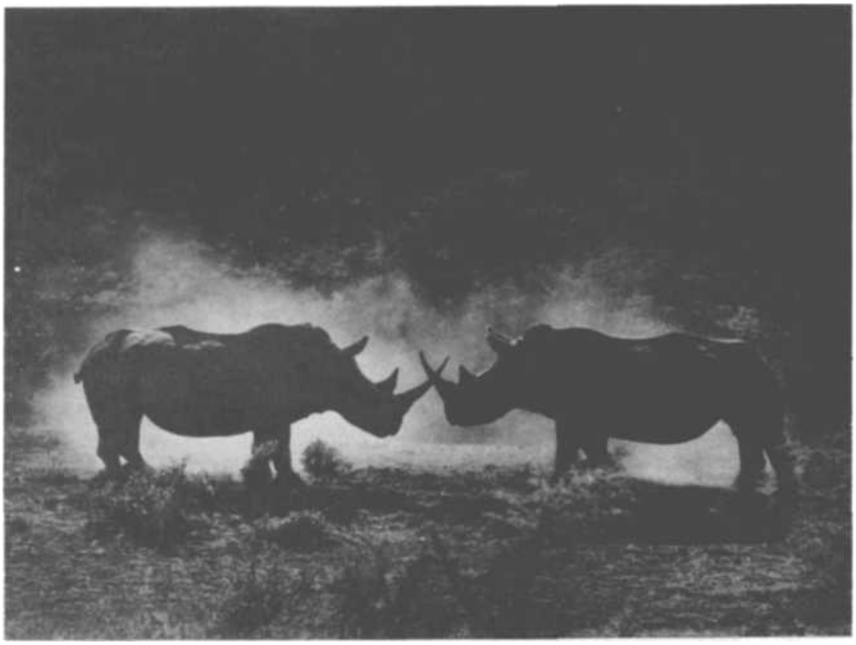

Plate II. Two territorial bulls stare at each other horn against horn during a border confrontation

Plate HI. A subordinate bull (on right) stands defensively giving the snarl-threat at the approach of a territorial bull

If confronted by a resident territorial bull while off his own territory during a journey to water, a territorial bull will also adopt the defensive snarl-threat stance with roars and shrieks. In one case a serious fight developed when a territorial bull returning from water attempted to cross the territory of a neighbouring bull, but was accosted by the neighbour at the boundary. There were long periods of slow horn against horn fencing with raised heads, with occasional sudden lowered head feints. These were interrupted by bouts in which one bull was able to strike through the defences of the other and deliver blows to the head, shoulders, and sometimes the body, with upward jabbing movements of the head and horn. Both bulls remained silent, apart from heavy breathing. The fight was still in progress after 35 minutes when darkness fell. The next day the wandering bull was still off his territory, and had a badly bloodied eye and numerous bruises and gashes. The resident bull showed only a few cuts. It seems significant that in this instance the trespassing bull did not demonstrate submission.

## 2. Changes in territory ownership

Because of the long duration of territory occupancy, changes in territory ownership are rare events. I observed in detail three such changes, which resulted from the ingress of a new bull and subsequent chain displacement of two further bulls. In one case the defeated bull had numerous bruises and gashes around the head, shoulders and sides; and I was able to glimpse a brief second fight in which the new territory holder laid into the former owner with repeated horn head to body blows, until the latter broke and fled after a few minutes. But in two of the cases, there were only a few superficial cuts on the deposed bull, so that the mechanism of the dominance shift was not clear.

In all of these transitions the deposed bull was not driven out of his territory, but remained there taking on subordinate bull status. In the first case this situation persisted for a few months, then the bull shifted a few kilometres and claimed another territory. The bull he displaced stayed on only a week, then took over the next-door territory. The third bull to be deposed was still present over a year later as a subordinate bull in the territory he had formerly held.

That violent fights do occur is evident from rangers' reports of bulls killed by fighting, and by the presence of subordinate bulls with numerous scars around the head, shoulders and belly regions. The horns of the rhinoceros are directly functional weapons, and social constraints are necessary to reduce the incidence of violent conflict.

A defeated territorial bull immediately ceased spray urination, and more gradually eliminated dung scattering, with an initial decrease in the number and intensity of kicks.

The reverse transition can also occur. Two of the four males which I knew as subordinate bulls in 1966 had by 1968 become territory holders, though not in the same territory they had formerly inhabited.

## 3. Territoriality and dominance

The approach adopted by a resident territorial bull on encountering another bull is essentially the same in all cases. The horn against horn stare is obviously a powerful intimidatory gesture. The course of the encounter depends on the response of the other bull. If the latter consistently adopts subordinate stance and vocalisations, attack is unlikely to be carried out. If submission is not shown, a fight can only be avoided by the intruder back-pedalling. In a border region, both bulls waver between attack and withdrawal, and a sequence of ritualised advances and retreats results.

All intruding bulls are potential territorial rivals, but an intruder is not driven out of the territory if he demonstrates submission when confronted. It appears that a territorial bull eventually becomes habituated to the presence of particular subordinate bulls on his territory. Regular testing serves to ensure that the dominance-subordinance relationship between them is maintained.

Spray urination is partly an assertion of dominance, and is not performed once a male leaves his territory, or loses his dominance within that territory. That dung scattering still occurs in these circumstances is probably a result of force of habit. While off his territory during a journey to water a territorial bull shows hesitancy and avoidance when he encounters other rhinos, whether bull, cow or adolescent.

Thus territoriality as shown by the white rhinoceros may be characterised as a spatially localised dominance by adult males.

### 4. Relationships with adolescent males

Adolescent males show nervousness of the close proximity of a territorial bull, and are occasionally chased. There are recorded instances in which young males have apparently been killed by horn wounds. However, most of the time the territorial bulls pay little attention to adolescent males, even when the latter are accompanying an oestrous female. Adolescents thus move relatively freely across the territories.

### 5. Relationships among cows and adolescents

Cows appear indifferent to the presence of other cows and adolescents in their vicinity. A cow may give snorts when another approaches to within a few metres, but on occasions two cows may come together to stand quietly with lowered heads in contact. This may develop into slow, gentle horn wrestling. Adolescents show interest in other rhinos, and more frequently approach for such naso-nasal contacts. These meetings can develop into prolonged and vigorous playful wrestling and chasing. Rather than avoidance, there seems to be a slight aggregative tendency among cows and subadults. In addition to the congregations at resting areas, there is also a noticeable clustering tendency in grazing distribution. At waterholes, where strangers are forced into close contact, repeated snorts and grunts are exchanged between cows, and one may sometimes drive another back with a clash of horns.

## D. COURTSHIP AND MATING

Reproduction in the white rhinoceros is not seasonally restricted, and births have been recorded in every month of the year. However, oestrus is apparently stimulated by a flush of green grass following a dry period. There is thus a mating activity peak through October-November-December, following the onset of spring rains, and subsequent calving peak through March-April-May. The gestation period is sixteen months. Oestrus can recur at intervals of about 30 days until fertilisation is achieved. The first post-partum oestrus may occur after six months, and intercalving intervals vary between two and three years.

A territorial bull will investigate any strange cow encountered on his territory. He makes a frontal approach accompanied by a hic-throbbing sound and stands staring at the cow from a range of a few metres, usually in a downwind position. A cow reacts to such an approach with snorts or the snarl-threat, and may sometimes drive a bull back with a clash of horns. Normally the bull then wanders on, but he may remain grazing in the vicinity of the cow for a few hours. If such an attachment persists for more than a day, it indicates that the cow is coming into oestrus.

The consort period may last for between five and twenty days, the bull simply accompanying the cow everywhere in her movements. The cow gives snorts of varying intensities of the snarl-threat if the bull approaches too close. The bull readily responds by giving way. However, if the cow wanders towards a boundary region, the bull then moves ahead, making soft squeals, to stand in front of her blocking her progress (Plates IV & V). Should the cow run off, he chases after her with loud wails and turns her back. In a few instances he may even drive the cow back with a clash of horns. Most commonly, however, such interactions are more subtle, with the bull quietly moving into a flanking position between the cow and the boundary, and the cow changing direction accordingly. These territory boundary blocking actions are commenced by a bull about 100 m inside the actual limits of his territory.

If the cow urinates, the bull investigates the site, nibbling at the damp soil then standing with raised head and wrinkled, parted lips. The posture, however, is not as exaggerated as *flehmen* in other ungulates. Though dung may also be sniffed, the flehmen response is restricted to urine testing, and may be exhibited also by calves and adolescents.

Plate IV. A territorial bull moves round to block the movement of an oestrus cow and her calf towards the territorial boundary

Plate V. A territorial bull (on right) determinedly blocks attempts by a cow and calf to proceed across a territory border. The cow gives the snarl-threat, while the bull counters also with the ears back posture

The onset of oestrus is apparent to the observer by the commencement of repeated hic-throbbing approaches by the bull. These approaches are made posteriorly with the head held high. Initially the cow wards off the bull with snorts, the snarl-threat, or a clash of horns. The bull readily yields, but makes another such testing approach a few minutes later. An accompanying calf or adolescent may block the approach of the bull with threat gestures, and the bull then circles round and tries from a different angle. After several hours the bull rests his chin on the rump of the cow, and after several such positionings, mounting attempts are made. The cow responds to these approaches by curling her tail and ejecting a squirt of urine, which is sniffed by the bull. She offers no other behavioural stimulus, other than by standing to receive the bull. After mounting several times intromission is achieved. Copulation lasts 20-30 minutes, with the multiple ejaculations indicated by quivering movements by the bull. It may take as long as 15-20 hours after the commencement of approaches before intromission is achieved. In only one instance was a repeated copulation observed, after an interval of three hours. The consort relationship is normally broken up 2-5 days after mating, but may continue through another oestrus cycle if fertilisation was not achieved.

Subordinate bulls normally do not form such consort relationships with cows and play no part in reproduction. In a single exceptional instance, a subordinate bull attached himself to a cow for several days at a time when the territorial bull was engaged with another pre-oestrus cow. When the first cow was ready for mating, however, it was the territorial bull who served her, while the subordinate bull wandered about agitatedly in the vicinity without interfering.

## E. MATERNAL BEHAVIOUR

The actual act of parturition was not witnessed; the cows evidently resort to secluded areas such as dense thicket or, occasionally, little-visited hillslopes at this time. However, some observations on newly-born infants were possible. The calf remains rather shaky on its feet for the first 2-3 days, and spends most of its time walking slowly round and round the cow, maintaining close bodily contact. The cow sniffs repeatedly at the infant, and will not leave its side. Aggressive gestures towards the observer were not made.

The calf is normally 3-4 weeks old before the cow reappears in her usual grazing areas. Both mother and calf keep within a few metres of each other. At any disturbance, the calf gallops off in front, with the cow following at its heels. The calf is attentive to any change in direction by the cow, and responds accordingly. However, it seems that usually the cow merely follows the direction of retreat chosen by the calf.

Nibbling at grass commences at an age of about two months, and by three to four months the calf is directing much time to grazing. Suckling however continues until the calf is well over a year old

Nursing is initiated by the calf, a thin whining squeal being made before commencing to suck. Suckling lasts 2-4 mins without the active pushing movements typical of many other ungulates, and is terminated by the calf turning away.

A young calf shows great curiosity in other rhinos, and will approach for investigation. The cow watches attentively, and will rush in at the slightest provocatioa Cows with small calves show less tolerance of the close proximity of other rhinos than those with larger calves. Playful horn wrestling and chasing often develop between two young calves while their mothers graze nearby.

Mother and offspring maintain a close bond for two to three years until the time comes for the cow to give birth again. The previous calf is then driven away and must seek out a new companion.

## F. INTEGRATION OF ADOLESCENTS INTO THE POPULATION

Following separation from its mother, the individual, which I shall now term an adolescent, wanders around forming temporary attachments with cows and other adolescents. Eventually a stable bond is formed, either with a cow lacking a calf, or with another adolescent. Such bonds are persistent, the same two individuals always being found together over periods of a year or longer, and rejoining after an accidental separation. The two animals keep close together while grazing, making occasional bodily contact, and co-ordinate their movements and activities. A hoarse panting sound is made at times and seems to have a proximity-maintaining function. Though adolescent groupings numbering several individuals are sometimes observed, additional animals seems to be treated as outsiders. Their proximity may be tolerated, but they are likely to be driven back if they make too close an approach.

Enduring bonds are most commonly formed with another adolescent of the same sex and of about the same age. In such pairs there is no obviously dominant individual or leader. Heterosexual pairs also occur and, in these, it seems that the female is the more active in directing movements. In cow-adolescent groups, each adolescent apparently bonds independently to the cow, who shows tolerance of their presence. Movements of such groups are controlled by the cow, though the adolescents may walk in front of her.

While some adolescents remained on in the study areas for over two years, others eventually disappeared. There were also strange adolescents which appeared, remained a few months, then vanished again, indicating nomadic tendencies. Adolescents which have been bonded to cows are most likely to stay in the area, even after their separation from the cow. This provides a mechanism by which dispersal movements may be balanced against calf losses. Adolescents, particularly young males nearing maturing, are most prominent in recently colonised areas.

Adolescence in females may be said to be terminated when the individual breaks away from her companions to give birth to her first calf at an age of 6½-7 years. Among males, adolescent bonds may persist until both individuals are almost full-grown. With time the males become separated and settle within a particular territory with subordinate bull status. There they remain until they reach virtually full weight and are able to challenge for ownership of a territory. By this time they are probably twelve or more years of age.

## DISCUSSION

The white rhinoceros is a herbivore which, through its great bulk, is almost invulnerable to non-human predation during its adult life. The pairing up of adolescents probably has a predator-defence as well as possible social-learning function, but the major selection pressure which is believed to favour the aggregation into large herds typical of other open-country grazing herbivores thus exerts minimal influence. With this prime adaptation this slow-moving, relatively slow-witted animal, relying mainly on olfactory cues for orientation, remained abundant and widely distributed through southern Africa, until the arrival of modern man with his weapons. The well ordered social system, which seems to promote a relatively high fecundity for an animal this size, has probably been a strong contributory factor to this success.

The long gestation period and slow growth to adulthood, which are also a consequence of large size, mean that there is no narrowly fixed optimum reproductive season. The resultant year-round mating activity, coupled with low predation pressure and relatively settled range occupancy, have been strong influences shaping social organisation. Thus we find that prime males maintain a fairly stable system of fixed territories, within which there is only a very slow turnover of individuals. Associated with them is a more mobile population of females, all members of which may be individually known to each other and to the males through repeated contacts over a period of many years.

The prime functional significance of territoriality seems here to be to regulate reproductive competition among males, by lowering the frequency of male combats, and allowing courtship and mating to proceed without disruption. Females and subadults do not exhibit territorial intolerance and, except for the brief period around oestrus, their movements are not restricted by the territorial behaviour of the males. Though there is pressure on surplus males to emigrate, there is no evidence that the rate of reproduction by females is limited by the availability of males to serve them. Mortality is currently low. Since marked habitat deterioration is occurring at existing population levels, it seems evident that territoriality cannot serve to regulate population growth within the carrying capacity of the habitat. Apart from a decline in fecundity and infant survival which may come into play at a later stage, the only apparent mechanism of population regulation seems to be the dispersal of adolescents into unfavourable habitat where their chances of survival may be low. This movement is now prevented by the boundary fence surrounding the reserve.

## MANAGEMENT IMPLICATIONS

The current natural increase of the white rhino population is nearly 10% per annum. It has become essential to undertake artificial control measures to limit population size to such a level as to ensure maintenance of the habitat and thus the continued survival of the species in this area. This is presently being carried out by a live capture and translocation program, which, in 1970, successfully removed nearly 200 rhinos from the reserve area.

While the aim of a zoological garden is chiefly to exhibit the physical features of different species, that of a game park must be to preserve representative natural communities with their ecologically and behaviourally adapted constituent species. Social behaviour patterns are as much species attributes as more readily visible morphological features, and physiological adaptations. They are of great potential interest, not only to ethologists and evolutionists, but also to a visiting public becoming increasingly well-educated as a result of recent popular literature on the subject.

The relatively stable, slow-changing social organisation of the white rhinoceros could easily be disrupted by the drastic culling measures which may soon become necessary. The problem is how to design management procedures so as to destroy the natural order in the population as little as possible; so as to work in with, rather than against, natural population regulatory mechanisms.

This ideal could perhaps be approached by setting aside certain zones of the reserve to be maintained as white rhino 'vacuums', by the constant removal of all animals which settle within them. The disturbing effects of culling operations could then be confined to these localities so far as is possible, though additional culling may be necessary to achieve population balance. It is, however, to be expected that these 'vacuums' would steadily be filled by surplus animals, mainly adolescents, dispersing out from the bulk of the population. The identity of these expendable individuals would be determined by social interactions among the animals themselves, rather than by the whim of a human management officer. This would permit the natural adjustments of the social order to changing environmental circumstances to have full play.

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**Paper No. 16**

# On the Bedding Behavior of Pronghorn Fawns

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## ABSTRACT

Fawns of the pronghorn (*Antilocapra americana*) are separated from their mothers and lie in seclusion up to 90 per cent of the daytime until three weeks or so following birth. Recurrent mother-fawn reunion are typically concluded by the fawn moving away from the doe and selecting its own 'bed'; this move-to-lie-secluded apparently has its inception at the birth site, and is described in detail. Our observations suggest that, until they are about three weeks old, fawns tend to seek seclusion in vegetative cover resembling that in which they were born. Sagebrush providing cover for which parturient does on our study area show preference is being sprayed with herbicides. An apparently reasonable question is raised: What will be the relation between reduction of sagebrush where it furnishes preferred fawning cover and the pronghorn's reproductive success in such areas?

## INTRODUCTORY NOTE AND ACKNOWLEDGEMENTS

This paper is largely an abstract of one section of a monograph on the behavior and socialization of pronghorn fawns, which I am writing in collaboration with Robert E. Autenrieth, formerly a graduate student at Idaho State University, now a Game Research Biologist with the Idaho Fish and Game Department. Our report is based on observations made over a period of 16 years. Special attention to behavior was undertaken in 1963, and is continuing; that effort was supported for four years by grants from the National Science Foundation which we gratefully acknowledge.

## OBSERVATIONS

Fawns of the pronghorn (*Antilocapra americana*) are routinely separated from their mothers up to 90 per cent of the daytime until three weeks or so following birth. Most of the time away from the dam is spent lying in seclusion, either as singles or as pairs of siblings, on 'beds' which the fawns select. The following presentation examines behavior relative to the young pronghorn's selection of bedding sites (cover) and, thence, an implication regarding management of populations of this game species. The findings reported here have, for the most part, been secured by observations on free-ranging animals in the Upper Pahsimeroi drainage of central Idaho.

Movements that characterize much of a pronghorn fawn's behavior for the first half-hour or so following delivery, during much of which time the neonate is being licked by the mother, include righting itself, raising and shaking the head, crawling, attempting to stand, standing, and walking. All or most of its movements soon show orientation to the doe, whether she is standing or lying down. The predisposition in newborn pronghorns to move toward the dam, even by crawling, is expressed as early as five minutes after delivery and before they gain their feet for the first time. Such approaches to the mother, also reported for other artiodactyls, appear to evidence 'the urge to follow' which Portmann (1961) considered present in precocial ungulates 'immediately at birth'. Significant to our exploration here, however, is the fact that pronghorn fawns also begin making short excursions *away from the mother* at the birth site—as soon as 43 minutes after being born (Bromley, 1967). Many of these early trips seem to be fortuitous (or aimless), but some conform to a pattern that is conspicuous in the fawn's behavioral repertoire for the next three weeks or so. This action, in which the fawn 'intentionally' leaves the doe and beds down, we are labelling 'the move-to-lie-secluded'.

A completed move-to-lie-secluded typically initiates a more or less extended period during which mother and young remain apart. Such intervals of separation are recurrent, perhaps experienced as many as 100 times by a given fawn. This course of events in the pronghorn is of special interest for several reasons, among which is the occurrence of essentially the same behavior in several species of African bovids (Estes, 1967; Leuthold, 1967; Walther, 1964, 1968).

As a rule, pronghorn does leave their recumbent neonates for the first time from three to six hours after parturition, either with the young still at the birth site, or after parent and offspring have moved away from the site together. At varying intervals for the next three weeks or so, the doe visits her offspring, effecting what we have labeled 'mother-fawn reunion periods'. Data on 61 reunion periods and 25 periods of separation, totalling 87 hours and 10 minutes and involving 29 does and 52 fawns, show reunion periods ranging from 2-46 minutes and averaging 18. 2 minutes, separation periods ranging from 50-488 minutes and averaging 187.6 minutes.

The principal activities of a reunion period are nursing, checking (doe noses fawn's rear), anogenital grooming, the relocation move, and the move-to-lie-secluded, with play often interposed by the young any time after the first round of nursing.

Because the relocation move appears to be prerequisite (along with nursing) to the fawn's moving away *and staying away* from the mother, brief attention to it is appropriate here. The relocation move results in no two successive periods of seclusion being, as a rule, spent on the same spot. Both mother and young typically participate in the move to a 'new' bedding site. They walk, trot and /or canter, and often interrupt the move with brief intervals of standing, looking about, and anogenital grooming; the fawns may also play or make abortive moves-to-lie-secluded. While we commonly say 'the doe moves her fawns', the action can apparently be initiated and the general direction established by either mother or young; however, the doe usually appears to determine the eventual course of the move, especially in the presence of disturbance.

Although highly variable, the move-to-lie-secluded typically comprises three phases: (1) the move away from the mother; (2) the search for and selection of a bedding place; and (3) the act of lying down. It also typically marks the conclusion of a mother-fawn reunion period. (While it is common for both of a doe's fawns to be involved in a reunion period after they are a few days old, my discussion of the move-to-lie-secluded will, for the sake of simplification, focus largely on the individual fawn.) Not until the neonate is several hours old does the 'move-away' of this behavioral sequence show the 'purposefulness' by which it can usually be recognized thereafter. The fawn walks away during its first several hours. Beginning when it is a day or so old, it will make the move either walking or running or both, sometimes interrupting this phase with play. At the birth site, the direction of the move-away apparently bears no relation to the position of the doe; after they are a day or two old; fawns generally move out laterally from or ahead of the mother, whether she is standing or on the move. Walther (1968) found that gazelle fawns also, at times, turn at a right angle to the direction of the mother's forward motion in order to lie down.

The search-and-selection phase usually lasts the longest and most clearly marks the move-to-lie-secluded. While it may begin imperceptibly, this phase becomes obvious when the fawn begins walking slowly and in a 'wandering' fashion with its head down at least some of the time. Upon stopping, a bed-searching fawn typically swings its lowered head slowly from side to side, apparently concentrating its attention upon the surface of the ground and perhaps the vegetative cover. A fawn may lie down on the first spot it examines closely in the course of a bed-search or it may examine a number of spots before going down. Movements suggesting 'indecision' sometimes prolong the action, and we have seen fawns take several minutes to search out and select a bed. The spot on which the fawn lies down may never have been laid upon before and will not be routinely used thereafter; the youngster makes no preparation other than by pawing—sometimes, and then only a few strokes—and/or turning partially or completely around on the spot before lying on it.

The route taken in the move-to-lie-secluded may be indirect; the distance which a fawn travels is, therefore, often greater than the actual distance from its mother at which it beds down. Both of these distances increase during the first few days after birth. Bromley (1967) found that a pair of neonates which he observed at close range 'tended to take longer trips from their mother' during their first few hours. A male fawn whose birth we watched made his first clearly distinguishable move-to-lie-secluded when he was 173 minutes old: he wandered about ten yards away from his dam, lay down, and remained recumbent 41 minutes, his longest rest period to that time. On the following day, when this fawn and his sister were 24 to 30 hours old, distances up to 30 yards were noted, and when the female fawn was 49 hours old, she searched for a bed at least 50 yards from the doe. The greatest such interval we have recorded for undisturbed animals was about 100 yards.

Commonly (perhaps typically) a pronghorn fawn begins its move-to-lie-secluded when the dam is standing still and sometimes by continuing on ahead of her when she ends a run. The doe appears to watch a bed-searching fawn, at least some of the time, and the fawn may look toward its mother a number of times. As soon as the fawn lies down, the dam may begin to feed, sometimes turning and feeding away from the bedded fawn or fawns, even trotting or cantering a short distance. She may stand for some time before feeding or moving off, or she may soon lie down. A doe that is apparently alerted or alarmed may hurry away before the fawn lies down. Infrequently we have seen does move to or near a fawn immediately after it goes down or investigate it closely several minutes later. A salient feature here is that, while the fawn moves to lie secluded, the mother generally remains in view of her young. She may be doing nothing more than showing attentiveness by virtue of which she memorizes the landmarks of the new bedding site. However, the pattern and timing of events often suggest that the doe actively elicits the move-to-lie-secluded. Stopping her forward progress (especially to end a cantering move), movements of the head, posture, scent, or vocalization are possible cues, but if any such signals are given they are so subtle or subdued that we have failed to detect them.

It is also conceivable that the mother's role in this interaction is passive in that she is simply the object away from which the fawn moves. That we see an abrupt reversal in fawn-doe response seems unquestionable: during much of a reunion period, a fawn approaches, follows, and walks or runs beside its mother, sometimes ahead of her, seeks a spot on which to bed, lies down, and does not follow her when she leaves the vicinity.

Whether or not the behavior of the mother is involved in eliciting the move-to-lie-secluded, the significance of this behavioral sequence, as regards our consideration here, is that the fawn *selects its own bedding site.* Bromley (1967) also noted fawns 'choosing their bedding areas', and Ingold (1969) emphasized that 'the fawns themselves invariably selected the precise spot on which they settled', Reporting his findings on four species of *Tragelaphus,* Walther (1964) says that the young, of its own accord, turns from the parent and finds a place where it lies down and remains while its mother moves further away; to this interaction Walther has given the name *Abliegen* (lying at a distance) and points out that, for those horned mammals in which *Abliegen* has been found, decisive participation by the mother has been only conditionally demonstrated. Referring particularly to *Tragelaphus,* he states that 'lying at a distance' is largely an active achievement of the young individual, especially after the first 24 hours following birth. Walther (1968) reports that a young gazelle also seeks out its resting place alone.

## MANAGEMENT IMPLICATIONS

Arising from these 'academic' findings and speculations are questions which may be relevant to management: What factors influence the pronghorn fawn's choice of a place in which to lie secluded? Do these young animals show attachment to or preference for 'the type of immediate environment first perceived' (Thorpe, 1963)? We know that the neonates of this species are socially imprinted on the mother within about two hours after birth. Do they also undergo habitat imprinting? Our findings suggest that, until they are about three weeks old, pronghorn fawns tend to seek seclusion in vegetative cover resembling that in which they were born. If so, what about birth sites? What kind of cover do parturient does select?

The characteristics of sites in which pronghorn does give birth show marked regional variations (Einarsen, 1948; Folker, 1956; Foree, 1960; Ingold, 1969), and even notable differences within our primary study area of approximately 27 square miles. However, our observations indicate that parturient does in the Upper Pahsimeroi valley tend to select birth sites where sagebrush (probably *Artemisia tridentata* in all instances) is roughtly 18-24 inches high: the sagebrush was of this depth at 12 of 17 birth sites observed, deeper than this (around 36 inches) at one site. At the other four sites, the vegetation was about six to ten inches high.

The stands of sagebrush of the intermediate depth are interspersed with the shallow cover on our area, occupy less land, and occur extensively as patches and strips along the edges of terraces and in swales and ravines where drifted snow increases the amount of available soil moisture. Of the 17 does whose behavior we have watched at their birth sites, five were seen deliberately moving into strips of sagebrush of the intermediate depth where they remained and shortly began showing symptoms of parturiency.

Of concern here is the destruction of sagebrush by spraying with herbicides. For example, in conjunction with introducing the rest-rotation system of grazing into the Upper Pahsimeroi valley, about 3000 acres of sagebrush have been sprayed within the last several months. I have been told by officials of the U.S. Forest Service that the objective is not to permit more cattle on the range but to secure better distribution of grazing. To the best of my knowledge, most of the sagebrush sprayed in this operation offered the kind of cover for which parturient pronghorn does show some preference.

I cannot make a clear and definitive case for the necessity of such fawning cover in the management of the pronghorn in any part of its range, but I think it is reasonable to ask this further question: What will be the relation between reduction of sagebrush where it provides preferred cover and the pronghorn's reproductive success in such areas? That relationship may be of particular importance if bed-searching fawns indeed seek the 'type of immediate environment' they perceive at the birth site. In this context, the fact that the move-to-lie-secluded is a relatively distinct and readily observed facet of habitat selection, and therefore apparently subject to experimental study, may be of special interest.

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**Paper No. 17**

# Courtship in the Pronghorn (*Antilocapra americana*)

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## ABSTRACT

Courtship behaviour in the pronghorn is described. Qualitative observations were made during five rutting seasons and quantitative data were gathered during three rutting seasons. Pronghorns were observed at the National Bison Range, Montana, and at Wind Cave National Park, South Dakota. The major findings and conclusions were as follows:

1. The territorial buck and the territory were the major features of the social organization during the rut. Territorial bucks performed 38 of 43 observed copulations.

2. The behaviour patterns and the typical sequence of activities leading to copulation are described. The buck uses visual, acoustic and probably olfactory signals to communicate with the doe.

3. Bouts of courtship varied in the number of behaviour patterns displayed and the performance of elements of behaviour patterns. The manner of termination of courtship bouts depended upon the readiness of the buck to court and upon the receptivity of the doe. Readiness of the doe was a function of her estrous condition and a function of the social status of the courting buck.

## INTRODUCTION

As the sole living antilocaprid, the pronghorn is a particularly interesting inhabitant of the prairies of North America. The literature of the pronghorn, however, is incomplete with regards to behaviour. The purpose of this paper is to describe courtship in the pronghorn. Our observations are compared, where possible, to those of other workers, including Buechner (1950), Cole and Wilkins (1958), Einarsen (1948), Gregg (1955) and Prenzlow *et al.* (1968).

Working independently, we observed courtship in the pronghorn at the National Bison Range (NBR) for five rutting seasons and at Wind Cave National Park (WCNP) for one season. Quantitative data used here was from 1969 and 1970 at NBR and from 1970 at WCNP. The animals were accustomed to and not afraid of people because of frequent tourist use and because there was no hunting on the study areas. We observed pronghorns with binoculars, spotting scopes and the unaided eye, from vehicles, on horseback, and on foot from distances as close as 5 m to as far away as approximately 2,500 m. Notes were recorded on tape, field notebooks, or on check sheets. Photographic equipment included 35 mm single lens reflex cameras, and super 8 mm and 16 mm movie cameras.

## SOCIAL ORGANIZATION

During the rutting season, the territorial system was well established, with mature bucks defending individual, spacially separate territories and with non-territorial

Fig. 1. Territorial buck with doe herd.

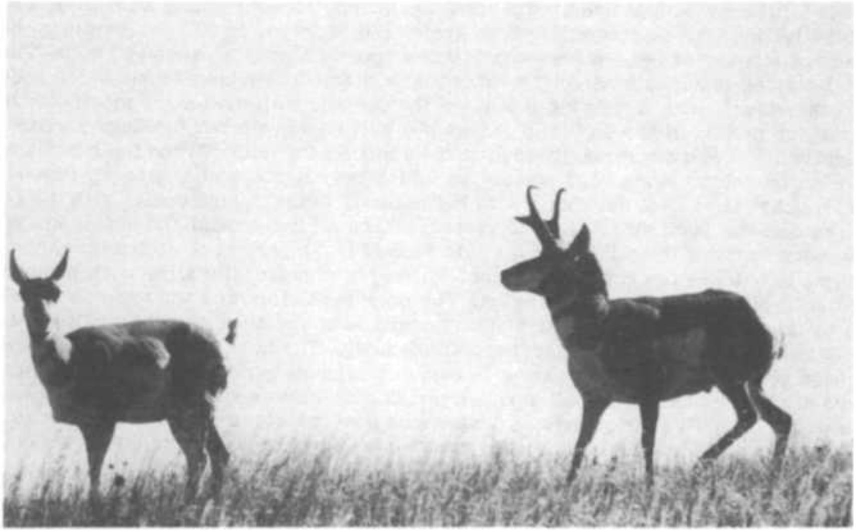

Fig. 2. Buck courting an estrous doe. Note the erect mane and median gland hair of the buck and the erect tail of the doe

bucks roaming the range in bachelor herds (Bromley, 1969). During the peak of rutting activity, the bachelor herds were smaller than in the summer, and does were occasionally separated from their young. As reported by Ingold (1969), does formed loose associations or doe herds, with the individual doe and her young being the most consistent unit.

Characteristic of territorial social structures of other ungulates (Buechner, 1961; Estes, 1967, 1969; Leuthold, 1966, 1970), the activity of the rut revolved around courtship of females and defense of territory by territorial bucks (TBs). The probability of breeding during the rut was related directly to the social status of the buck. Territorial bucks accounted for 694 of 1, 010 bouts of courtship and 38 of 43 copulations. Does which approached a territory were herded into the area by the TB and the buck actively attempted to retain the does on his territory. Often the buck would attempt to restrict does to a small, depressed area in his domain, such as a head of a draw or swale. In these situations the buck remained uphill and to the rear of the doe herd when not actively courting does or confronting rivals (Fig. 1).

## COURTSHIP BEHAVIOUR

The repertoire of courtship behaviour in the pronghorn from the initial sexual approach by the buck to copulation is a continuous and variable flow of activity which is not easily separated into phases or placed in a stereotyped, action-reaction context. To simplify description, the following is an account of a buck courting a doe with the normal fixed action patterns in the usual sequence.

### Courtship Behaviour Patterns.

The sexually aroused buck announces his intentions to the doe by emitting a high-pitched whine, which smoothly decreases in pitch and suddenly becomes a low, gutteral roar. Simultaneously, the buck's body becomes erect, with legs straightened, neck vertical, and top of nostrum horizontal. Also occurring during the whine is erection of the mane and hair of the median gland. If the doe is receptive she responds to the whine by raising her tail above the horizontal, exposing her swollen, pink and grey vulva (Fig. 2).

With his body erect, the buck walks with short, prancing steps toward the doe. When about 5 m from the doe and approaching her rump, the buck starts waving his head laterally, the nose moving through an arc of 180 degrees. In 233 observations the average number of head-waves was 3.9 per approach, with a range of 1 to 9. The head-waving is accompanied by a low volume, staccato, sucking sound, which occurs simultaneously with a chewing motion of the jaw and with the tongue moving in and out of the mouth. If the doe is in estrus she will stand with her hindlegs spread slightly apart and occasionally look at the approaching male. When the buck is within 1 m of the doe he stops head-waving, looks toward the doe, walks directly to her rump, and touches the top of her rump with his brisket. Maintaining contact with the rump of the doe, the buck slowly lifts his forequarters off the ground and moves his hindquarters forward by walking on his hind legs (Fig. 3). The buck slides forward until his penis touches the vulva of the doe. Moving his hindquarters, the buck prods the doe until his penis enters the vagina. The buck rocks forward and touches the withers of the doe with his muzzle. Copulation occurs when the buck rapidly straightens his back and jumps with his hind feet simultaneously. The hind feet of the buck leave the ground (Fig. 4). Does lost interest in bucks immediately after being bred and were bred only once. Gregg (1955) reported one doe which was bred twice in about one and one-half hours. We observed no conspicuous post-copulatory behaviour such as described for the Uganda kob (*Adenota kob thomasi*) by Buechner and Schloeth (1965).

Earlier descriptions of courtship in the pronghorn appeared in the works of Gregg (1955) and Prenzlow *et al.* (1968). These authors noted the head-wave and Gregg observed the erection of the median gland hair patch and the chewing motion of the jaw in the courtship routine of the buck.

In his courtship routine the buck utilizes at least two, and perhaps three, modes of communication to signal his sexual interest to the doe. Visual components of his

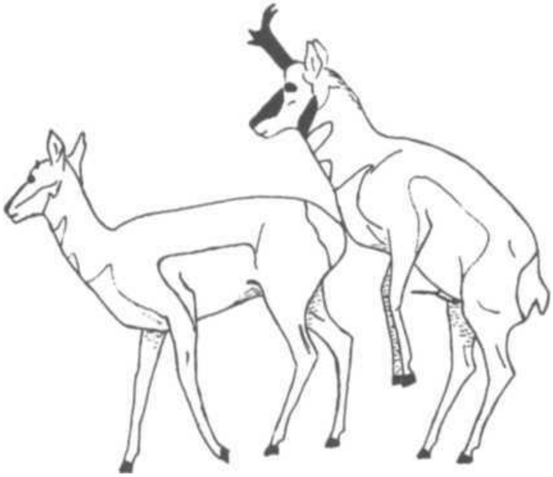

Fig. 3. Buck attempting to mount a doe. Drawn from 35 mm slide.

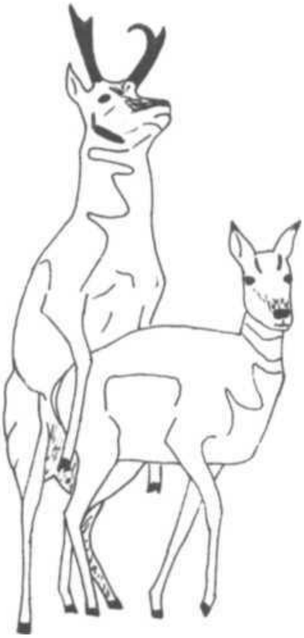

Fig. 4. Copulation. Drawn from 35 mm slide..

approach include the erect stance, rapid, prancing gait, erect patches of hair, and head-waving. The head-waving is a striking part of the display and probably draws the doe's attention to the patch of black hair on the neck and the cheek patch, and to the horns, a point also raised by Prenzlow *et al.* (1968). Also, by waving his head, the buck avoids staring directly at the doe, which eliminates an aggressive element. The raised tail of the doe in response to the whine may be a visual signal of receptivity by the doe to the buck, however this tail movement is certainly not always given and bucks performed the head-wave to does whose tails were not up. However, there is little doubt that the whine is a signal. The sucking sound made by the buck when he is close to the doe, is a second acoustic signal. The sucking sound may mimic the sound of a nursing fawn and function as an appeasement gesture.

Olfaction is possibly a third means of communication utilized by the buck. Concomitant with the whine is the erection of the median gland. Recently, Moy (1971) suggested that odor from the median gland could function in alarm and perhaps in sexual behaviour. The odor from the median gland of a buck which had just died at WCNP was strong and musky and different from the scent of the cheek patch or the rump glands. In bucks, this gland is erected during both alarm and courtship situations, which supports Moy's suggestion. Additional olfactory signals may come from the cheek patch, which overlies the subauricular gland, as suggested by Seton (1929) and Moy (1970). Only bucks have these and according to Moy (1970) the size and activity of the gland parallel the testis cycle. Muller-Schwarze and Muller-Schwarze (in press) observed that a burst of scent comes from the buck with each head-wave. In addition, does on 31 occasions sniffed the cheek patch (Fig. 5). At least four of these does were bred shortly after they investigated cheek patches. In all but two cases, bucks mounted does who investigated their cheek patches. In one observation a TB and an estrous doe were surrounded by 18 bachelor males when the doe rubbed the buck's cheek patch. Before the TB had been rubbed, he would only court the doe after one of the bachelor bucks attempted courtship, but 64.3 sec after the doe rubbed the cheek patch, the buck bred the doe.

A detailed and complete comparison of courtship behaviour in the pronghorn to courtship in the true antelopes will not be undertaken here. However, one similarity is apparent immediately. The raised head, erect body carriage, and prancing gait typical of the courtship of the buck pronghorn are also found in the male courtship repertoires of some true antelopes, including Uganda kob (Buechner and Schloeth, 1965) and topi (*Damaliscus korrigum; Walther,* personal communication). This common ground

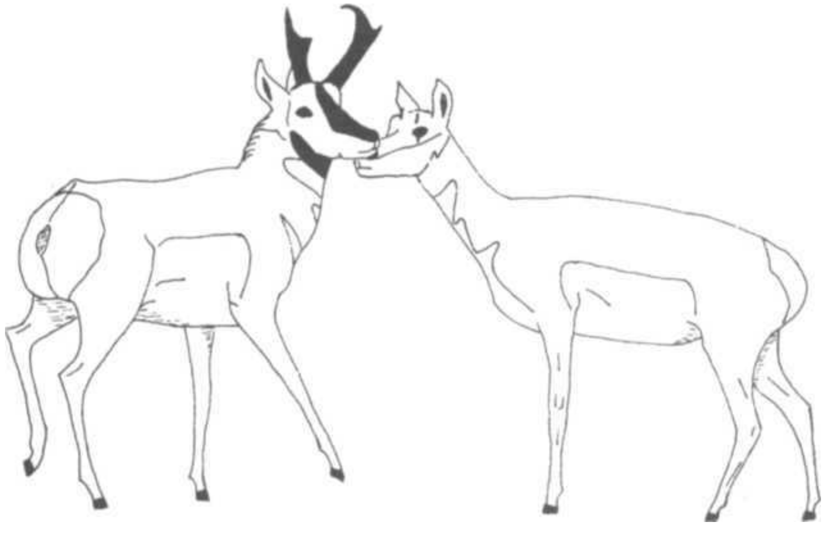

Fig. 5. A doe investigating the subauricular gland of a courting buck. Drawn from 35 mm slide.

between two distantly related lines of artiodactyles (Romer, 1966), suggests convergent evolution. The elements of the prancing approach are quite opposite from the slow gait, crouched body posture, and lowered head of a male about to deliver a blow with his horns. The threatening male appears ready to attack without radical change in body position. This is an application of the principle of antithesis proposed in 1872 by Darwin (1965) and applied to the rutting behaviour of the mountain goat (*Oreamnos americanus*) by Geist (1965).

The buck performed flehmen in response to odors from female urine, as do other male ungulates. In the pronghorn, flehmen is not directly connected with courtship nor is it restricted to territorial males. When a buck performs flehmen, he investigates, with his nose, female urine which has fallen to the ground, draws back his upper and lower lips, raises his head and slowly swings it laterally, and licks his nose. Flehmen is followed immediately by pawing the urine-soaked ground with the front hooves, sniffing the ground, and urination and defecation on that spot, as described by Gregg (1955). Male Thomson's and Grant's gazelles perform urination and defecation in linked, sequential manner too (Estes, 1967;Walther, 1964, 1968). We concur with Walther who felt that the conspicuous performance of elimination by the territorial buck advertises his presence. We suggest that this is another example of convergent evolution between these two lines of medium-sized, plains ungulates.

In contrast to the behaviour of male gazelles and Waterbuck (*Kobus defassa*; Spinage, 1969), buck pronghorns did not commence active courting immediately after investigating urine from estrous females. However, bucks did seem to perform flehmen and linked urination and defecation more fully after smelling urine from estrous or near-estrous does.

### Variability of Courtship Bouts

Variability on courtship is illustrated by 14 bouts of courting by one buck a single doe on the same day. He performed the whine 10 times and head-waved only 3 times. In addition to variability in completeness, the behavioural elements of courtship were not always performed uniformly. The whine and roar varied in duration, volume and pitch. After what sounded like a normal whine, one buck roared more loudly than usual and then lunged toward the doe. Another element subject to change was the head-wave. In 31 observations, courting bucks held their heads with the sides of their faces toward the does and waving was omitted completely.

The complex nature of courtship in the pronghorn is further illustrated by the manner of termination of bouts. In 1010 records of courtship, 43 resulted in copulation, 22 ended when the buck apparently lost interest, 26 ended when the courting buck left the doe to drive off other males, and in the remaining 919 cases the doe stopped courting activity by moving away from the buck. The way does avoided courting bucks probably reflected variations in estrous condition, past experience and variations in the social status and maturity of the courting bucks.

Only does with swollen vulvas were mounted by bucks. Even does in the peak of estrous usually moved away from courting bucks. Eleven does were observed continuously for an average time of 74. 8 min before they were bred. These does were courted 222 times during this period; in 109 bouts the does moved off before the bucks got within 1 m; in 10 bouts the bucks touched the rumps of the does with their briskets before the does moved away; in 18 bouts the bucks started to slide up onto the rumps of the does before the does moved away; in 84 bouts the bucks fully mounted the does; and in 11 of the full mounts the copulatory thrust was observed. Does which were not in estrus would usually start moving when the buck began prancing or before.

In spite of considerable variability, a general pattern of avoidance behaviour in does can be described. The retreating doe lowered her head to near the vegetation and twisted her neck at the same time. These movements were often accompanied by a flip of the tail, a lowering of the rump and/or a slight lowering of the whole body. In addition to this behaviour, does utilized barriers such as clumps of shrubs and trees to separate themselves from courting bucks.

The similarity between the avoidance behaviour of the female pronghorn to that described for the doe blacktail deer (*Odocoileus hemionus columbiana;* Geist, 1966) and for the cow elk (*Cervus elaphus;* Geist, 1966; Struhsaker, 1967; McCullough, 1969) suggests convergent evolution of this behaviour. This similarity may be due to the need for an unambiguous signal for non-receptivity. The lowered head, twisting of the neck, lowered body and movement away from the courting male are in sharp contrast to the raised head and stationary body displayed by the receptive female in response to courtship.

Even though a generalized avoidance behaviour in the doe pronghorn can be recogrnized,the performance of the behaviour was highly variable. Of 483 observations of avoidance behaviour, does walked away from bucks in 235 bouts, ran in 174 bouts, and jumped away followed by walking or running in 74 bouts. Dipping and twisting of the head and lowering of the rump and/or body occurred along with walking away in at least 123 cases and with running away in at least 70 cases. In 667 observations of the behaviour of bucks after does exhibited avoidance behaviours, bucks ceased interacting in 60. 5 percent, initiated a second sexual approach immediately after the doe stopped moving in 25. 5 percent, and chased does in 14 percent. Closer inspection of the data shows that the more complete the avoidance behaviour of the doe, the more likely courtship would stop. In 76.3 percent of 192 records of full avoidance behaviour, including twisting the neck, bucks terminated courtship, whereas in only 21 percent of 235 observations of the doe simply walking away from the buck, did the buck stop courting.

Bucks chased does through complex series of loops and curves. Similar descriptions of the buck-doe chase are found in Buechner (1950), Einarsen (1948) and Prenzlow *et al.* (1968). We observed that the behaviour of the chasing buck frequently included the aggressive elements of lowered ears and neck; deep, guttural roar, and hooking with the horns. The doe ran away from the buck until the buck reached a position parallel to her, at which point she veered away from the buck. When the buck was parallel to or slightly ahead of the doe he often lowered his head and neck and moved his horns toward her. On two occasions bucks knocked does down during chases. Chases were often complicated by the addition of other males. We have seen up to nine bucks chasing one doe. The chase lasted a few seconds to as long as 15 min and usually ended when the doe stopped running. Distances covered by the chased doe may exceed 5, 000 m.

Does responded differently to courtship from the different classes of bucks. We have already noted that TBs accounted for 68. 6 percent of all observed sexual approaches and 88. 4 percent of recorded copulations. Table 1 also documents the relative success of TBs. Does consistently ran from groups of courting bucks, which were usually composed of non-territorial bucks. In 147 of 174 chases by non-territorial yearling and adult bucks, there were two or more bucks trying to court the female. TBs were also harassed by groups of courting males and in 61.1 percent of 22 chases that resulted from sexual approaches by TBs there were three to nine other males attempting to court the doe.

TABLE 1. RESULTS OF COURTSHIP BY THREE CLASSES OF BUCKS AT NBR

| Class of buck | Results of courtship in per cent | | | Total bouts |
|---|---|---|---|---|
| | Chase | Doe moved away | Full or partial mount | |
| Territorial | 7 | 45 | 48 | 469 |
| Non-territorial adult | 57 | 24.2 | 18.8 | 149 |
| Yearling | 36.8 | 50.7 | 12.5 | 122 |

In comparison to courting TBs, non-territorial bucks courted does more rapidly and appeared more persistent than TBs. Does confronted by non-territorial bucks often ran from them and were chased (Table 1). These chases tended to attract other bachelor males and were the longest chases we observed. The harassment by non-territorial bucks undoubtedly contributed to the high breeding success of TBs. When does which were being chased entered territories, the territorial bucks ran to the chasing animals and challenged the harassing bucks, allowing the does to stop running. That the territory is often a sanctuary from the over-zealous courtship of non-territorial bucks was also noted by Cole and Wilkens (1958).

Orians (1969) has theorized that in polygamous societies of mammals and birds, the female should select her mate. Since parental care from the male does not occur in ungulates, polygamous societies can exist where each male potentially can breed many females but where each female is bred only once per reproductive cycle. Females may choose between many possible mates and, according to Orians, should secure the best possible genes for their future offspring. The breeding system of the pronghorn is polygamous, and does should select their mates. Even though TBs performed a disproportionate share of the breeding, it cannot be concluded from our observations that mate selection did occur. Two factors cloud the issue. First, does could remain on the territories because of harrassment by groups of courting bachelor males. Secondly, unpublished data from WCNP indicate that forage may better on territories than outside of them, which raises the possibility that does could spend a disproportionate amount of their time on territories for nutritional reasons alone. While these considerations do obscure the truth, we believe that Orian's hypothesis is viable and that it should be tested under experimental conditions.

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**Paper No 18**

# Agonistic Behavior of Territorial Pronghorn Bucks

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## ABSTRACT

Territorial behavior of pronghorn (*Antilocapra americana* Ord) bucks was observed independently for six summers, five rutting seasons, and one full winter and spring at the National Bison Range, Moiese, Montana, and Wind Cave National Park, Hot Springs, South Dakota. Pronghorn bucks were territorial from late March until early October and during this time they drove other males from their territories. Five basic phases were involved in territorial encounters: (1) stare at intruder, (2) vocal display of the territorial buck's presence with a snort-wheeze call, (3) approach intruder, (4) interact with intruder, and (5) chase or withdrawal of intruder from the area. Phases may be omitted from an encounter or the encounter may terminate at any point. Occasionally snort-wheeze vocalizations were sufficient to drive an intruder from the territory, particularly yearlings. The call seems to function as a display of activated male dominance and not territorial advertisement *per se*. A territorial buck's rate of approach (walk or run) was dictated by the age and social position of the intruding male and how deeply the interloper had penetrated the area. Behavior during an approach was highly variable and again depended on the aforementioned factors. Interaction phases were variable and no two were alike, but a general pattern of feed-thrash-mark-walk-threaten was noted in some encounters. Some of the variability seemed to be due to the same factors that regulated the territorial male's rate of approach. Chases were the most frequent manner in which territorial encounters ended. Eleven chases crossed territorial boundaries and resulted in dominance reversals. Chases were more frequent in encounters with bucks low in the social hierarchy than with those in higher positions. Serious fights were rare in the pronghorn, but did occur at times. Fighting behavior and skin defenses in the pronghorn are described, and it is noted that they fit the predictions of Geist's (1966) theory based on the horn morphology of the pronghorn. Some comparisons are made between the territorial systems of the true antelopes in the family Bovidae and that of the pronghorn.

## INTRODUCTION

The pronghorn is unique among North American large mammals in the extent to which prominent markings are localized on the head and neck, and in the casting of the horn sheaths. Its taxonomic position as the only extant member of a family (Antilocapridae), which was highly diverse during the Miocene and Pliocene of North America and is of uncertain origin (Simpson, 1945:157), makes this medium-sized ungulate (males 41. 5 kg to 73. 5 kg, females 41. 2 kg to 52. 7 kg; Mitchell, 1971) an interesting part of the region's prairie fauna. Our goal in this paper is to describe the agonistic and related behaviors that are used to defend a territory. When feasible, our observations will be compared to those other workers have made of both the pronghorn and the true antelopes of the family Bovidae.

Field work was carried out independently at the National Bison Range (NBR), Moiese,

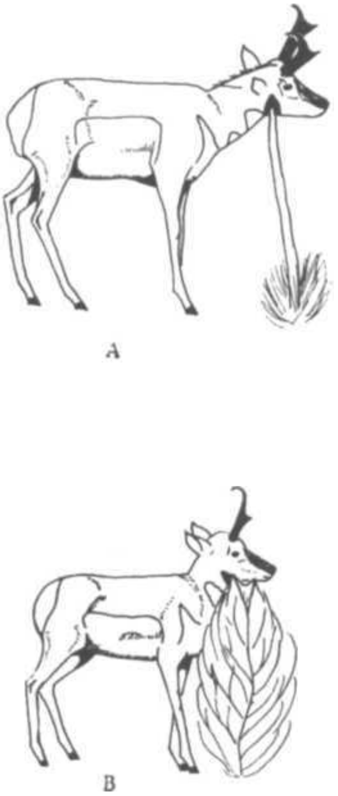

Fig. 1 Two bucks scratching their cheek patches (subauricular gland) on vegetation (note the parallel position of the display), 15 m inside buck A's territory (drawn from a 35 mm slide).

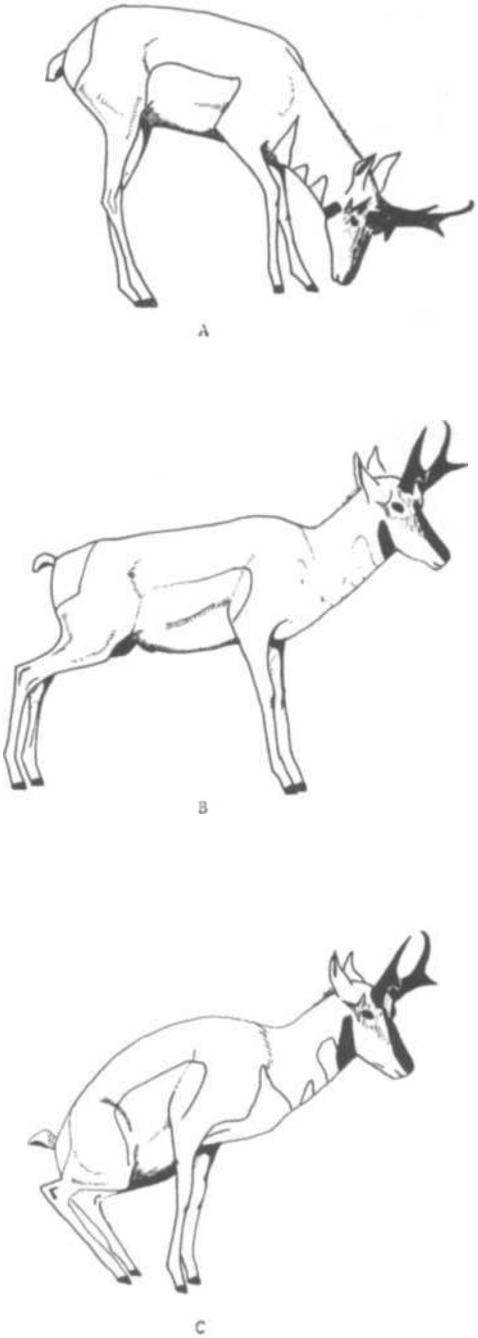

Fig. 2 A territorial buck going through the linked urination-defecation sequence (SPUD): (A) sniff and paw ground, (B) stretch and urinate, (C) squat and defecate.

Montana and at Wind Cave National Park (WNCP), Hot Springs, South Dakota. Territorial behavior was observed for six summers, five rutting seasons, and one full winter and spring. Animals were observed with binoculars, spotting scopes, and the unaided eye from vehicles, on foot, and on horseback. Observational distances varied from 5-10 m up to about 2. 5 km. Notes were recorded on tape, field notebooks, or check sheets. Behavior was recorded with 35 mm single lens reflex cameras and with 16 mm or super 8 mm movie cameras.

## TERRITORIALITY

Mature pronghorn bucks hold territories from early spring (March-April) until late fall (October), after which they join with does, fawns, non-territorial bucks and other territorial bucks (TB), to form large winter herds. Unlike the small territories of the Uganda kob (*Adenota kob thomasi;* Buechner, 1961), the territories of the pronghorn provide the TB, and any does that may be with him, sufficient forage. Although distinct boundaries between territories were not always evident, the bucks consistently defended their area against intrusions by other males. Territories were marked by scent and visual presence of the TB, as earlier speculated by Bromley (1969).

Tall vegetation was marked by secretions from the subauricular gland or cheek patch. Moy (1970) described this gland and found its size and activity is probably related to testis size and activity. The use of the gland to mark vegetation on the territory may be analogous to the marking of vegetation with the preorbital gland by certain gazelles (Walther, 1964, 1968; and Estes, 1967) and the marking of the ground with the pre-orbital gland by the wildebeest (*Connochaetes laurinus; Fstes,* 1969). Cheek patch marking (scratch cheek patch = SCP) follows a basic pattern of: sniff vegetation, mouth it or nip off end of stem, and then rub the gland up and down the plant stem (Fig. 1). Bucks sometimes re-marked the same plants, but did not seem to use this behavior to delineate a consistent boundary.

Elimination of urine and feces was accomplished with a linked sniff-paw ground-urinate-defecate sequence (SPUD), which was noted by Gregg (1955). The postural changes are extreme (Fig. 2) and are similar to those described for Grant's and Thomson's gazelles (*Gazella granti, G. thomsoni; Walther,* 1964, 1965; and Estes, 1967). Each element of the series is performed in exaggerated form by the TBs, in

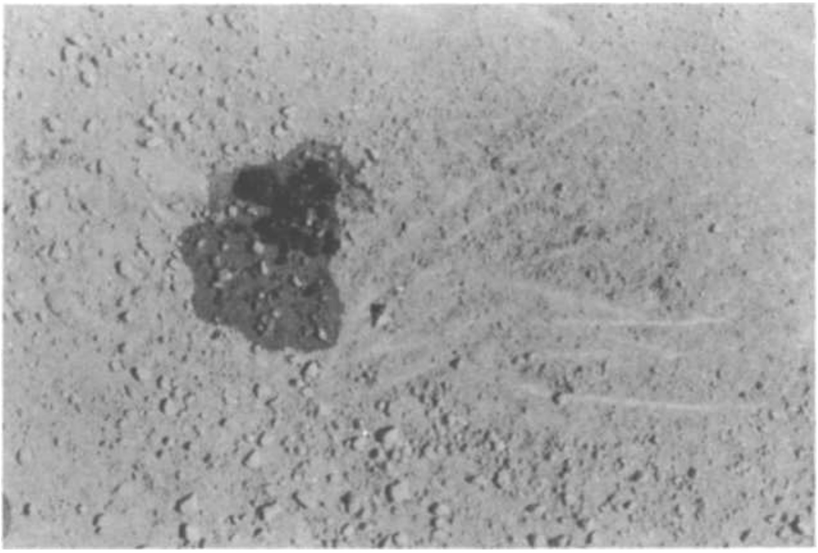

Fig. 3 A typical buck scrape showing the position of the feces and urine and their relationship to the paw marks.

contrast to the often incomplete performance by yearlings and two-year-old bucks of the bachelor herds. Pronghorns have large sack-like interdigital glands (Moy, 1971) and so the pawing before urination-defecation may serve to deposit this scent on the area marked (Figure 3). This form of marking did not seem to indicate a precise boundary, but scrapes were re-marked on several occasions.

Overt territorial defense lasted from about mid-March until early October, and during this period 93. 4% of TB's agonistic encounters with other males occurred on or within his territorial boundaries. Thus, agonistic behavior of pronghorn bucks is best viewed against the framework of territoriality.

A TB's defense of his area was variable and many behavioral acts might be used during an encounter (see Table 4). Estes (1969) noted that no two territorial defenses were the same in the wildebeest, and this observation is also true for the pronghorn. Because of this it has not been possible, so far, to establish a stereotyped action-reaction type of frequence, but most encounters consisted of part or all of five basic phases: (1) stare at intruder, (2) vocal display of the TB's presence, (3) approach intruder, (4) interact with intruder, and (5) chase or withdrawal of intruder. Any phase may be skipped or an encounter may be terminated at any phase. This general description agrees with the progression of aggressive displays used in territorial defense noted for the pronghorn by Bromley (1969).

All medium-sized animals, regardless of species, were watched closely as they entered a territory. A TB would stare for as little as 10 second to over 25 minutes ($\overline{X}$ = 1. 75 minutes) before he reacted to the presence of the other animal. If it was a pronghorn, the TB might display his presence on the area vocally with a snort-wheeze call (this is the 'laugh' reported by Gregg, 1955). The vocalization starts with a loud, medium-pitched snort, which is followed by a series of shorter bursts of sound that descend in pitch and volume until the call is terminated. As he calls, the TB pumps his sides and probably his diaphragm. The later bursts have a wheeze-like quality and are not as clearly differentiated from each other as the first and second bursts. The initial snort was held longer (1-2 seconds, $\overline{X}$ = 1. 2 seconds) than subsequent ones (1-1.3 seconds, $\overline{X}$ = 0. 8 second), but each buck varied the pattern, rate, and descent of pitch and volume in such a way that a human observer could identify individual bucks by this call. No proper analysis of the call was made with sonograms, but analysis would probably reveal differences not detected by us. In 83. 5% of the observations the snort-wheeze was associated with erection of the median gland (see Moy, 1971 for description of this gland), mane and upper $^1/_3$ of the rump patch (Figure 4).

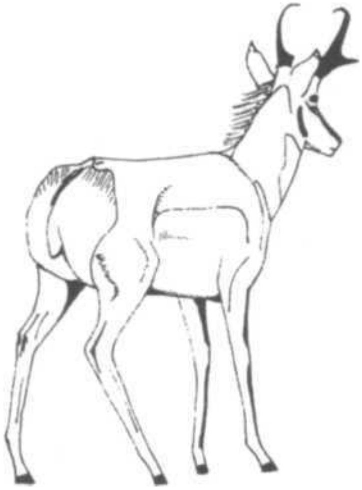

Fig. 4 Stance of a buck during the snort-wheeze call: mane, median gland, and upper $^1/_3$ of rump patch erect.

In 70 of 288 encounters the intruding buck left the territory after only the snort-wheeze call. Yearlings showed a greater tendency to flee as a result of the call than older age classes. (Table 1). There was also a difference in the response based on the time of year. From April 16 through September 6, bucks fled in 31 of 69 encounters (45%), while during the rut they fled in only 39 of 169 cases (25. 5%), significant at the 95% level ($X^2$ = 8. 44). Similarly all but 2 of the yearling encounters in which they did not flee from the call were during the rut.

TABLE 1. RESPONSE TO THE SNORT-WHEEZE CALL BY AGE CLASS OF BUCK.

| Age | No. times received call | Reaction of Buck | |
|---|---|---|---|
| | | Ran off | Remained |
| yearlings | | 31* | 24 |
| 2- and 3-year olds | 26 | 14 | 12 |
| greater than 4 years old | 131 | 22* | 109 |
| mixed groups (3-38 bachelor males) | 16 | 3 | 13 |
| Total | 228 | 70 | 158 |

* Difference significant at 99% level, $X^2$ = 12. 39.

The snort-wheeze does not seem to be related solely to territorial behavior in the pronghorn. We have heard the call preceding and during courtship on numerous occasions, while bucks were herding does on their territories, and we have also heard bachelors use the call (always by the dominant male) during seven hierarchical disputes. It therefore does not seem to function as territorial advertisement *per se,* as noted for the 'whistle' of the Uganda kob (Leuthold, 1966) and for the grunting of territorial wildebeests (Estes, 1969). Rather it is more like the roaring display of the impala (*Aepyceros melampus*), which functions as an 'expression of activated male dominance' (Schenkel, 1966 and Leuthold, 1970). It may also be similar to the bugle of bull elk (*Cervus elaphus*), from the descriptions of its use in Struhsaker (1967) and in McCullough (1969). The interpretation of the snort-wheeze as a display of dominance and not territorial advertisement is further supported by a review of the encounters in which the vocalization occurred. TB's used the call 469 times in response to a specific intrusion by another pronghorn on their territory and only 59 times without intrusion. The call was not frequent ($\bar{X}$ = 0. 34 per hour of observation) and at the NBR it never exceeded 7. 2 calls per hour of observation, even during the rut. These numbers are for all bucks within hearing range on any given day and are not solely those of a single territorial male.

Males that did not leave the territory in response to the snort-wheeze were approached. The rate of approach depended on at least two factors: (1) the distance of intrusion into the area, and (2) the age of the intruder. Intruding bucks that were half-way or more (75-180 m, depending on territory size) to the center of the area, before being discovered, elicited a rapid approach by the TB, and they did so more often (83. 5%) than did bucks near the boundary (38. 8%). Yearlings were approached at a lope or run more frequently (82. 3%, Table 2) than other age classes (45. 9%), significant at 99% level (t = 21. 1). This is noted especially when the boundary data for yearlings are compared to similar data for older males (Table 2). Rapid approaches usually led to running chases and the intruders were driven from the area. Chases and other types of interactions will be dealt with later.

Pronghorns near (30-75 m usually) the limit of the territory were approached more cautiously (Table 2). In some cases the TB loped or trotted at first, but when he was 40-80 m ($\bar{X}$ = 68 m) away he slowed to a walk. As he slowed down he lowered his head to the level of the withers, and depressed his ears (Fig. 5). When he was 15-25 m from the intruding buck his walk became a slow, stiff, deliberate gait until he was standing broadside to him. This broadside threat display is similar to the threat display noted by Prenzlow *et al.* (1969). In 75. 6% of the encounters the display was

TABLE 2. RATES OF APPROACH AND THEIR OUTCOME BASED ON DISTANCE INTRUDING MALE WAS WITHIN THE TERRITORIAL BOUNDARY

| Intruder ½ way or more to center of territory | | | | | | | Intruder near boundary | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age | Year Buck | Chase | >Year Buck | Chase | TB | Chase | Year Buck | Chase | >Year Buck | Chase | TB | Chase |
| Fast Approach | 56 | 55 | 110 | 107 | 16 | 15 | 109 | 99 | 20 | 16 | 1 | 1 |
| Slow Approach | 0 | 0 | 22 | 18 | 14 | 11 | 36 | 15 | 96 | 40 | 20 | 2 |
| No Approach | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 2 | 3 | 0 |
| Total | 56 | 55 | 132 | 125 | 30 | 26 | 145 | 114 | 134 | 58 | 24 | 3 |

broadside, but the orientation varied up to 45° and in one case it was frontal. If both bucks displayed, it was usually paralled (84%, 35 of 43 encounters), but various different angles from this position were observed, though they never exceeded 45° from the parallel axis. In all cases the median gland was at least partially erect on both bucks.

Partial erection of the mane and upper $^1/_3$ of the rump patch, and a slight raising of the ears was noted in some encounters (Fig. 6). There is some indication that only bucks which were losing their confidence showed these deviations from the normal display in which the ears are fully depressed, and rump patch and mane compressed. The parallel display may lead to parallel walking in the head-low posture (Fig. 5)

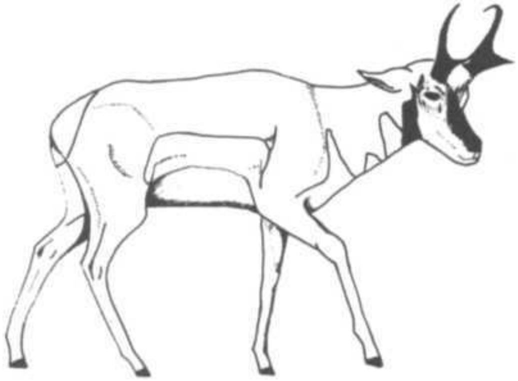

Fig. 5 This demonstrates the head-low, ears-back walking position which is used during a slow approach. Note the mane and rump patch are compressed. The same position of head, ears, and general body conformation is maintained in the standing broadside threat display.

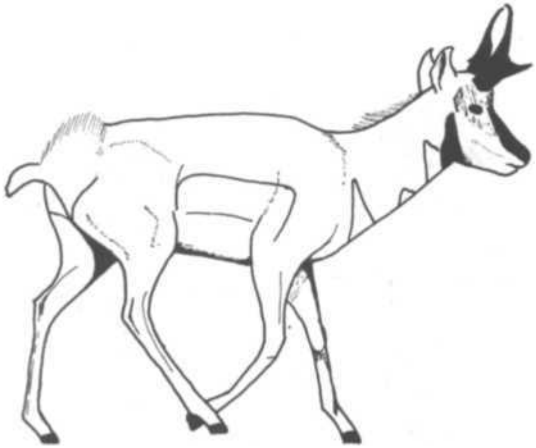

Fig. 6 This buck has lost his confidence in an encounter with the buck in Fig. 5. Note the tail is raised, upper part of the rump patch and mane are partially erect, and the ears have moved to a neutral position.

(23 encounters) or a closer approach (9 encounters) by the TB. In these 32 encounters the intruding buck gave ground to the TB and, as he did, a slight erection of the mane and rump patch and lifting of the ears was noted. In 29 cases a chase ensued 5-64 second ($\overline{X}$ = 23.4 seconds) after the intruder gave ground and showed piloerection or raised ears. The other three encounters were between territorial neighbors near the boundary, and as the buck entered his own area again his ears were depressed fully and mane and rump patch compressed.

In about 43% of the slow approaches the TB did not walk directly to the intruder, but engaged in several types of behaviour on his way. As a TB moved toward the other male he often marked (both SCP and SPUD) or thrashed vegetation with his horns. At times he would stop and feed, either with or without actually ingesting plant material, and occasionally he gave the snort-wheeze call. In one case it was given six times during this phase. Intruders were often active during this time and would go through marking, thrashing or feeding activity. This was especially true of territorial neighbors who always engaged in some type of behavior while being approached. A survey of 100 slow approaches by TBs indicated that yearlings were more apt to simply watch the TB as he approached (22 of 36 cases) than older age classes, which watched in only 24 of 64 cases. So far no specific sequence of acts has been noted other than a general feed-mark-thrash-walk pattern. Table 2 shows that slow approaches were elicited more often by older bucks near the territorial boundary than by yearlings near the boundary.

An interesting variation of the TB's slow approach is the cheek patch display, which develops from the head-low, ears-back approach. As the slow stiff walk begins the TB raises his head above the level of his withers, tilts his muzzle up, and slowly rotates his head to the side, ears depressed. He may hold his head rigid or rotate it slowly through a 180° arc, and in this attitude display the cheek patch and offer a broadside view of the horns (Fig. 7). There is a general erection of the neck hair, but not of the mane. The mane may be partially erect, but in 36 of 40 encounters it was not. The TB continues his approach until he is 1 to 10 m from the intruder

Fig. 7 As the territorial buck approached the intruding yearling buck, he gave the cheek patch display. Note the head is raised above the level of the withers and is rotated to the left. In this case the muzzle was not fully elevated.

and then stands in a rigid cheek patch display. The most frequent orientation was frontal (23 of 40 cases), but the display may assume any orientation (i.e. broadside, rear, or at an angle).

We feel the use of the cheek patch display indicates a high level of confidence in the TB, or any buck, using it. Two lines of evidence seem to support this interpretation. First, in the large bachelor herd on the NBR (36-47 head) there were many individually known animals (by ear tags, horn form, color patterns), whose hierarchical position was known. In 131 of 132 encounters in which the cheek patch display was used by a bachelor male, it was directed at a buck at least two or three steps below him in the hierarchy. On only one occasion was it oriented toward a male higher in the hierarchy than the displaying animal (see fight behavior section). Secondly, although TBs used the display rarely (33 of 564 encounters, at the NBR), only 6 were near the boundary. At the NBR it was directed primarily at yearlings and two-year-olds, rarely at a larger male (three times).

Teeth grinding, along with the snort-wheeze, was the only other vocalization noted during the approach phase. As the TB approached, he ground his teeth, and this could be heard by an observer up to about 10 m. It was associated with 175 of the 290 territorial encounters where the observer was close enough to hear the sound. A buck might continue to grind his teeth during the standing broadside or parallel walking displays, but it was not heard during the cheek patch display. Teeth grinding during agonistic encounters has been reported in the tule elk (*Cervus elaphus nannodes;* McCullough, 1969).

When the snort-wheeze or approach did not drive the intruder from the area an interaction phase began. There was a steady flow of activity, and many acts were used and reused so that a general pattern of feed-thrash-mark-walk-threaten was apparent, but this was not a rigid sequence. It must be noted that the bucks may have been interacting to varying degrees during the approach, but at this point we refer to close range activity where it was clear that the bucks were aware of and responding to each other.

As a territorial buck approached to within 15-25 m of the intruder he reacted to any type of behavior the other male was displaying. If the intruder was marking, thrashing, etc., then the TB usually responded with the same act. After responding he approached more closely (10-20 m), as noted earlier, and gave either a broadside threat or a cheek patch display. At this point, if the intruder had not fled, the TB began to initiate more acts and the intruding buck generally responded with the same act. Once the TB started to initiate the acts, he pushed the encounter by moving closer. Acts were usually (52 of 71 encounters) carried out in a parallel position (Figs. 1 and 8), but all orientations were observed. TBs initiated 553 of 913 acts (61%) during these encounters.

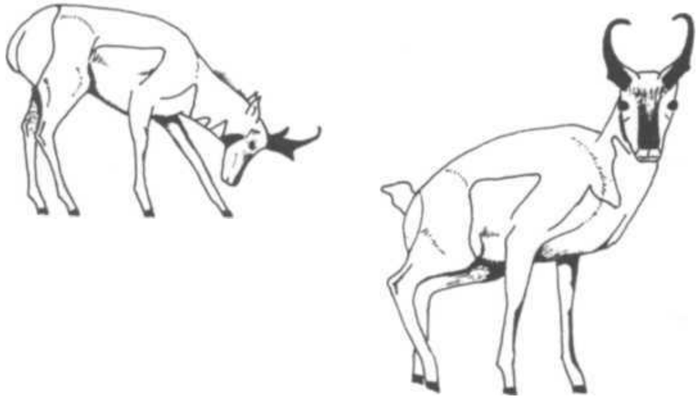

Fig. 8 These two bucks went through the SPUD sequence in parallel. In this encounter the territorial buck responded to the initiative of his territorial neighbor, who invaded his area.

In most of the interactions (50 of 71) a point was reached where the other buck no longer responded to the TBs initiative and simply watched. This usually led (47 of 50) to a strong threat (broadside 25, cheek patch 4, head-low, ears-back approach 18) by the TB; in 32 encounters the intruder was herded from the territory at a walk, and in 18 encounters he was chased off at a run. 21 of 71 interactions did not follow the above termination pattern and they are listed in Table 3.

TABLE 3 OUTCOME OF THOSE INTERACTIONS THAT DID NOT FOLLOW THE USUAL TERMINATION PATTERN FOR TERRITORIAL ENCOUNTERS WITH AN INTERACTION PHASE.

| Bucks' Activity | Number | Ended in Chase | Intruder walked off or herded from territory | Intruder ran off |
|---|---|---|---|---|
| Fight | 12 | 4 | 6 | 2 |
| Both thrash | 2 | 1 | 1 | 0 |
| Both SCP | 2 | 2 | 0 | 0 |
| TB snort-wheeze | 2 | 1 | 1 | 0 |
| Both SPUD | 2 | 1 | 1 | 0 |
| Touch horns | 1 | 0 | 0 | 1 |
| Total | 21 | 9 | 9 | 3 |

Fig. 9 This is a territorial buck during a running chase. Note: (1) median gland is erect, (2) mane is fully erect, and (3) ears are almost fully depressed.

Most (385 out of 564*) territorial encounters ended in a chase in which the intruder was driven from the area at a run (Fig. 9). In 15 cases the opponent ran off without a chase, in 121 encounters he was herded from the area at a walk, and 12 interactions ended in other ways. During the chase a TB might utter a low guttural roar (36 times), generally given when the TB was 3-5 m behind the intruder, but in 9 cases it preceded the chase. In 24 encounters the roar preceded an attempt by the TB to hook the fleeing male with his horns. While in pursuit the TB depressed his ears, erected his mane, median gland, and on 13 occasions the ugper $^1/_3$ of his rump patch (Fig. 9).

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* Thirty-nine of the 564 encounters are excluded from the tally due to possible human interference.

Chases ranged from 15 to 20 m up to about 5 km ($\overline{X}$ = 520 m) and lasted from a few seconds to about 10 minutes ($\overline{X}$ = 43 seconds).

When a TB reached his territorial boundary the chase was terminated 93. 2% of the time. In 27 encounters the intruder was pursued beyond the territory, and in 11 cases, when territorial neighbors were chased, dominance reversal occurred as the boundary was crossed. In all the latter cases the boundary was crossed several times in both directions before both TBs stood and displayed at each other. The first display used after the reversals was always the broadside threat followed by markings with the linked urination- defecation act or the cheek patch gland

Occasionally approaches and displays were not sufficient to eject the intruder from a territory, and serious fights ensued. Combat was rare and of 1877 buck-buck interactions observed at the NBR only 10 involved fighting. Five additional fights were seen at WCNP. Of the total 15 fights noted, 14 occured during the rut. Conditions which caused these fights were variable: five involved boundary disputes between TBs, with no females present; six involved TBs near a boundary, but with estrous females present (Fig. 10); two involved disputes over estruous females not on a territory (one between yearlings and one between a TB and a large non-territorial male); and two involved non-territorial males for the apparent purpose of settling their relative dominance (one between yearlings, and one between older non-territorial males).

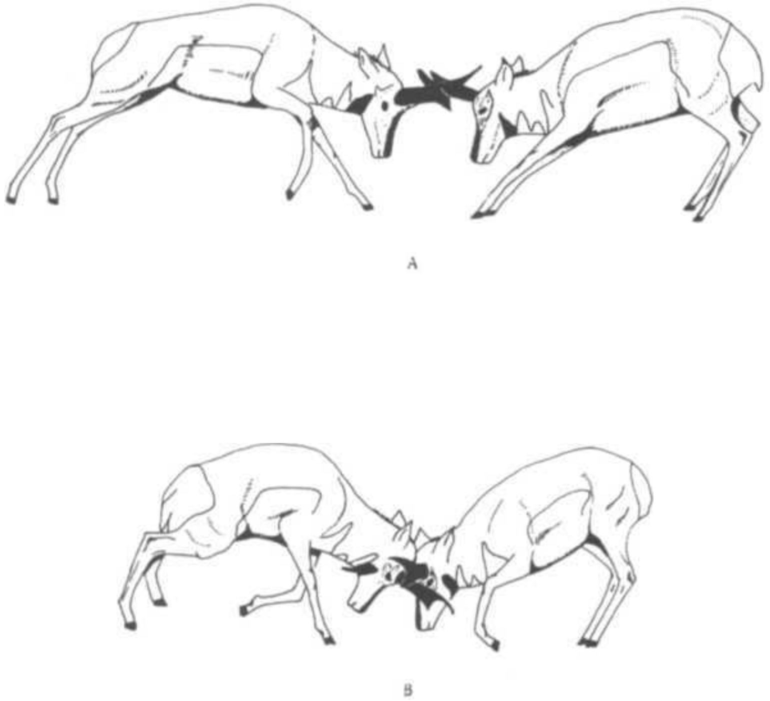

Fig. 10 These two territorial neighbors fought near their boundary and in the presence of an estrous doe. In A, the initial clash is shown and the prongs made good contact, fighting horn to horn, but in B the prongs did not meet and the bucks are fighting head to head.

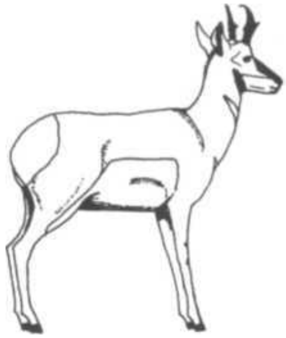

Fig. 11 This shows the submissive posture of the pronghorn. Note this yearling buck's head is up, ears are in a neutral position, and his body is in a hunched position (compare Fig. 5).

The eleven fights between TBs occured near territorial boundaries. Three fights ended with the TB defeating the intruder and one fight was lost to the intruder. Losers were chased from the territory in three fights and in one both bucks walked away from each other after one buck assumed a submissive posture (Fig. 11). Seven ended in draws when both bucks suddenly raised their heads and walked off simultaneously (five fights) or when one of the two ran after an estrous female which had moved away during the fight (two fights). As the TBs walked off after their encounters, they marked with their cheek patches and thrashed vegetation until they were 25-40 m apart. At 25-30 m, at the NBR, they either uttered only the snort-wheeze (three bucks) or marked with urine and feces and snort-wheezed (seven bucks). The call-mark sequence may indicate the retreat position or holdings of a buck in the same manner as noted in fighting gazelles (Walther, 1968).

All fights were preceded by a slow approach with head-low, ears-back, and mane and rump patch compressed. At 0. 5 to 1. 5 m all stood head on, and stared at each other for up to 6 seconds. Contact was usually made in one of two ways: in nine fights the bucks suddenly clashed together with no apparent intention movements; and five fights commenced after the two bucks gradually and simultaneously lowered their heads and slowly engaged horns. One yearling fight was preceded by a cheek catch display by a yearling ('Silver-red' = SR) which had been courting an estrous female. As SR displayed, the other yearling ('Torn-right-ear' = TRE), which was higher in the bachelor hierarchy, lunged and delivered a blow to SR's shoulder causing a serious injury.

Fights consisted of a series of thrusts and counterthrusts with the horns, much like a fencing match, with the apparent goal of goring the opponent. When the bucks were locked together head to head, each male attempted to force his adversary off balance by pushing him back and twisting his neck. Also, each buck tried to gain an uphill position during the battle. In four fights, both males backed away from each other only to suddenly clash together again.

Fights were short, the average time for 15 fights being two minutes. Several resulted in injuries. Five animals were clearly injured in the 15 fights, but 11 other injured animals, probably the victims of fights, were seen. Non-lethal horn penetration of the neck was observed in a fight between a TB and a large non-territorial buck at WCNP and a dead non-territorial male found at the NBR had deep puncture wounds in the lungs and heart, presumably from horn penetration.

The severity, style, and frequency of fighting in the pronghorn were predicted by Geist (1966) from horn morphology. The theory states that in species where the horns are relatively short and dagger-like, combat will be rare but very serious, and combatants will fight in an anti-parallel, broadside orientation, as reported for the mountain goat (*Oreamnos americanus*; Geist, 1964). In species where the horn is branched, as in elk, or where the horn is curved, as in bighorn sheep (*Ovis canadensis*), combat will be more frequent and less serious than in mountain goats, and the opponents will both deliver and defend against blows with their horns (Struhsaker, 1967; McCullough, 1969; and Geist, 1966).

The horn of the pronghorn is sharp-pointed, curved only on the distal $^1/_3$ portion, and slightly branched; therefore, combat in this species should be infrequent, occasionally serious, and head to head. These predictions are supported by our data. Judging from the size of the prong, it is predicted that it should not always catch the opponent's prong during a thrust, and that adversaries should alternate horn to horn and skull to skull contact during a fight. Figure 10 illustrates this inefficiency of the prong.

Geist also noted that in species which had dagger-like weapons the skin was thickened in areas where horn penetration was most probable. In the pronghorn buck the skin of the head and neck should be thicker than the skin of the rest of the body. In contrast to the buck, the doe has diminutive horns and there should be no thickening of the skin in the doe. We can report measurements from only one buck, and one doe, but they are in agreement with the prediction. The adult buck was found dead on 12 October 1970 at WCNP approximately ½ hour after it was shot. The hide was skinned down to the pastern joints; cut into strips of 10 cm. in width from the center of the neck to the tail and the center of the neck to the nose; and then it was measured every 5 cm along the posterior edge of each strip. The average of 67 measurements of skin thickness of the head and neck region was 3. 2 mm and the average of 142 measurements of the body was 1. 7 mm. Thus the skin of the head and neck was thicker than the skin of the body, significant at the 99% level (t = 5. 51). The skin of the neck was enlarged by the subauricular glands, which measured as much as 9 mm; however, one measurement of non-glandular skin was 7 mm. Also, the body skin measurements were increased by the skin of the rump patch, which averaged 3 mm, and this might reflect both the erectile quality of the rump and the possibility of horn penetration during flight from a chasing buck. At least one and probably two of 13 TBs at WCNP and two of 15 TBs at the NBR were gored in the rump during the 1970 rut.

The doe was shot by a hunter in southwestern South Dakota, near the WCNP area, on 3 October 1971. One half of the hide of the doe was measured in the same way the buck's hide was measured. Thirty-two measurements from the head and neck region averaged 2 mm and 60 measurements from the body region averaged 1. 9 mm. There was no significant difference between the averages. From these limited data it appears that skin thickness in the head and neck region is sexually dimorphic in the pronghorn. It seems therefore, that Geist's (1966) theory correctly predicts the nature of combat and defensive development of the skin in the pronghorn from the morphology of the horn.

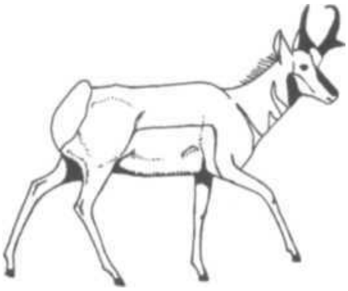

Fig. 12 This is the typical alarm posture with the rump patch and mane fully erect and the ears in a neutral position. The median gland is normally erect in this posture.

TABLE 4. LIST OF ACTS USED IN A SAMPLE OF 125 RANDOMLY SELECTED TERRITORIAL INTERACTIONS AND THE NUMBER OF TIMES EACH ACT WAS USED.

| LOCOMOTION | TB | Intruder | Both |
|---|---|---|---|
| Approach | | | |
| Fast | 43 | 0 | 0 |
| slow | 82 | 0 | 0 |
| grind teeth | 16 | 0 | 0 |
| not grind teeth | 11 | 53 | 47 |
| unable to determine if teeth ground | 88 | 72 | 78 |
| Closer approach in head-low, ears-back position | 128 | 3 | 7 |
| AGONISTIC AND RELATED DISPLAYS | | | |
| Broadside threat | 116 | 8 | 22 |
| Cheek patch display | 16 | 0 | 0 |
| Parallel walk in head-low, ears-back position | 0 | 0 | 103 |
| Thrash vegetation | 87 | 17 | 43 |
| Stare (>1 m apart) | 37 | 2 | 18 |
| Submissive posture | 0 | 37 | 0 |
| Play (cavorting) | 3 | 18 | 2 |
| SCP | 124 | 34 | 29 |
| SPUD | 88 | 16 | 22 |
| MAINTENANCE ACTIVITIES | | | |
| Feeding | | | |
| actual feeding | 18 | 43 | 24 |
| fake feeding | 11 | 23 | 16 |
| Scratching | 2 | 11 | 0 |
| Lay down | 1 | 0 | 0 |
| Chew cud | 2 | 0 | 0 |
| Shake body | 16 | 22 | 0 |
| Grooming (mouth or with horn) | 23 | 31 | 3 |
| ALARM | | | |
| Alarm posture | 0 | 19 | 0 |
| Snort | 0 | 27 | 0 |
| Stamp, stare at some point away from TB | 0 | 23 | 0 |
| FIGHT ACTIONS | | | |
| Stare (<1 m apart) | 7 | 0 | 8 |
| Lower head and stare | 0 | 0 | 4 |
| Move horns and make horn to horn contact | 0 | 0 | 4 |
| Clash | 0 | 0 | 1 |
| Fight | 0 | 0 | 2 |

Table 4—continued

| | TB | Intruder | Both |
|---|---|---|---|
| VOCALIZATIONS | | | |
| Snort-Wheeze | 72 | 2 | 0 |
| Roar | 2 | 0 | 0 |
| TERMINATION ACTIVITIES | | | |
| Herd intruder from territory | 37 | 0 | 0 |
| Chases | 140 | 3* | 0 |
| Chase with roar | 2 | 0 | 0 |
| Chase with hook | 1 | 0 | 0 |
| Both walk off | 0 | 0 | 11 |

* These 3 chases included dominance reversals and this is why the territorial buck was chased.

## SUMMARY OF ACTS USED DURING AGONISTIC ENCOUNTERS

In order to demonstrate more fully the behavioral repertoire of the pronghorn buck in a territorial encounter a random sample of 125 encounters was analyzed (Table 4). Certain acts listed need some amplification as they have not been discussed as yet. The submissive posture (Fig. 11) is used more typically in bachelor encounters, doe-doe encounters, and buck-doe encounters. With the head held up (weapons neutralized), ears in a neutral position, and the hunched stature of the animal, the submissive posture is clearly the antithesis of the threat display (Fig. 5).

Alarm behavior occurred in 19 encounters: in 12 cases it was displayed by yearlings and in 7 by larger bucks. This may indicate a greater tendency for the yearlings to react with alarm and show a lack of confidence during the interaction. The alarm posture (Fig. 12) we noted was similar to that reported for the pronghorn by Einarsen (1948), and Buechner (1950).

In the fight actions section a progression can be noted from a close range stare to a lowered head stare, then touch horns and fight. This is the typical sequence noted for bachelor buck fights which are typically 'low key' and usually consist of fencing with the horns, and wrestling with the head and neck. Serious fights were rarely observed in bachelor groups. This sequence was seen only 8 times in the 564 territorial encounters we observed and may not be typical of TB fights in general.

## COMPARISON OF THE PRQNGHORN'S TERRITORIAL SYSTEM TO OTHER TERRITORIAL UNGULATES

The pronghorn's territorial system resembles those reported for the Grant's gazelle (Walther, 1965, 1968; and Estes, 1967) and the impala (Leuthold, 1970) in that territories tend to be large (0. 23 km$^2$ to 1. 61 km$^2$), spread out and with few common boundaries (no-man's land separating territories by up to 0. 63 km), and that territorial neighbors interact rarely. In this they contrast with the more strongly territorial Thomson's gazelle (Walther, 1964; Estes, 1967), Uganda kob (Buechner 1961, 1963, Buechner and Schloeth, 1965, and Leuthold, 1966), and wildebeest (Estes, 1969), which tend to have smaller territories, common boundaries, and interact frequently with their neighbors. Unlike Grant's gazelle, impala, and Uganda kob, but similar to Thomson's gazelle and the wildebeest, olfactory marking with glandular secretion is an important part of the pronghorn's expression of territoriality.

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Paper No. 19

# Sexual and Aggressive Behavior of Adult Male American Bison *(Bison bison)*

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## ABSTRACT

Copulation in bison takes place in the context of a tending relationship that lasts from a few minutes to a few days. Flehmen usually accompanies the initiation of tending. Several mounting intention movements usually precede copulation.

Bison are primarily dominance organized. The dominance relationship is less stable in large populations than in small ones. Fighting is primarily head-to-head ramming with a great deal of force. It has a high potential for physical damage and even death. Threat behavior includes head-on threats, broadside threats, nod-threats, bellowing, snorting and stamping. Submissive behavior includes passive avoidance, a wide range of turning away movements, and grazing. A dominant animal often responds to the other animal's submission signal with a mounting intention movement.

## INTRODUCTION

The data reported here were collected in the course of field observations on bison in two locations. The primary study area has been the National Bison Range in western Montana. The bison population there is maintained at approximately 350 head excluding calves. This population is in two approximately equal groups. Each group is moved four times a year through a series of fenced enclosures. Each enclosure includes about 2,000 acres. Most members of the herd are effectively constrained by the fences and cattle guards which surround these areas, but mature bulls can cross the cattle guards both by jumping them and by walking on the rails. This, combined with their occasional resistence to being driven by the range personnel when a move is under way, results in their location being somewhat unpredictable.

The second herd is located on Catalina Island, California. This herd is estimated at about 400 animals excluding calves. They have access to an area about 76 square miles which is completely unfenced. However, only about 60 square miles of the island is actually frequented by the bison. Both herds graze year-round for their food supply. Neither ever has any supplemental feeding.

The ecology of the two areas contrasts sharply. The study areas in the National Bison Range are primarily rolling grassland with a few steep areas and a very small amount of coniferous forest. The range has been well managed for a number of years, consequently grass is well established and seems luxuriant by ordinary grazing standards. Catalina Island has more frequent and steeper divisions of the land. Moreover, the graze is much more widely scattered. During the early years of the European invasion of North America, Spanish ships deposited domestic goats on Catalina and a number of other islands off the shores of California. Without predator control the population expanded exponentially. The native flora, which had not adapted to the demands of a large herbivore population, was eliminated in some areas, and badly damaged elsewhere. The goat population is being controlled and the range is recovering, but at present graze is very sparse. A scrub oak forest covers a good part of the area, and there are large stands of cactus.

My observations on the National Bison Range include 1,100 hours of observation during the breeding season, evenly distributed over six breeding seasons from 1966 through 1971. The Catalina Island herd was observed for 50 hours during the 1971 breeding season. The field notes were recorded on a tape recorder for later transcription. These notes are supplemented by approximately 6 hours of motion pictures and 1200 still photographs.

Both herds function as tourist attractions and so are well adapted to the presence of motor vehicles. Consequently an observer can drive to within 20 yards of the animals without disturbing them. The great bulk of the observations in both locations were made from jeeps.

## GENERAL SOCIAL ORGANIZATION

Mature male bison are peripheral to the primary social organization. Except during the breeding season (July and August) they are either solitary or in small, temporary groups. Females, on the other hand, are almost never alone and they and the young bulls (up through three years of age) that stay with them are almost always together in the company of at least a few other animals. As the rut approaches the gregariousness of the cows seems to increase and so larger groups are typically seen during the rut.

The size of these groups is the only difference observed so far in the behavior of the animals in the two locations. Group size on the National Bison Range during the rut reached 174 (excluding calves) and averaged 57. On Catalina Island during the rut the largest group was 97 animals and the average on 17. Shackleton (1968) observed that bison groups were smaller in the wooded habitat of Elk Island National Park than on the National Bison Range.

Mature bulls join these herds and spend most of their time during the rut inside them. The herds drift over the range as a body, frequently moving from good pasture to the few watering areas, and sometimes marching or stampeding several miles. These movements are initiated and directed by mature cows. Mature bulls come and go from the herd during the rut as individuals. They stay in the herd for a while, leave for a day or two, and then return. This pattern continues until the rut is over. Bulls also come and go from the cow herds at other times of the year. It appears that the rut is different primarily in that they come more often and stay longer.

## PHYSICAL CHARACTERISTICS OF MATURE BISON

### Sexual Maturity

Female bison ordinarily first breed as two year olds, delivering their first calf three years after their own birth. Male bison are sexually mature by their third year, but do not reach full growth until they are at least six. Because of the competition of larger bulls, they rarely breed before they are five.

### Sexual Dimorphism

There is a great deal of sexual dimorphism in bison. On the National Bison Range mature males weigh about 2, 000 pounds and mature females about half that. Not only are the males larger but they have somewhat different shape. Their hump is relatively higher and their neck is relatively much thicker. Their skull is wider and their horns are much thicker, particularly at the base.

In both sexes a cape of woolly hair covers the neck and forequarters, extending down the forelegs so that the bison has pantaloons which end abruptly about 12 inches above the ground. This development of cape and pantaloons is much more pronounced in males. The distribution of hair on the head is even more distinct. Both sexes are bearded, but the beard on the male is substantially heavier. For the first couple of years the head hair is practically the same on males and females, but the female's head hair essentially stops growing around this time while the male's continues to grow. As they mature this heavy growth of curly hair gradually forms a dense rather resilient mass, covering the head. This mass is about two inches deep where it begins above the muzzle and as much as four or five inches deep at the level of the eyes. The hair continues to grow on the upper part of the head until in most bulls five or six years old the space between the horns is completely filled with it. This mass undoubtedly absorbs some of the shock of the physical encounters between bulls. Both the head hair and the beard of mature bulls (and only mature bulls) decreases dramatically after the rut.

## SEXUAL BEHAVIOR

### Tending

The basic breeding pattern of the species is called a 'tending' relationship (McHugh, 1958). A tending pair is established by a bull approaching a cow and staying with her; keeping other bulls away if necessary. He stands very close to the cow facing in the same direction. A grazing herd of bison drifts over the range fairly rapidly and the gregarious cows try to keep up with this movement. However, when being tended they are usually intercepted by the tending bulls who run beside and a little ahead of them and stop them by swinging their heads across the cows' line of travel. The parallel position of a tending pair is illustrated in Fig. 1.

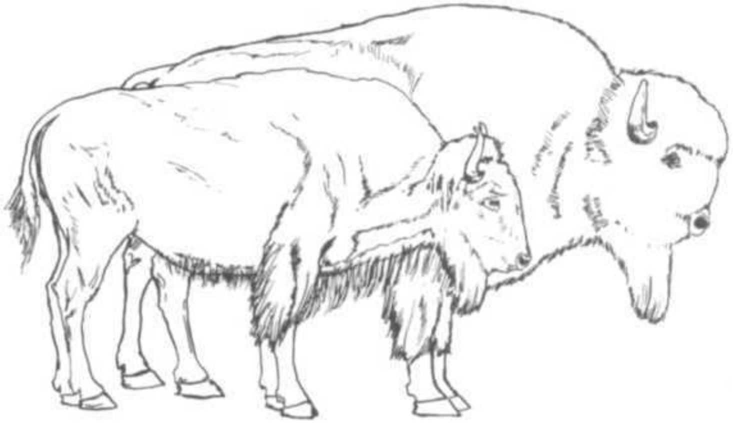

Fig. 1. Tending. If the cow starts to move away the bull intercepts her and swings his head across the line of her movement.

The length of a tending relationship can vary from a few seconds to several days. It is ended when the bull leaves, either voluntarily or under pressure from another bull. The duration of the period in which cows are attractive to bulls (as indicated by their being constantly tended) varies greatly from cow to cow. It is frequently as short as one day, but occasionally as long as ten days.

McHugh (1958) has described the tending relationship of *B. bison* as basically controlled by the cow. I feel obliged to disagree to some extent. Despite the herding behavior of the bull, the cow does generally determine the location of the tending pair, and she can, of course, refuse to stand for service. By refusing to stand for some bulls but standing for others she can, and occasionally does, excercise some options in the selection of her calf's father. On the other hand, cows may show a marked preference for a particular bull but be ineffective in implementing that preference. I've observed two instances in which a cow showed a marked preference for a bull who was subordinate to her tending bull. These cows repeatedly broke away from their tending bull and joined the subordinate bull. However, the subordinate bull was immediately supplanted by the more dominant bull and, after several of these attempts, finally pursued at a gallop until he retreated about one-third of a mile from the herd. These cows did not join the preferred bulls again and the bulls did not return that day.

On two other occasions tending bulls preserved the tending relationship by controlling the behavior of the cow more directly. Both instances involved relatively young (four year old) bulls who were tending mature cows. Both bulls had been subjected to a more than normal amount of unusually intense horning in the head and side. Neither bull retaliated during the period of horning. However, immediately following a horning bout the cows started to move away by rotating from the head-to-head parallel position to a head-to-tail parallel position. The cows' heads were swung low during this turn and in both instances the bulls kicked the cows in the head with a side-wise thrust of the hind foot. This kick was never observed in any other context but was powerful and effective. The sound produced was very similar to the sound of a small caliber rifle, and the cows swung immediately back to the head-to-head parallel position. They then stood very near the bulls with their heads held slightly higher than normal and rotating on their neck while their eyes blinked rapidly. They remained standing quietly beside the bulls for some time afterward and did not resume horning them.

A tending bull is usually tolerant of mild aggressive behavior on the cow's part (such as butting and horning him firmly but not hard in the flanks, ribs, or head) and such behavior on the cow's part is very common. Occasionally a tending bull will lick a cow's hair with repeated tongue strokes like those used by a cow on her calf, but this behavior is rare. All parts of the cow's body seem equally likely to be licked in this way. The only responses regularly stimulated by the cow are flehmen and mounting intention movements.

Flehmen in bison is so similar to flehmen in other ungulates that it is probably best described by reference to Fig. 2.

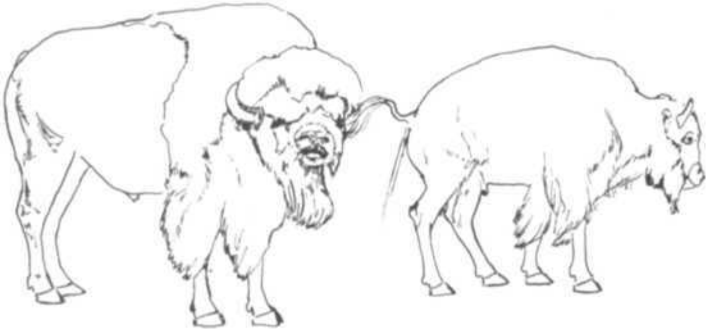

Fig. 2. Flehmen. Here the response follows licking in the cow's stream of urine. Other stimuli, including blood, can also produce flehmen.

The most common occasion for flehmen is the sniffing (and sometimes licking) of the vulva or urine of a cow. It most commonly occurs when a bull first approaches a cow. However, a bull frequently approaches and tends a cow without making the investigatory responses that lead to flehmen. The vulva or urine of a cow produce flehmen in all ages and both sexes. Other stimuli (e.g. a bloody wound, amniotic fluid) can also produce flehmen.

The mounting intention movement is the first stage of the copulatory pattern. A copulating bull steps toward the cow, puts his chin on her back and lifts his front legs from the ground while sliding his chin and brisket up her hips and back until his forelegs are clasped around her flanks in a full mount. A mounting intention movement consists of the first stages of the sequence. The bull steps toward the cow and swings his chin toward the level of her hips. This movement is often preceded or accompanied by a soft panting sound.

Most mounting movements are not completed. Usually the cow steps quickly away when the bull begins the mounting sequence or pants. When this happens it looks as though the bull 'tried' to mount the cow and she 'refused' to permit it. But even if the cow stands, the mounting sequence is frequently incomplete. A bull may stop at any point in the sequence, but most commonly he stops at the point where his chin is lifted to the level of the cow's hips and he has swung toward the cow with a short half step

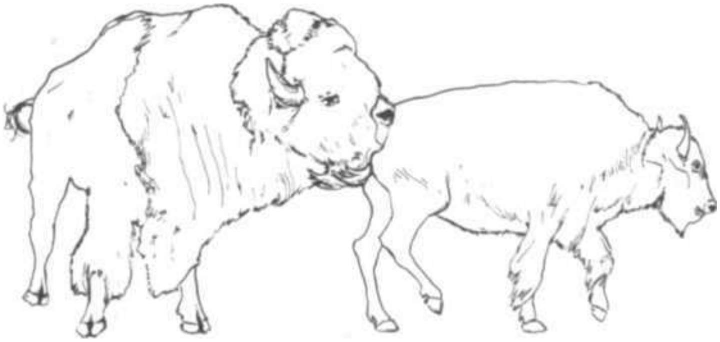

Fig. 3. Mounting intention. The bull has swung his head up and toward the tended cow, his beard trailing behind the movement. She has jumped forward and away.

or a mere shift of weight in her direction. Since this gesture occurs so frequently in this degree of completeness, I have isolated it as a unit of behavior and call it the mounting intention movement. This movement is illustrated in Fig. 3.

Occasionally the cow seems to become receptive when the bull is not ready to copulate. She will stand perfectly still during mounting intention movements, and may begin to mount the bull and/or rub his sheathed penis with her nose or lick it with her tongue. She may also push him about with her horns in a way that seems unique to this situation, setting the points against his rib cage or shoulder and gently but firmly pressing them against him forcing him to move sideways.

When they copulate the cow usually stands until the bull has mounted, then starts to run or walk fast when he penetrates or just before. The bull runs behind on two legs until he has penetrated, thrust once or twice, and (presumably) ejaculated. On the fairly frequent occasions when the cow starts to run before he has penetrated this involves a run of 20 to 30 meters at a good speed. Fig. 4 illustrates copulation.

After copulation the cow arches her back, usually urinates, and holds her tail straight out behind her, gradually lowering it to a normal position over a period of four to eight hours. Most cows stand for only one copulation, and exceptions to this rule appear to be unrelated to the length of time they are tended.

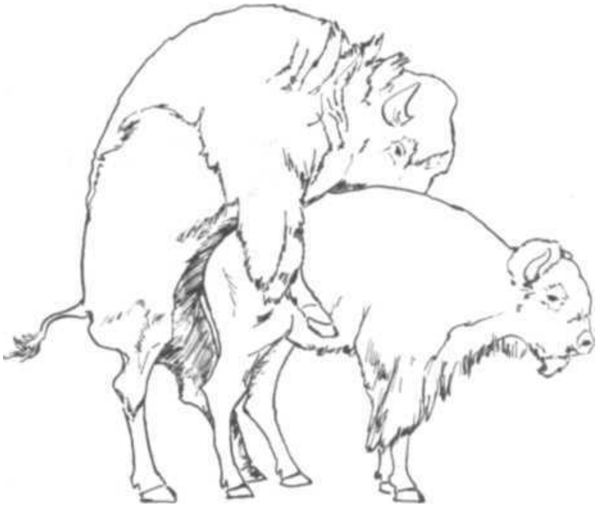

Fig. 4. Copulation. Cows often begin to run just prior to or immediately upon penetration. Bulls can run rapidly in this position up to 30 yards.

## AGGRESSIVE BEHAVIOR

At any one time during the rut, only a small number of the cows in the herd are attractive to bulls. The number of attractive cows always seems to be substantially smaller than the number of mature bulls, consequently there is a good deal of competition between the bulls.

If bison are placed along the reduction-of-fighting-mechanism continuum from completely territorial to completely dominance organized, they fall very close to the dominance end. The only space from which they exclude other bison is a small circle (with a radius of 10 to 25 feet) around a cow they are tending.

Their dominance relationships are established by, and expressed in, four basic patterns of behavior: (1) fighting, (2) passive avoidance, (3) threats, (4) submissions.

### Occasion for fighting

Serious fighting among males has never been observed in animals less than four years old. The most serious fights occur during the rut, but they are nearly as frequent when neither bull is tending as when one is tending and the other challenges him. In fact, bulls frequently abandon a cow they are tending to cross the herd and fight.

Fights tend to occur in clusters concentrated in fairly short periods of time. While only eight or ten fights will occur in a herd of 35 mature bulls on many days during the rut, there are periods when the frequency of fights is very high. I call these periods 'fighting storms'. An example occured one day with about 15 mature bulls in the part of the herd that was visible. Fighting suddenly grew very intense. This storm lasted only 22 minutes, but during that time we recorded 12 fights in which 7 different bulls were involved. The most active bull was involved in 10 of the fights. There were other fights in this group during this period, but our concentration in identifying the individuals involved in previous fights precluded our recording of them.

### The forms of fighting

The energy that bison use in overcoming one another during fights is transmitted by the head in one of two basic ways.

The first is by a straight push, lunge or charge in which one animal simply sets his head straight in front of his body and moves into the other with an impact that depends upon his rate of movement. The contact can occur at speeds ranging from a slow walk to a full gallop. Most such impacts are a result of a short charge or lunge in which the animal is at a walk or dead standstill only a few feet from the opponent and accelerates from that position. The special morphological features of the male, and especially the thick cushion of hair on the front of the head, absorb the shock of these contacts very well, even when it occurs at a full gallop. I have seen a bull take the impact of a galloping charge squarely while standing still, slide backward ten to fifteen feet, counter-attack immediately, and win the fight.

The other basic way of transmitting energy to the other animal is by 'hooking'. In hooking the animal starts with his head substantially to one side (usually about 45 degrees away from the direct line of his body) and uses the muscles of his head and neck combined with a side-ways thrust of his forelegs to accelerate his head and slam his horn or forehead into his opponent. The force of these hooking attacks can be very substantial. This is most clearly demonstrated when the hook contains a strong upward component. The force of such blows can lift the opponent's forefeet from the ground.

A particular fight is not confined to either of these strategies, but often includes a mix of them. Blows are almost never delivered to any part of the opponent other than the head. Much of this localization of impact is accounted for by the fact that the opponent maneuvers to intercept the attacks with his head, but it is also true that when an opponent's flank or side is exposed the bull with the advantage frequently stops his attack at that point and shifts to a position in which he can again direct his attack toward the opponent's head. Occasionally, however, he presses home the attack when the opponent is vulnerable and rather frequently pierces the opponent's rib cage or abdomen with a horn. Serious injury and death are likely to result.

Since fighting represents such a high level of energy expenditure and risk, it is not surprising that behavior patterns that can settle disputes in the absence of fighting, or terminate fights without damage, are rather well developed. There are two basic ways of resolving conflicts without fighting: passive avoidance and signalling.

### Passive avoidance

Passive avoidance is the behavior which is most commonly substituted for fighting. The phrase refers to those occasions when one bull simply yields to another without fighting or challenging. Passive avoidance may take place while the approaching animal is still at some distance (e.g., when a tending bull leaves quietly well before his challenger arrives.) The challenger is identified as such by means of behaviors which seem classifiable as threats since they frequently precede the initiation of fighting.

## THREATS

### Auditory threats

Of several such behaviors, the one that operates from the greatest distance is an exchange of bellows between two bulls. The bellow is emitted only by mature bulls and resembles a lion's roar. An exchange of such bellows may take place between a pair of tending bulls, a pair of bulls in which one is tending and one is alone, two bulls both of which are alone, or among several bulls. Bulls two hundred yards apart and out of sight of each other may exchange bellows. Exchanges of bellows may simply stop after a while but frequently bellowing bulls approach each other. Occasionally a bull will break off a tending relationship to get closer to a bull with whom he has been exchanging bellows.

There are two other auditory stimuli produced only by mature male bulls and only in aggressive situations: snorting and stamping. Both occur as accompaniment to the walk of a challenging bull, and frequently these behaviors occur together. A challenging bull often walks stiffly ('hesitation walks', McHugh, 1958) and brings his front feet down hard (stamping). He may also expel his breath explosively through his nostrils (snorting). Either of these behaviors can occur without the other, but when they occur together (as they often do) they are timed so that the moment of expulsion of breath and moment of impact of the feet coincide. The snort may alternate with bellows without the walk changing.

Stamping produces a sound on many surfaces, and when seen from the front enhances the advancing bull's movement and size by increasing the motion of the pantaloons which surround his front legs. The snort may be a specialized exaggeration of a sound made by many bison under other circumstances. Investigation of a new object by bison often includes substantial snuffing—inhaling deeply through the nostrils and then expelling the breath through the nostrils quickly and rather explosively. The snort of the bull bison appears to be an elaboration of this investigatory breathing pattern that has taken on communicative significance.

### Pawing and wallowing

A comfort behavior which often occurs during aggressive behavior of mature males is wallowing. During much of the summer large areas of a bison's coat are heavily infused with dust; the result of wallowing. Wallowing occurs in special areas where the bisons have torn the sod from the ground with their horns. The exposed soil is stirred several inches deep by horning and dried to the consistency of flour. The size of wallows ranges from a rough oval a minimum of six feet across on the long axis, to areas of widely variable form eight to ten times as large. All bison wallow: they walk into the wallow, frequently paw or horn the loose dirt and then lie down on their sides and roll laterally toward the top of their back, usually throwing loose dirt up onto their belly with their forelegs as they do. They may wallow on one side, or both sides but contrary to some reports (e.g.,Garretson, 1938) I have never seen adult bison roll from side to side on their backs. The loose dust which this behavior packs into the animal's coat greatly reduces the suitability of the coat as a habitat for insects. Consequently, bison are often relatively undisturbed by insects in areas where domestic cattle are seriously harassed.

Contending bulls sometimes paw loose dirt up toward their bellies with their forefeet. In addition, they may wallow. Wallowing during these interchanges takes place in an already established wallow if one is convenient. If not, a male frequently makes one or two passes through the sod with a horn, throws himself down on one side and goes through wallowing motions. Without any loose dust this behavior cannot serve the normal function of wallowing. Occasionally a bull urinates into the wallow before wallowing. One of the animals may move away either during or after wallowing, but the interaction usually continues past wallowing, and wallowing is far from universal in threat interactions. Threats other than bellowing, stamping, snorting and wallowing generally take one of three clearly distinguishable forms of postural display.

### Head-on threat

This form of threat is simply a head-on approach indistinguishable from the preliminary movements of a charge. This approach can be varied in rate all the way from a standstill to a gallop but usually occurs at a slow walk. A variant is the lunge in which the aggressor rushes one or two bounds towards his opponent with his head down and nose tucked back as if in a full charge but stops abruptly short of the other animal and tosses his head up. Lunges always seem to be directed toward clearly subordinate animals. During lunges and head-on threats the tail is often held high in the air, like a living question mark.

### Nod threat

This kind of threat interaction usually develops from a head-on approach but occasionally develops from a broad-side threat interaction (which will be described later). The two animals approach very close to one another then stop with their bodies oriented toward one another, and their heads swung to one side (either the same or opposite sides) and held fairly high. At intervals varying from a few seconds to one minute, both animals abruptly swing their heads down and then back up again in a matched movement. The interaction may go on like this for several minutes and can be terminated either by a submission signal (to be described later) or fighting. If the animals fight the contact is initiated while the heads are low and to one side. The initial blow in a fight that starts in this position is a hook to the opponent's head. The bulls are standing so close together that this blow can reach the opponent without either animal moving its feet and the opponent nearly always intercepts the hook with a corresponding hooking movement. A fight preceded by nod-threatening is frequently interupted by bouts of nod-threatening. Once contact has occurred the attack may take other forms. The posture and movement of a nod-threat are illustrated in Fig. 5.

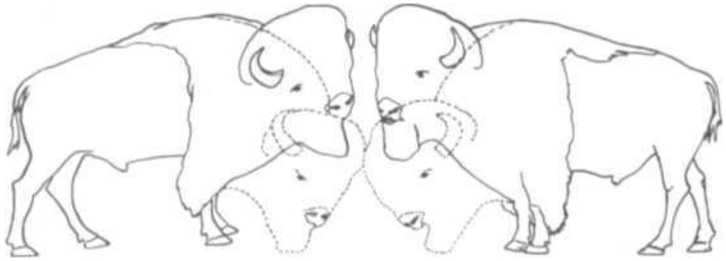

Fig. 5. Nod-threat. The solid lines show the high point of the up-swing and the dotted lines the low point of the down-swing. In the latter position the bull's beard rests on the ground.

### Broadside threat

This threat pattern seems to come closer to the classical concept of a display than any other behavior in the repertoire of bison. Threatening animals stand broadside to their opponent at a distance of 10 to 25 feet. The neck is not bent at all. The head and body form an absolutely straight line and the head is carried at about the elevation normally associated with walking or a little higher. Bulls often bellow during a broadside threat. When they do their back arches, their belly lifts, and their head lowers a few inches, but without turning or swinging laterally. If the opponent moves away, the aggressor may move to reestablish the broadside orientation. Such re-orientations are made with a slow, stiff walk. If both males are threatening they stand parallel to each other facing either in the same or opposite directions. The direction of facing seems to be entirely determined by the direction in which the animals have approached each other. While animals in a head-on approach often have their tails high in the air, animals in broadside threat rarely elevate their tails, and in fact, usually stop the normal tail swinging of animals chasing flies from their anus. A broadside threat is illustrated in Fig. 6.

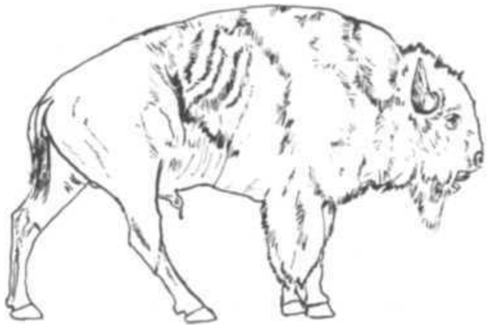

Fig. 6. Broadside threat. As the bull bellows his belly lifts, his head is depressed slightly and the tip of his tongue curls up to touch the roof of his mouth.

## SUBMISSION

### Submission signals

Both threats and fights are terminated by a submission signal from the opponent. There is no unvarying postural or vocal signal; instead there is a long gradation of postures and movements which carry the bulk of the submission signalling burden. This signal appears to be derived from turning and moving away and varies all the way from the minimum of swinging the head and neck aside, to actually turning away and running. A variant of this signal is a sequence in which the retreating animal backs directly away from the opponent swinging his head quickly from one side to the other. This movement may be repeated a number of times resulting in a series of movements somewhat analogous to a man shaking his head 'no'.

Submission during a broadside threat interaction is a special problem, because of the close relationship between the broadside threat posture and the submission or withdrawal signal that terminates other aggressive interactions. The submitting animal can, and often does, shift out of the parallel relationship by walking or turning away. It is possible, however, for him to withdraw from the threat interaction without shifting out of the parallel orientation. To do so he initiates the only other submission signal in the repetoire of the mature male bison: he drops his head to a grazing position and often begins to graze. The grazing that occurs as a submission signal usually involves the eating of a few mouthfuls of grass and then stopping, whereas an ordinary grazing bout lasts substantially longer.

### Reaction of winner to submission signals

The most common response of a winning bull to a submission signal is to break off the interaction and go about his business. But a surprisingly common response, especially at the termination of a broadside interaction, is to make a mounting intention movement, often complete with the panting vocalization.

The occurrence of the mounting intention in this context has been described previously (Egerton, 1962) and interpreted as a threat behavior. However, it rarely occurs before the opponent starts to submit and in view of this timing it may be better interpreted as a response of the winning animal to the submission of the loser. Its significance in this situation seems quite unclear. One is tempted to think that perhaps it has no signal value at all, but simply indicates that a submitting male elicits some of the same reactions from a dominant male as does a female. This behavior does, however, frequently stimulate a response by the losing male. He is likely either to accelerate his departure or begin to threaten again himself.

Another less frequent response by the winner is to go to a wallow, urinate and then roll in it.

### Dominance relationships

The stability and consistency of the dominance relationships of bison have been studied by McHugh (1958) and Egerton (1962). Both these studies reported on the structure of small groups of animals: McHugh studied a herd of 16 with two mature bulls and Egerton studied a herd of 25 with four mature bulls. Moreover, dominance interactions were probably exaggerated in both herds by the fact that they were confined to small areas and fed in troughs part of the time.

Both reports indicated very stable relationships. McHugh reported no reversals between the two mature bulls in his herd while Egerton reported only 6% reversals (involving only one pair of animals) among the four mature bulls in the herd. Neither study reported triangles among the mature bulls.

I recently studied the dominance relationships of mature bulls in a breeding herd containing 35 mature bulls on the National Bison Range. The resulting dominance relationships were rather less consistent than those reported in the previous studies. Reversals accounted for 12% of the outcomes of aggressive interactions and there were a number of triangles.

## DISCUSSION: (a) SEXUAL BEHAVIOR

The description of *Bison bison* sexual behavior reported here is quite similar to the description by McHugh (1958) and is also similar to Jaczewski's (1958) description of sexual behavior in *Bison bonasus*, differing primarily in that *B. bonasus* cows are described as typically standing for repeated copulations while *B. bison* cows rarely do.

The sexual behavior of *B. bison* is also similar to that of domestic cattle (Schloeth, 1961). There are, however, some significant differences. Domestic cows ordinarily stand quietly during copulation; *B. bison* cows rarely do. Also, domestic cows usually stand for repeated service while *B. bison* rarely do. Finally, tending pairs of domestic cattle usually stand parallel and head-to-tail, while *B. bison* stand parallel and head-to-head as does the Gaur *Bos gaurus* (Schaller, 1967). Fraser (1968) has suggested the head-to-tail relationship facilitates maximal pheromonal stimulation between the pair. The head-to-head stance of bison would lack that characteristic, but may have developed to keep the bull ready to intercept the frequent movement of the cow.

## (b) AGGRESSIVE BEHAVIOR

### Dominance

The dominance relations among the 35 mature bulls studied here are less stable than in previous studies of bison (McHugh, 1958; Egerton, 1962) or domestic cattle (Schein and Fohrman, 1955). There are several possible reasons for this.

The first is that the animals do not know each other as well. In contrast to the earlier studies, the subjects of the study had a range of several square miles. The amount of area available, combined with the generally asocial behavior of mature males, would lead to a small number of contacts outside the breeding season. Moreover, those contacts that did occur would generally be neutral because, again in contrast to the previous studies, there was no supplemental feeding of this population. Supplemental feeding, with its dual consequences of crowding and competition over a limited resource, greatly increases interaction and the development of strong dominance relationships.

Another probable cause of the relatively instable and inconsistent dominance relations reported here is the larger number of animals in a single age-sex class. This means that there will be more of the very small differences in size, strength, experience and aggressiveness that lead to reversals.

The final factor, especially in accounting for the inconsistencies (triangles) in dominance relations, are the fighting storms. Fighting a long series of rivals in a short period of time could easily lead to a loss to a lesser fighter through temporary factors such as fatigue or injury. If dominance relations established through wins and losses in fighting are challenged only occasionally one would expect a number of triangular relationships.

All the differences between the present study and the studies it is compared with above, are in a direction that makes the present study more relevant to the behavior of bison in their natural state. The fact that the dominance organization observed is weaker than previously reported raises questions about the degree to which this organizational principal operated in natural populations of bison. Studies of the home range of unrestricted bison become invaluable here.

### Threats

Geist (1964) has suggested that the threat behaviour of artiodactyls can be classified in three main categories: (1) rush threat, (2) weapons threat, (3) present threat. The threat behavior of the mature male American bison fits into such a classification scheme fairly comfortably, with some modification required to include everything. Some behavior appears to fall into both the rush threat and weapons threat categories. This is primarily because bison so commonly fight with a head-on attack that a straight-ahead approach necessarily involves a weapon presentation. Moreover, there appears to be some display features in the head-on approach. One of them is the auditory accompaniment of a slow head-on approach which often includes bellowing, stamping and snorting. It is possible that characteristics of these sounds correlate well with the size of the particular animal and thus could present size information in the same way as the broadside display.

The broadside threat display fits very comfortably into the 'present threat' category. The widespread occurrence of this display in bovids is documented in reviews by Schloeth (1958) and Geist (1966). Schaller (1967) describes it in detail in *Bos gaurus.* It is interesting to note that in bison the broadside stance not only displays the bull's overall size and his weapons, but also displays the depth of the shock absorbing hair on the forehead.

Signalling submission by turning away in varying degrees of completeness is a characteristic shared with domestic cattle (Schloeth, 1958). Schloeth also notes that a submitting bull is likely to engage in a brief bout of grazing immediately upon submitting.

The tendency of males to roll in a wallow, after urinating in it either before or after winning an agressive encounter, seems to be difficult to interpret. Marking objects or locations with urine is reported in a number of species and is assumed to have a territorial function. A number of primates soak the palmar surfaces of their hands and feet with urine (Andrews, 1963) but the assumed function of this behavior is to mark the surfaces that the animals will later walk on, thus being simply another mechanism for territorial marking. Since American bison are not territorial this behavior cannot have a territorial function for them.

Hediger (1968) provides a highly detailed description of European bison bulls wallowing in their own urine, then marking trees as territorial boundaries by rubbing their urine-wetted hump against them. Other detailed descriptions of the behavior of European bison (e.g., Jaczewski, 1958) mention neither territoriality nor rolling in urine-wetted wallows. Schloeth (1958) cites Hediger's statement about European bison and adds that Garretson (1938) reports that American bison bulls sometimes roll in wallows after urinating in them. (I have reexamined Garretson's writing very carefully without being able to confirm Schloeth's attribution). He also explicitly denies the occurrence of such behaviour in *Bos tanrus.*

Getting fresh urine in the hair is also reported in other ungulates.

Among other reports Espmark (1964) reports that in *Rangifer tarandus L.* rutting bulls urinate on their hind legs, and Lent (1965) reported the same phenomenon in *Rangifer tarandus groenlandicus.* Schaller (1967) observed a rutting male hog deer (*Axis porcinus*) twice urinate on a spot before lying down in it. McCullough (1969) reported that bull tule elk spray urine on their bellies during the breeding season, and Propst (1971) reports that billies among the feral goats on Catalina Island, California, urinate on their beards at least part of the year. Müller-Schwarz (1971) reports that both sexes and all ages of black-tailed deer urinate on their legs and rub them together.

Espmark (1964) interprets this behaviour as serving to mark a 'moving territory' with the bull as its center and only reference point. This use of the concept of territory has the unusual feature of making the defender and the thing defended (and therefore the possessor and the thing possessed) identical.

Lent (1965) takes a different, tack, suggesting that the tended cow marks the center of a moving territory and is the thing defended. This use of territory has the unusual feature of making the thing defended different from the thing marked, and the territory not only able to change location when a tended cow moves, but able to change identity when the tending bull shifts his attention to a different cow.

McCullough (1969) argues that the function of this behavior in tule elk is to communicate the bull's physical condition to potential rivals, via the odor of the metabolites in the urine. (As a busy, non-feeding harem bull's condition declines through the rut the odor of his urine would change correspondingly: rivals would attack when the odor indicated a weakened bull.) This is a most stimulating and ingenious hypothesis but at the present time there is no evidence for a key link in the chain of reasoning, namely that rivals do in fact respond to the change in the odor of the harem bull's urine. It would be possible, though not easy, to test this link experimentally and the hypothesis seems well worth the effort.

One alternative, or perhaps additional function self-marking might serve (at least in bison) is to permit or facilitate individual recognition in low light. There is a good deal of nocturnal activity in bison during the rut. Perhaps the odor of the bull's urine permits him to use pre-established dominance relations more effectively in the dark.

## ACKNOWLEDGEMENTS

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The figures were drawn by (Mrs.) Yoshie Kyhos.

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Paper No. 20

# Rutting Behaviour of Newfoundland Caribou

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## ABSTRACT

The breeding behaviour of caribou (*Rangifer tarandus*) in Newfoundland was studied during the fall rutting season for 10 years. Prior to the rut males and females were mostly segregated. In mid-September there was a fall shuffle in which stags joined female groups. The week prior to actual breeding animals banded together in small companies, usually with only one dominant stag present. In this pre-rut period there was considerable agonistic behaviour between males and between males and females. It is believed the function of this behaviour was to establish dominance relations prior to actual breeding. Common breeding displays seen in this period and described in the paper include: bush gazing, bush thrashing, hock rubbing, mock battles, dominance battles, sparring and rearing, and flailing. During the actual rut (October 8-18) females that were in heat were tended by males; the males courted and tested the females by a vacuum-licking display called slurping. Large-antlered stags did most of the breeding. It is hypothesized that the force of natural selection declines more rapidly with age in males than in females because older males are not permitted to breed females. If this hypothesis is valid it would suggest that males grow older faster than females, and there is a preponderance of females in caribou populations because males reach senility at an earlier age than females.

## INTRODUCTION

The Wildlife Division of the Newfoundland Provincial Government studied fall breeding behaviour of caribou (*Rangifer tarandus*) in Newfoundland for 10 years (below). In addition, the behaviour of a captive herd (5 or 6 animals) were observed for three years. Also I visited Mr. Albert on the Gaspé Peninsula of Quebec to watch caribou in September and October, 1959.

*Years and study areas*

| | |
|---|---|
| 1952 | Sandy Lake, Badger (Fig. 1) |
| 1956 | Avalon Penisula and Sandy Lake, Badger |
| 1957 | Sandy Lake, Badger |
| 1958 | Sandy Lake, Badger |
| 1959 | Sandy Lake, Badger, Mt. Albert, Quebec |
| 1960 | Avalon Peninsula, Captive herd |
| 1961 | Sandy Lake, Badger, Captive herd |
| 1962 | Sandy Lake, Badger, Brunette Island, Captive herd |
| 1963 | Sandy Lake, Badger, |
| 1964 | Sandy Lake, Badger |

The habitat at Sandy Lake consisted mostly of open landscapes with extensive areas of sedge marshes and Subalpine dry barrens. Also there were some 'islands' of closed canopy forest and some lichen woodland stands. The lichen woodlands consisted of thinly-scattered forests of open-grown and unpruned conifers surrounded at

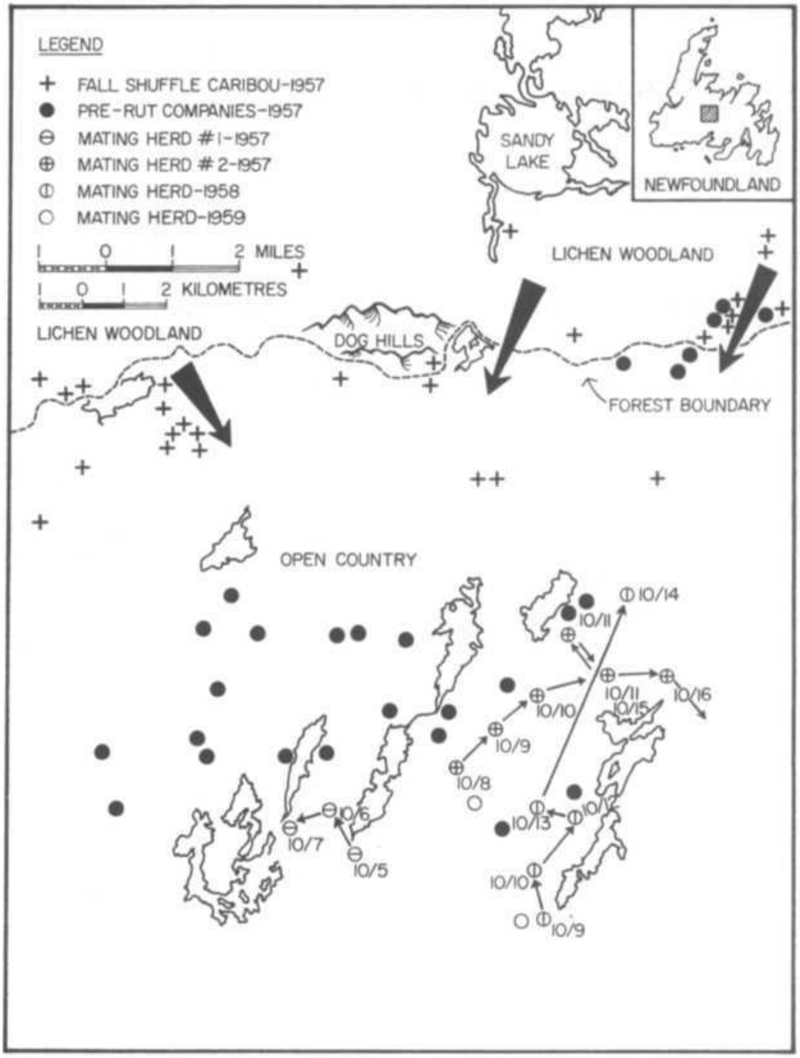


Fig. 1. The study area at Sandy Lake, Badger. Large arrows indicate direction of fall shuffle.

ground level with *Cladonia* lichens (see Bergerud, 1971a, Fig. 2 and Bergerud, 1971b, frontispiece). The tree cover on the Avalon Peninsula was composed of islands of closed-canopy conifers surrounded by large bogs (see Bergerud, 1971b, Fig. 19).

A description of Brunette Island is found in Mercer (1966). The Brunette study involved only 10 animals. Nine wild does were introduced to the Island in June, 1962, and a hand-reared stag (4½ years-old) was released in September, 1962, to breed the females.

The primary technique was the continued and undisturbed field observations of breeding caribou for approximately 500 man days. I drew two-dimensional antler diagrams with the aid of a 20 x spotting scope to recognize individuals. For stag classifications I used face profile and antler size to distinguish yearlings, 2-year-old stags, and senile stags (showing regressing antlers based on characteristics of beams spindly, few points and asymmetry).

## HERD STRUCTURE

### Fall shuffle

In both the Sandy Lake and Avalon Peninsula study areas, males were partly segregated from females during the summer; they used more timbered areas while females visited more open habitats. Normally, insect harassment eased about mid-September and the males left their summer haunts and moved towards open country and the females (Fig. 1). Counts made of males and females in the transition zone between the forests and the open barrens were biased towards males (Table 1).

TABLE 1. COMPARISON OF THE PERCENTAGE OF MALES SEEN BETWEEN AGGREGATION PERIOD AND THE TOTAL SEX RATIO WITH HERD STRUCTURE DURING BREEDING.

| Year | Total Adults in Sample | Percentage of Adult Males | | | | Total Sex Ratio* ♂/100 ♀ | Herd Structure‡ |
|---|---|---|---|---|---|---|---|
| | | Fall Shuffle | Pre-Rut | The Rut | Post-Rut | | |
| 1952 | 290 | – | – | – | – | 48 | RC |
| 1956 | 164 | – | – | 36 | 28 | 33 | RC & MH |
| 1957 | 826 | 47 | 33 | 48 | 31 | 35 | MH |
| 1958 | 453 | 48 | 33 | 42 | – | 37 | RC & MH |
| 1959 | 302 | 39 | 31 | 39 | – | 34 | RC & MH |
| 1960† | 142 | – | – | 37 | – | 37 | RC & MH |
| 1962 | 376 | 29 | 25 | 42 | 33 | 29 | MH |
| 1963 | 180 | – | – | 26 | – | 26 | MH |
| 1964 | 138 | – | 31 | 27 | – | 27 | MH |

* Sex ratio for all 4 aggregation periods.

† The Avalon Peninsula Herd; other years for Sandy Lake, Badger.

‡ RC = Rutting Company

MH = Mating Herd

The first observation of does and stags together in 1957 was on September 15 when two stags had joined a group of females and were sparring. The next day a medium and a large stag were chasing does.

In 1958 a stag that had been solitary all summer first joined two does on September 16 (Bergerud, 1972). An aerial survey the next day showed 15 single stags, 25 single does, 18 groups of 2 or 3 females and 12 companies with both males and females. Two stags were sparring.

Earlier in the century Millais (1907) said stags were in the timber along the Garder River on September 14, 1903, and said it would be a fortnight before they joined the does on the open marshes. In 1905 Millais found the males still in timber as late as September 25 and attributed their late emergence to the severe winter of 1904-05 which he felt delayed sexual development and retarded antler growth.

### Pre-rut

The animals in the pre-rut period (defined as October 1-8) were usually associated in small groups (2 to 20 animals) in which one stag was active investigating and herding females and threatening subordinate stags; the group had one obvious dominant male. I call such groups rutting companies. These aggregations were not harems (cf. Espmark, 1964a). Seldom were the same animals seen together on subsequent sightings. An individual was not a member of any specific social group. A common sequence was for a large antlered male to join a group of females. For a time he would be active herding and threatening. But such bouts of activity were not continuous. Eventually he might leave the group, presumably to seek out females elsewhere; he might simply get left behind by the group while he was resting. The doe group might then separate into subcomponents and meet other female parties and associate with other males.

Usually there were many pre-rutting companies quite near each other (Fig. 2). The nearest adjacent cluster of companies might be 20+ miles distance. I suspect that many of the animals in such a concentration, especially the males, became familiar with each other through interactions in the pre-rut interval. Perhaps these concentrations qualify as demes.

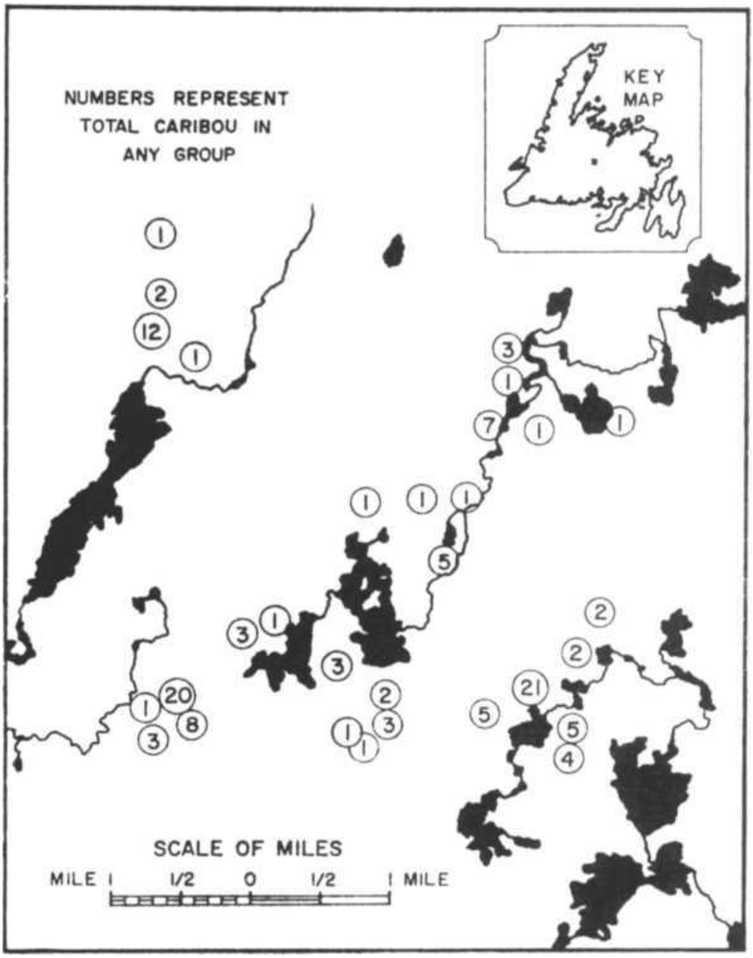


Fig. 2. Typical spatial distribution of animals on October 2. Conceivably all these animals could unite in one herd in the mating interval October 9-18.

Most of the single animals in this period (Fig. 2) were: (1) large antlered, sexually active stags that were moving between doe groups (Fig. 3) called 'travelling stags' (Millais, 1907); (2) small antlered stags (satellite or bachelor stags) that usually kept their distance from groups that were dominated by a large stag; and (3) senile stags with regressed antlers that took little interest in breeding activities.

The 'travelling stag' component included both stags seen to dominate other males in serious fights and stags that were defeated. I do not imply that these latter animals were of inferior physical status. In fact, they represented the sexually most active stags. At one moment they were in charge of a group of females; later they were on their way to find other females.

Fig. 3. A travelling stag searching for does. He is panting (vocalization of aroused mature male).

Fig. 4 A mating herd of caribou with several large stags. Note difference in wariness between males and females-0 of 4 males alert (including a male calf), whereas 5 of 6 females alert. Senile stag at left is 'bush-gazing'.

The travelling stags' located caribou groups by orientating on the sounds of stags clashing antlers, beating trees, and vocalizing. Also they tracked herds. We followed one stag that visited the exact site where a herd had been the previous day. He lowered his head, scented the ground and then followed the scent of the herd until he came up with them one mile away. The more I studied these animals the more I felt they knew each other and knew where to find each other.

There was usually only one dominant stag per small aggregation. However, in groups of 20 or more animals there were at times several large stags (Fig. 4). It was not always obvious if *one* stag was in command of the group.

Between years (based on three rutting seasons) there was a significant difference in the number of females associated with large, medium and small stags; there were

TABLE 2. HERD STRUCTURE IN THE PRE-RUT INTERVAL COMPARED IN THREE YEARS.

| Year seen, Size of Dominant Male | Number of Companies in Sample | Number of Satellite Males per Company | | Average Number of Females per Company | Per cent Females in Company |
|---|---|---|---|---|---|
| | | Small | Med.-Large | | |
| 1952 | | | | | |
| Large | 12 | 1.7 | 0.7 | 4.2 | 55 |
| Medium | 10 | 0.8 | 0.1 | 2.7 | 30 |
| Small | 5 | 0.2 | – | 2.4 | 15 |
| 1958 | | | | | |
| Large | 28 | – | 0.3 | 3.1 | 91 |
| Medium | 6 | – | – | 1.5 | 9 |
| Small | * | – | – | – | – |
| 1959 | | | | | |
| Large | 9 | – | 1.0 | 4.8 | 31 |
| Medium | 28 | .04 | – | 3.3 | 67 |
| Small | 1* | – | – | 2.0 | 2 |

* Very few young stags in populations because of high calf mortality in 1956 and 1957 (Bergerud, 1971b)

TABLE 3. ASSOCIATION OF STAGS AND DOES DURING THE FALL AT SANDY LAKE

| Dates | Total Caribou Observed | Percentage of Animals ♂♂with♀♀ | | ♀♀with♂♂ | | | Average Size of Herds |
|---|---|---|---|---|---|---|---|
| | | 57-58 | 59 | 56 | 57-58 | 59 | |
| September 24-30 | 77 | 39 | – | – | 52 | 50 | 2.3 |
| October 1-8 | 1301 | 72 | 52 | – | 90 | 68 | 4.1 |
| October 9-18 | 913 | 95 | 52 | 97 | 95 | 96 | 10.0 |
| October 19-25 | 609 | 91 | – | 88 | 95 | – | 5.8 |
| October 26-31 | 796 | 88 | – | – | 85 | – | 5.5 |
| November 1-14 | 411 | 86 | – | – | 74 | – | 5.4 |
| November 15-30 | 728 | 62 | – | – | 54 | – | 5.9 |

more females per group where a large stag was present than when a medium or small stag was present (Table 2). Large stags were vocalizing and thrashing trees more often than were the young stags. These sounds advertized their presence and we observed females frequently joining such groups. Secondly, the large stags appeared better able to control the straying of females. We made observations in which small stags could not prevent females from leaving their rutting companies.

The average number of animals per group in October increased over the years 1957 to 1967 (Bergerud, 1972). This increase was concomitant with a decline in males per females from 1 to 2 in 1957, to 1 to 4 in 1967 (Bergerud, 1971b). Since females invariably initiate movement in rutting companies and lead such groups, they should have been responsible for the increase in herd size with a decline in males. Females sought males when approaching estrus and in heat (latter section). They were agonistic towards other females who approached them while they were being tended. With a reduction in the number of stags, pre-estrus females would likely be more mobile. This could lead to larger herds.

The intensity of the pre-rutting activities of males seemed to vary between years. In 1957 and 1958 most of the males were associated with the females in the period October 1-8 (Table 3). However, in 1959 many stags were seen that were not with females.

The entire tempo of sexual activity seemed reduced in 1959 compared to 1957 and 1958. Further, in 1957 and 1958 most of the stags seen had large antlers, whereas in 1959 most of the males seen had medium antlers (see Table 16). The winter of 1957-58 was one of the mildest on record for Newfoundland; in contrast, the winter of 1958-59 was one of the most severe (Bergerud, 1971b, Fig. 6). Perhaps winter nutrition played a role in the physical conditions and sexual activity of males, as suggested by Millais in 1907.

However, even in 1959 most of the females were associated with males in the breeding period, October 9-18 (Table 3), and 91% of the females gave birth to calves the following spring (Bergerud, 1971b).

The most distinctive feature of the pre-rut period was that many animals met and interacted, somewhat analogous to a 'get-acquainted social affair.' The large sexually active stags 'made-the-rounds' and visited many temporary groupings of does. Agonistic behaviour was frequent between stags and between does and stags.

These interactions probably established dominance relations between males as well as between males and females. The actual breeding period was brief, lasting from October 9-18. This left little time for sorting out status.

Another possible function of the accelerated rate of interaction in this period is that it may have synchronized heat in females. The caribou in captivity came into true heat each year (1960, 1961 and 1962) about October 25, approximately 10-11 days after the breeding period in the wild. However, the captive animals appeared to experience a silent heat on the same date that wild animals were being bred (Bergerud, 1961). Social stimulation (possibly also mobility) may play some role in the maturation of psychological heat with physiological heat so that they both occur simultaneously.

### Rutting period

The herds increased in size just prior to breeding (breeding interval, October 9-18). In some years females joined into large herds in which a single male could not prevent the many other large males from associating with the females; I call these mating herds. In other years the does did not combine in large herds (Table 1) and the herd structure resembled that during the pre-rut period. If there were many stags in the population, rutting companies, not mating herds, were the rule (Table 4).

The formation of a mating herd was observed on October 5, 1957. Six caribou met a company of 21 animals. The master stag of the smaller group became defeated in an ensuing fight. On October 6 the group had increased to 52 caribou with 5 large stags. The herd was no longer one stag's domain. All of the large stags 'tolerated' the presence of each other but were 'on guard' when passing, tilting their antlers towards

TABLE 4. ACTIVITY OF KNOWN INDIVIDUALS OCTOBER 5-6, 1957.

October 5

Rutting Company No. 1 (6 caribou)

Stag #41 active "panting" and following does. Individuals include large stag, #41, does 42, 43, 44, 1 anterless doe and 1 yearling doe

Rutting Company No. 2 (21 caribou)

Large stag #49 active "panting" and chasing does and other stags. Individuals include stag #49, medium stag #51, small stags 46 and 50, does 45, 47, 48, doe 1 calf, 2 yearling does, 11 antlerless does.

Rutting companies meet and stags 41 and 49 fight (49 defeated).

Rutting companies travel together #49 quiet and #41 active "panting".

Large stag #52 joins herd.

#41 moves towards #52 but #52 turns aside.

Herds separate at dark with most of the animals moving on. #41 remains behind, chasing 43 so that she remains behind.

Continue moving, stags #49, 52, 51, 50 and does 42, 45, 48 and others.

Remain behind #41, 43, 44, 46, 47, doe 1 calf, 40, 2 yearling does, 3 antlerless does.

October 6

#52 leaves group

Rutting companies together with the addition of a 3rd group (total 45 animals). Very large new stag #65. #49, 41 and 62 all active.

Very large stag #54 joins herd (he was with 2 small stags Oct. 5).

Upon Joining herd #54 pushes with #51, #65 comes to meet #54 but no battle, #54 approaches #41 but #41 turns aside, #54 locks antlers with #62 but #62 gives up immediately, #54 and #49 lock antlers and fight hard—#54 wins. Stags active all day chasing and panting.

their rival. On October 8 another group joined them and the dominant stag of this group was defeated by a stag from the mating herd. The next day the herd grew to 76 animals as part of the original herd met another mating group. Two stags fought on this occasion. By October 11 there were 176 animals. By that time the stags were paying little heed to each other and were intent on chasing females; the accelerated action of the animals precluded any further note taking. I have never since observed such a frantic period. It was obvious that many does were approaching heat simultaneously (note brief calving interval in 1958, in Bergerud, 1972, Table 3). When the herd was visited on October 14 activity had slackened appreciably and breeding was in progress. By October 16 the herd was reduced to 60 animals with only two copulations recorded throughout the day. A considerable daily turnover of members was evident from changing sex ratios during the day and from different total counts of 113, 67, 94 and 88 animals. There were still many animals nearby, but they were scattering.

The formation of the mating herd at Sandy Lake in 1958 happened almost overnight. During the first week of October several rutting companies were encountered daily.

On October 8 three rutting companies were watched. The next day the caribou were gone. The only animals found in a day's walk were five travelling stags searching for females. The same day an assistant located the mating herd of 84 animals 3.5 miles from where the rutting companies were the prior day.

An island-wide aerial survey on October 13 and 14, 1958, days in which many females were bred, showed animals in the following groupings:

1. 9 single animals, 1.3 per cent
2. 17 rutting companies
   Mean size 4.8 animals, 16.5 per cent
3. 7 mating herds (294 caribou), 42.2 per cent
4. 4 clusters of rutting companies, each concentration limited to less than 16 sq. miles (279 animals), 40.0 per cent

In 1959 a small mating herd of 40 animals was seen October 8. Prior to that date only rutting companies had been seen. Another mating herd was seen October 11 (20 animals with 5 large stags). All the animals did not join mating herds at Sandy Lake in 1959 as in 1957 and 1958. Again in 1956, L. Tuck (Canadian Wildlife Service Officer) reported a similar herd division at Sandy Lake. On October 12 he watched a mating herd of 73 caribou, including 15 large stags; and the same day he saw three rutting companies.

### Post-rut

The mating herds disbanded each year after October 17. Superficially the groups in the post-rut period resembled the pre-rut groups. Often there was only one large stag per company. The stag was quiet and did not chase and herd subordinate males. No increase in the herd size was found in October 26-31, 1958, when some breeding occurred (likely a second estrus). Some segratation of the sexes occurred in November, but many of the stags remained with does throughout the winter (Bergerud, 1972, Table 2).

## AGONISTIC BEHAVIOUR

The herd structure of caribou is quite open (cf. Lent, 1965). Females were always permitted to join herds. Stags were able to join large mating herds but were frequently unable to associate with does if they were in small rutting companies in which a dominant stag was active. Although herd structure was open, we did note a number of agonistic displays both within and between the two sexes.

### Threat behaviour of large stags

The most common threat was the antler presentation of stags. If the threat was addressed to a small stag (presumably a subordinate) or to a doe, the presentation was a brief tilting down of the head.

The frontal view seemed a consistent component. Large males had white shoulders and mane and a dark face (Fig. 3). A sudden dichromatism resulted when a threatening stag turned quickly head on and lowered his head so that the antlers and dark face contrasted against the white mane (see sketch in Pruitt, 1960, p. 8). The long neck mane would exaggerate the size of the animal from the front. Thus, the dimorphic sexual coloration may function both for sex recognition and intimidation. The mane is not as noticeable in small stags and is poorly developed in yearlings.

If a threatening stag was sufficiently aroused he might follow the antler presentation with a few quick steps forward, antlers down and pointing forward. This movement often resulted in an active chase.

If a chasing stag was able to come abreast of a female he might rake her side with his antlers (three observations). In the case of overtaking a male he attempted to ram into the side of the animal. I saw one stag bowled off his feet and killed in this manner. Normally, chases were short and the threatening animal did not overtake the pursued.

Usually when a doe strayed from a rutting company the dominant stag walked towards her vocalizing; she usually turned back and joined the other females. If the doe had wandered far before being noticed, a stag would frequently break into a run and angle towards her obliquely, in which case she usually circled back. On only nine observations did a stag flank a female and turn her back; six of them involved aggregations with only a stag and a single doe. On three occasions the doe did not circle back but ran from the stag (a small stag in all cases).

The extent of harassment of small males in a company depended on the sexual stimulation of the dominant stag, as well as on the sexual behaviour, especially licking, of small satellite stags. At times a stag was able to join a herd and associate with the does only to be driven from the group hours later. During the middle of the day and in hot weather the activity of the dominant male was at its lowest level. The drive to isolate the females from the other males also waned near the end of the sexual period of each stag (Bergerud, 1960).

When subordinate stags were successful in associating with a group of does that had an active dominant stag, they appeared to be on guard and aware of the dominant stag's location. With so many does coming into heat within a few days in Newfoundland, the stags devoted most of their time after October 9 to the does; chases were necessarily short so that the stags could get back to the does.

### Threatening and fighting involving females

I noted a good deal of fighting between adult does and young stags. We recorded 12 interactions between yearling males and does; females dominated in 10 cases. They butted heads in four observations and reared and flailed in 8 cases. In seven encounters involving small stags, probably 2½-years-of-age, the male dominated 5 times. These encounters usually occurred when the stags showed sexual interest in the females.

The most common interaction between females was between two antlered does. In 11 observations, 4 were antler threats, 6 resulted in antler fighting and one was rearing and flailing. We did not record an actual fight between an antlered female and anterless females. I believe that antlered females usually dominate antlerless animals (see Table 5; cf. Espmark, 1964b). When two antlerless does fought they usually reared and flailed (Fig. 5), but sometimes butted heads.

TABLE 5. SOCIAL HIERARCHY OF 9 WILD DOES OBSERVED FOR 20 DAYS ON BRUNETTE ISLAND IN OCTOBER 1962

| Dominance Rank | Weight in Pounds* | Presence of Antlers (Y or N) | Number of Interactions Observed | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 1 | 214 | Yes† | – | – | – | – | – | – | – | – |
| 2 | 195 | Yes | 2 | – | – | – | – | – | – | – |
| 3 | 188 | Yes | – | 1 | – | – | – | – | – | – |
| 4 | 193 | Yes | 2 | 4 | 3 | – | – | – | – | – |
| ft | 195 | No | 1 | – | – | – | – | – | – | – |
| 6 | 178 | No | 1 | – | – | 2 | 3 | – | – | – |
| 7 | 212 | No | – | – | – | – | 3 | 1 | – | – |
| 8 | 171 | No | – | 1 | 4 | – | 2 | – | 1 | – |
| 9 | 172 | 1 antler | 7 | 1 | 2 | – | 1 | – | 1 | 3 |

* June figures

† Largest antlers

Threatening and fighting between females usually resulted from the following: (1) new animals joining a herd; (2) a doe being tended by a stag, fighting or threatening another animal; or (3) driving up other animals lying down.

The following notes provide a description of interaction involving new animals joining a herd:

> October 9, 3:28 p.m.
>
> Doe and calf running 2 miles away. They swim lake and come to herd (1♂, 5 ♀♀ and 2 ♂♂ calves). One doe watches their approach at ¼ mile. When doe approaches they both rear. Female calf with new doe rears at male calf who ran. Now both male calves approach and start rearing at female calf that retreats. At *least* two other does rear when new doe joins herd. Herd was laying down but new arrivals get the herd moving. Two does rear so close that their heads are over each others necks. Stag ran towards new doe panting (vocalizing).

Notes taken on an observation of driving up behaviour were as follows:

> (Nine does on Brunette Island—No. 1 refers to alpha animals and No. 9 to omega).
>
> October 10, 10:30 p.m.
>
> Doe 1 (see Table 5) stands up, stretches and with her antlers drives up doe 9. Four more does get up. 11:00, other does lay down. No. 1 stands up and rakes at tree. 11:06, doe 1 drives up doe 9 and doe 8. No. 9 goes and lays down. No. 1 drives up doe 9 up again. 11:09, doe 8 runs at doe 9 and pushes at her with head. No. 9 runs. Doe 2 walks towards 9 and 9 runs. 11:15, stag gets up. Five does get up. 11:16, stag drives up 2 more does with antler threat.

We noted many observations of calves interacting. The usual situation was for a male calf to rear and flail at a female calf; the male usually dominated.

### Behaviour of subordinate stags

Small stags and does revealed their subordinate position to large stags by avoidance or flight. If a large stag approached a herd *without vocalizing* (passive approach), a threatening advance of the master stag usually turned the new arrival aside without a battle. The newcomer normally held this course until the resident stag was nearly on him and then he turned, slowly moving off so that the antlers of the two animals *would not touch* (30 observations). The dominant stag then usually vocalized, turned, and retraced his steps back to his does.

I do not interpret the broadside display of the stag turning aside as a superiority display. Rather it seemed to indicate that the animal was not ready to attack but expressed a readiness to ward of an attack if the other animal continued. There was one observation in which the stag waited too late to turn aside. As he started his slow turn his antler touched those of the other stag. He then turned head-on and fought a hard battle in which he was killed. We also observed three cases in which a large stag stopped advancing, but rather than turn aside began to feed. The other stag in each instance then turned and returned to the herd.

### Sparring

Sparring is defined as a non-belligerent match between two animals, usually involving stags. In sparring some gentle pushing resulted, but mostly the action was a sideways twisting of heads as animals tried to obtain an advantageous hold with their antlers (Fig. 6).

If one animal got his head turned or twisted in a disadvantageous position, he would start to pivot using his hind legs. His opponent, in trying to maintain his advantage, also had to pivot. At times the circling was quite rapid as one animal tried to get his antlers unlocked and break loose.

Sparring matches were continually in progress in October, the earliest recorded September 18; and it was not unusual to see three pairs of stags sparring at the same moment in a herd of 50 or 60 animals. Two yearlings sparred intermittently for 7.5

Fig. 5. Two antlerless does rearing. Note that the ears of the aggressor (on right) are inclined back

Fig. 6. Two stags sparring in a mock battle. Note that they are not pushing.

hours. Bachelor groups were found adjacent to the large rutting companies as a result of the association of the small and medium antlered stags seeking out each other as sparring partners.

Sparring between does was only recorded once in the wild, but captive females sparred frequently with each other and with young stags. An interesting observation was of a doe that sparred with her own male calf. The doe and calf were released into a new pen containing other animals on October 1. The calf had nursed prior to release. In the new pen the doe immediately began to drive the calf. By October 2 the calf no longer tried to associate with its mother. However, the calf and doe sparred together non-belligerently on October 21.

TABLE 6. COMPARISON OF THE STAG'S SIZE (BASED ON ANTLERS) TO FREQUENCY OF VARIOUS BREEDING DISPLAYS AT MT. ALBERT, SEPTEMBER 16-OCTOBER 29. *

| Size of Stag | No. of Different Stags in Sample | Number of Stags Seen: Panting | Slurping | Dominance Battles | Mock Battles |
|---|---|---|---|---|---|
| Large | 11 | 11 | 7 | 5 | 2 |
| Medium | 8 | 2 | 7 | 2 | 7 |
| Small† | 7 | 1 | 4 | – | 6 |
| 2-years | 5 | – | – | – | 4 |
| Yearlings | 7 | – | 1 | – | 6 |

* Stags recognized by antler diagrams.
† Probably mostly 3-years-old.

### Dominance battles between stags

Dominance battles occurred frequently between large antlered stags (Table 6 gives an idea of the frequency of this and of various other displays according to age). These battles were brief and serious, frequently resulting in the death of one of the combatants.

Any large stag that vocalized when he approached a herd (active approach) also normally challenged the resident stag in a dominance battle. The time interval in which the animals actively battled was quite brief. The following times were recorded in seconds: 5,7, 10, 15, 22, 24, 27, 30, 40, 76, 120, 238. The length of time of the fight was related to how evenly matched the combatants were in size. In the 4-minute contest the stags were very evenly matched and they had to cease shoving several times to rest, with their antlers still meshed.

Seventeen of the longer dominance battles recorded occurred in the following situations:

1. Two stags chasing the same doe (7)
2. A new stag joining a large herd of caribou which contained many stags (3)
3. The meeting of two rutting companies (4)
4. A challenger stag attempting to take charge of a rutting company (3)

Conflicts arising from the chasing of the same doe followed a pattern somewhat different from those arising from the other three situations. Usually, one stag was pursuing a doe when another stag joined the chase, running parallel to the first stag and angling in towards the doe. The stags always tilted their antlers toward the opponent. The instant the antlers touched the chase was momentarily abandoned as the combatants strove to push each other. After the fight, the victorious stag continued following the doe or rushed at other does, or even locked antlers with another stag who had become aroused by the action of does and stags rushing about. I do not think the parallel movement of these two stags is a broadside superiority display. They were both simply trying to keep up with the same female. Frontal display rather than side-on displays seemed the approach used to threaten and intimidate opponents.

An example of two dominant stags with does meeting and fighting was seen on October 9, 1957, One herd of 35 animals, including 10 stags, approached another herd of 36 caribou with seven stags. When the two groups were about 50 yards apart the approaching group stopped and a large stag left the herd and slowly walked towards a large stag emerging from the second group. They walked together slowly with a stiff-legged gait, with heads down, and fought for 10-15 seconds. At the sounds of the battle, caribou ran towards the combatants to watch; a doe almost got caught between the animals in her attempt to get a better look. A small stag started to mount a doe and there was considerable activity as stags showed increased interest in the does. The defeated stag left the herd and lay down while the victorious stag was busy vocalizing and chasing.

In three contests between a stag in charge of a rutting company and a challenger, the former dominated in each case. Possibly stags with females were victorious because: (1) they were in a higher state of sexual stimulation due to the presence of does; (2) in the process of 'holding' does they had acquired experience in fighting (Collias, 1944); (3) they were perhaps psychologically unprepared for defeat, whereas challenger stags may be slightly more prone to 'giving away'; and (4) they may simply be bigger.

### Mortality

Agonistic behaviour between large stags resulted in considerable mortality. The following observations were made:

1. Two sets of locked antlers found
2. Two pairs of stags found dead within a few feet of each other
3. The remains of two stags at Mt. Albert, Quebec, that died in the previous rutting season
4. A stag that was pushed into a bog hole and probably drowned
5. Observation of a dominance battle in which a stag was mortally wounded
6. A mature stag found dead immediately after the rut (signs of struggle)

In addition to these 13 large stags, one small stag was found dead with an antler puncture and two does were found with antler stabs. The small stag had probably been caught by a large stag, while the two does presumably would not stand for the stag and were charged broadside.

On October 15, 1957, in a herd of 67 caribou there were 25 stags; four stags had broken antlers, two stags were noticeably limping, and 5 stags were covered with mud. I had previously observed one of the muddy stags having his head pushed underwater and held during a serious fight.

## PREMATING STAG BEHAVIOUR

Several basic stag displays were first seen in the first week of October prior to coitus activity in the second week of October. The signal function of these displays was not readily clear to the author and I discuss these displays here rather than under the heading of *agonistic behaviour.* They consist of panting, hock-rubbing, bush-gazing and bush-thrashing.

### Panting

Large dominant stags produce a hoarse guttural sound which has been termed bugling (Dugmore, 1913), grunting (Henshaw, 1970; Lent, 1965), roaring (Fraser, 1968), snorting (Meschaks and Nordkvist, 1962) and rattling (Espmark, 1964a). I think the sound is best described as panting. The head is usually held horizontal, mouth open, and the sound produced by repeated rapid expirations of air from throat and chest.

The frequency and loudness of panting reached a peak each year prior to the actual breeding. The earliest panting was heard October 4, 1957; October 1, 1958; and October 1, 1959. The latest panting was heard October 27, 1958 (3 stags), except for a single stag heard on October 31 of that year. Both early and late panting was low in tone. Also the panting of senile stags was soft.

I have not heard vocal sounds in wild males between the age of 7 months (calf grunting for dam) and 3 years-of-age. However, a captive stag, without competitors, first showed signs of trying to vocalize when 29 months of age. He was able to perfect the sound during a 30 day period (Table 7). His first vocalization came when he was highly stimulated by females in heat and was breathing hard from physical exertion (Table 7).

TABLE 7. MATURATION OF VOCALIZATION IN A CAPTIVE 2½ YEAR-OLD STAG. NO VOCALIZATION HEARD BETWEEN 7 AND 28 MONTHS OF AGE. NO SOUNDS HEARD IN INTERVAL BETWEEN DATES LISTED BELOW.

| | |
|---|---|
| October 14. Doe probably experiencing a silent heat. | |
| 12:38 p.m. | Stag runs at doe slurping. |
| 12:40 | Stag appears to be *panting* but makes no sound. |
| 12:41 | Stag seems to *pant* again. |
| October 16. Doe probably still experiencing a silent heat. | |
| 11:13 p.m. | Stag walks towards doe slurping, makes a sort of convulsive shudder, and pants or grunts once. |
| October 25. Doe believed to be in heat from 8:49 a.m. | |
| 12:42 p.m. | runs at doe, mounts, falls off, *coughs,* and walks away. Slurps, tries to mount, can't seem to get up, *coughs* and heaves, |
| 12:54 | slurps, mounts, falls off, stands heaving, *coughs* twice. |
| November 15. Doe believed to be in heat from 12 noon. * | |
| 3:13 p.m. | Stag mounts 11 seconds, ♀ walks away, ♂ gets off, *pants.* |
| 3:17 | mounts 9 seconds, ♀ walks, ♂ follows *panting.* |
| 3:20 | follows hooking at him, he tries to mount, turns away and *pants.* |
| 3:25 | tries to mount, falls off, *pants.* |
| 3:27 | tries to mount, falls off, *panting* heavily, |
| 3:30 | mounts 11 seconds, *panting* very heavily. |
| ___† | |
| 6:17 | turns and *grunts* and slurps at ♀. |
| 6:24 | runs at ♀ grunting, |
| 6:25 | mounts 3 seconds; ♀ walks away; ♂ follows; ♂ turns and *grunts.* |
| ___† | |
| 9:15 | slurps at doe then *grunts.* |
| 9:30 | runs at ♀, antlers down, then puts head over ♀ back, slurping, ♀ stands, |
| 9:39 | tries to mount but couldn't make it, *grunts* and turns away. |

* Observer was H. L. Russell who termed the more perfected sound grunting rather than panting contrary to the author's use of the words,

† Doe not released to stag from 3:31 to 5:59 or 6:31 to 9:09.

Panting occurred in the field when:

1. A 'travelling' stag searched for does (3 observations 1957-59)
2. A 'travelling' stag approached a human who was imitating panting (2)
3. The dominant stag of a rutting company saw the approach of a. challenger stag (4)

4. A challenger stag approached a herd (4)
5. The victorious stag vocalized after a dominance battle (2)
6. A stag was stimulated by doe's urine (5) or her presence (43)

Panting occurred most when stags were standing, but we did hear it several times from stags lying down who panted when females walked by.

The captive stags appeared to address their panting to females in heat. They were silent between estrus cycles. They did not pant in stag versus stag interactions even though a sexually aroused male was in an adjacent pen and sparred with the stag panting and tending does.

Panting is probably a display of dominance and threat. It probably indicates a high level of stimulation. Panting was heard most often in both the wild and captivity just before a female would stand. It was also common after the stag dismounted.

If a stag had established himself as the dominant stag in a herd he was normally the only male in that group that panted. Nine recognizable stags in 1959 panted when they became dominant stags in a company, but were quiet elsewhere when they were subordinate to other stags. Panting in the latter situations would have attracted the attention of the dominant stag and might have resulted in their expulsion from the group.

Panting of a dominant stag likely served the purpose of mate indentification of does. Four does in heat were seen to seek the association of a dominant stag panting in a rutting company.

Panting likely helped caribou find each other. The sound was audible to the human ear on still days at distances up to 200-300 yards. Five caribou (three stags, two does) were attracted to a rutting company on October 8, 1957, during 6½ hours of observation, by the panting of the dominant stag; visibility was limited to approximately 200 feet by fog. Another herd kept in view for four hours as it travelled 2¼ miles through a partially forested area changed in number as follows: 2, 3, 4, 5, 6, 4, 5, and 3. The panting of the stag could have enabled the individual animals in this group to find the herd while they were feeding.

## Hock-Rubbing

A self-marking display recognized only 7 times was trampling (Espmark, 1964a) or hock-rubbing. In this movement a mature stag would take rapid short steps with his hind legs and shift them under him (Fig.7). During this movement the stag urinated a small amount of urine on the hocks. The animal then turned his hocks inward and appeared to rub his tarsal glands together.

I would suspect that this self-marking served a role in the olfactory stimulation of females approaching heat. However, the display was recorded in an interaction between males, as has been noted in reindeer (Espmark, 1964a).

Notes taken on two occasions were:

> October 14: two large stags clash antlers momentarily but do not fight, each male draws his hind legs up and rubs his hocks.
> October 2: stag walking behind female, stopped, pulled up his hind legs and rubbed hocks and then bush-gazed (he was still there an hour later).

Captive immature stags on a few occasions drew the hind legs under them, hunched their backs and seemed to strain. They did not urinate or rub their hocks. These immature stags smelled musky even though they did not urinate on their hocks.

## Bush-Gazing

Mature stags frequently stood in a 'dejected posture' with neck and head drooping and the eyes partially closed (Fig. 8) (cf. Millais, 1907; Dugmore, 1913). Small antlered stags did not bush-gaze. The earliest we observed this behaviour was October 1 and it was not seen after the middle of October. This behaviour was one of the most common and it could be considered as the basic posture of a large, sexually interested male.

Fig. 7. A stag with his hind legs hunched under him in partial 'hock-rubbing' display.

Fig. 8. 'Bush-gazing'.

This behaviour could be the waiting posture of a dominant male. From this position he can move to challenge approaching males, threaten straying females, and test females approaching heat.

Bush-gazing often occurred in a rutting company when sexual activities has declined, e.g. when the does reclined and small stags ceased showing interest in females. From this position the stag had a commanding view and could continue to advertise his presence while he awaited further developments.

Bush-gazing was also part of the tending behaviour of a stag courting a female (later section). Between displays in which he tested her readiness to stand he would bush-gaze.

Some display sequences involving bush-gazing were:

bush-gaze → antler threa → bush-gaze
bush-gaze → low head-stretch towards female → pant
bush-gaze → pant → bush-gaze
antler threat → rub hocks → bush-gaze

Caribou bothered by flies in the summer assume a similar position (also estrous females) in which they droop their neck and head. They seem to be agitated and waiting (perhaps waiting a further fly attack). However, if the flies become less bothersome they seem to relax and resemble bush-gazing stags—with eyes mostly closed, sleeping on their feet.

### Bush-Thrashing

Another behaviour manifested only by mature stags was the beating of solitary larch (*Larix laricina*) and black spruce (*Picea mariana*). The activity was sometimes violent with both up-down and sideways motions. Small trees were frequently killed by this activity. To be suitable the trees had to be limber and offer some resistance.

The action was not always vigorous; sometimes the tree thrashing is of an intensity similar to that of small stags sparring. The possibility that the displays serve as an auto-erotic function should be considered (Darling, 1937). Erection was not a common accompaniment of the display.

The pattern was frequent in mating herds when there were many large stags and there was a high level of sexual activity. However, it was also performed by lone stags. The display should assist females in locating and distinguishing mature, sexually stimulated males.

## MATING BEHAVIOUR

Mating depends upon the readiness of the female who in turn stimulates the stag. The stag appears capable of breeding the doe over an extended period if he is sufficiently aroused by the stimulus of a doe in estrus. Although the female sets the basic pattern, the stimulating actions of the male may be important to ensure that psychological heat coincides with physiological heat.

As indicated in Table 8, the food intake of stags during the mating period was reduced; however, stags continued to rest, although less frequently, throughout the mating interval. The dominant stag was often the last animal to lie down and the first to become disturbed. When he was sexually stimulated he might raise his head while reclining and pant, often without apparent stimuli. If greatly aroused, it was common for the stag to remain standing in the bush-gazing pose while the rest of the herd bedded. He often 'broke' from this pose quickly to run in a low-stretch posture at does or to herd and drive the females.

### Dominance between males and females

It is likely that a stag may have to dominate a doe to be able to court and breed her. During the rutting season only small stags and does had dominance interactions involving fighting, and these were mostly between antlered females and males with similar size antlers.

TABLE 8. OBSERVATIONS OF THE BEHAVIOUR OF A 4½ -YEAR-OLD STAG* WITH 9 FEMALES ON BRUNETTE ISLAND, 1962.

| Hours Observed | Oct. 10<br>6 Hrs. | Oct. 12<br>5¼ Hrs. | Oct. 14<br>6 Hrs. | Oct. 16<br>6¼ Hrs. | Oct. 18<br>8 Hrs. |
|---|---|---|---|---|---|
| Stags displays recorded | | | | | |
| Slurping | 13 | 5 | 22 | 23 | 14 |
| Mounting attempts | – | – | – | 11† | – |
| Herding does | 3 | 5 | 2 | 4 | 1 |
| Panting | – | – | 1 | 2 | – |
| Bush-gazing | 1 | 1 | 3 | 4 | – |
| Bush-thrashing | 2 | – | 3 | – | 1 |
| Sniffing and licking | 2 | – | 2 | 2 | 2 |
| Percentage of time observed | | | | | |
| Feeding | 37 | 53 | 33 | 45 | 9 |
| Lying down | 44 | 26 | 36 | 36 | 40 |
| Active or Bush-Gazing | 19 | 37 | 31 | 18 | 51 |

* Stag was hand-reared and released to does on September 28; no other stags on the island.

† One female bred.

In the captive studies young stags and older females invariably fought when they were placed together after being separated. The most serious fight occurred between a 2½-year-old stag and a 3½-year-old doe. The doe fought extremely hard but was clearly overmatched. Another 2½-year-old stag and a 4¼-year-old female fought daily for several weeks but seemed almost evenly matched. The numerous interactions recorded in three years from the captive herd showed that males would dominate females of a similar age. Further, two 2½-year old stags dominated two 3½-year-old does and a 3½-year-old stag dominated two 4½-year-old females.

I compared the dominance ranking between the captive males and females of different ages with the mean weight and antler length of *wild* animals of similar age. A good correlation existed between dominance and antler size (Table 9). I would argue that males should be able to dominate females in the rut if they are of similar weight or have antlers of equal size. Possibly females can dominate males if the female has antlers of equal size but outweighs the stag by 20 pounds or more. Age *per se* may be a less precise criterion for dominance between young males and older females since young stags frequently are larger than older females.

The breeding studies on penned caribou in 1960 (one stag and two does) provided information for a comprehensive analysis of stag aggressive behaviour in securing dominance over the females. In applying these observations to wild stock some possible bias must be considered:

1. Although the 29-month stag had reached puberty and appeared more fully developed than a stag of comparable age in the wild, he was not yet mature since he had difficulty panting.
2. The stag lacked sexual finesse. His only sexual experience prior to the study was breeding of a doe when he was a yearling.
3. The stag was prevented from breeding by a canvas halter.

TABLE 9. COMPARISON OF DOMINANCE RANK SECURED FROM CAPTIVE ANIMALS WITH THE WEIGHT AND ANTLER LENGTH OF WILD ANIMALS OF SIMILAR AGE (DIRECTION OF ARROW INDICATES DOMINANCE IN CAPTIVITY).

| Animal | Males | | Females | |
|---|---|---|---|---|
| | Weight (lbs.) | Antler Length (in.) | Weight (lbs.) | Antler Length (in.) |
| 1.5 | 169 | 8.3 | *→ 167 | 7.0 |
| 2.5 | 210 | 10.0 | → 200 | → 8.0 |
| 3.5 | 232 | 15.2 | → 226 | 9.2 |
| 4.5+ | 293 | 24.1 | → 234 | 9.6 |

Sample sizes for weight were 35 males and 60 females. Weights taken in November. Sample sizes for antlers were 29 males and 45 females.

* Presumed, not observed.

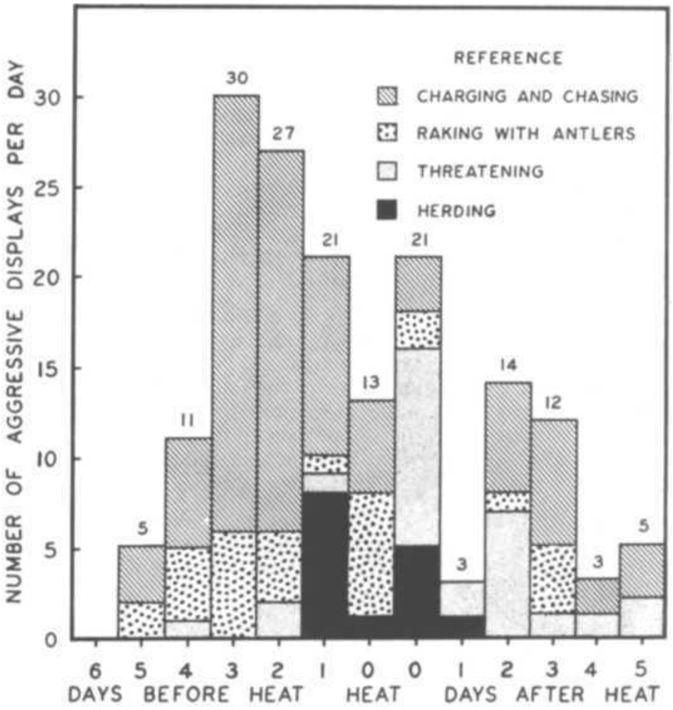


Fig. 9. Comparison of the aggressive displays of a captive stag with the dates of the estrus sequence in two does.

4. The enclosing fence modified his herding and chasing patterns to some degree (enclosure 1/8 acre).
5. The stag was free from the competitive influence of other stags (a yearling stag could be seen in an adjacent pen and the animals sometimes sparred through the fence).

The stag's aggressive behaviour was categorized as: charging and chasing, herding, raking of does with antlers and threatening by a brief lowering of his head.

Aggressive activity was pronounced three days before the does came into heat (Fig. 9). He frequently charged (head down) and chased the does at a hard run around the yard, swiping at them with his antlers. The continued harassment by the stag resulted in the does becoming nervous and reluctant to enter the stag's pen.

The stag's activity and driving appeared to be directed at boxing the does into a corner approximately two days before they came into heat. When one of the does was released from her holding pen the stag would chase her to the opposite corner of the breeding yard, adjacent to the other doe who was still in her holding pen. The same procedure was true when the second doe was released.

The day prior to the first heat each doe had learned the corner in which she should remain if she wished to avoid being driven. This compliance lessened the frequency of aggressive incidents by the stag (Fig.9). The stag's aggressive actions were then restricted to threatening and short runs, similar to a wild stag in charge of a rutting company. The stag's aggressive behaviour declined on the first day of heat (Fig. 9) because the does would not leave his side even though he raked them with his antlers.

One of the two does had a second estrus. In this case the non-estrus doe was still kept cornered adjacent to the doe in heat but when the doe in heat was released she was not herded over next to the non-estrus doe. This suggests the possibility that in a rutting company there may be one or more nucleus does that are closest to estrus around which the stag herds the other does.

During the first week of October stags in the wild are frequently seen chasing does, especially solitary ones. Later when does are associated in companies, the quickest method for a single, straying doe to obtain relief when the stag chases her is to get back as quickly as possible to the other does—in a manner of speaking, to get back in her corner. The stag's charging and chasing drive is reinforced by the sight of running or straying females apart from the other does.

In early November, the breeding pen was divided into two sections and a yearling male was placed in one half with one of the does. Under the stimulus of the competitive stag each male kept his respective doe in the corner opposite the dividing partition, the maximum distance from the other stag.

### Stag recognition of does in heat

As the captive does approached heat there was a noticeable increase in the tempo of the stag's activities (Fig. 9). Probably the doe's physiological condition stimulated the stag as early as three days prior to heat. We were not able to discern any change in visual, auditory or tactile sign stimuli displayed by the doe prior to heat that might stimulate the stag. The increased stimulation must depend on scent stimuli.

In the captive herd, the 2-year-old stag normally smelled and licked the does' external genitalia each time they were released to his company. On one occasion a doe apparently came into heat while she was in her holding pen. When she was released at 7:35 she walked to the lower end of the yard with the stag slowly following. At 7:40 the stag sniffed the doe's vulva and, without any other preliminaries, mounted her. In the next 40 minutes he attempted to mount her 33 times. Seven hours previously, his activities consisted only of chasing and licking at her.

In the wild, stags frequently approach reclining does in order to smell their external genitalia (27 observations). The females always got to their feet as the stag approached. The stags would then smell the ground that was directly beneath the female's tail; often females defecated while resting and pellets were also smelled. On three occasions a small stag, after smelling the ground, attempted to mount a doe as she got up. The doe struggled to escape in all three cases.

The smelling or eating of the doe's urine was observed on 42 occasions in the field, with pawing accompanying the act in 10 instances. One stag kept his nostrils in the hole he had created in pawing for 2 minutes. At times the stags rubbed their muzzles in a sideways motion in the urinated area. The urine of female calves and yearlings was also investigated. Stags occasionally curled up their lips (Flehmen) after smelling the doe's urine or vulva. Yawning was also displayed by the stag. Of 15 yawns recorded, 10 occurred after smelling urine or a doe's vulva. Plants and soil that are urinated on were readily eaten. The stomach contents of one stag contained ½ cup of gravel, accumulated from eating urine-soaked dirt. The investigation of does' urine occurred only during the mating interval. The record of 19 observations in Newfoundland was:

October 13-3 observations

October 14-4 observations

October 15-2 observations

October 16-10 observations

There was no noticeable increase in the frequency of urination by the captive does in 1960 while they were in heat.

**Slurping**

When a doe was approaching heat or in heat, a tending stag constantly made short runs at her in a low-stretch position directed at the head of the female. Usually the stag was standing in a parallel position to the female and slightly behind (Fig. 10). As the stag approached the female's head, he tilted his muzzle up and twisted his head away from the female, minimizing the doe's view of his antlers (Fig. 10). It is my impression that as he turned and twisted his head there was more white of his eye showing. The turning and twisting of the stag's neck and head displayed the white shoulder and mane to maximum view.

Fig. 10. A tending stag in low-stretch display, panting, while doe rubs her head on vegetation (sketch by Penny L. Brown).

Fig. 11. A tending stag licking the vulva of a doe (sketch by Penny L. Brown).

Frequently a stag flicked his tongue in and out near the end of the low-stretch approach. This licking made a slurping sound against the upper palate. I call the *combination* of the low-stretch run and tongue licking, slurping. Vacuum licking was seen only after the low-stretch advance. However, panting commonly followed a low-stretch movement rather than licking. The low-stretch → pant sequence was most common when the female would not stand or when she shifted her hind quarters to prohibit mounting. The low-stretch → tongue licking pattern was the rule when the doe would not stand and the stag was attempting to mount.

The broad-side, low-stretch run accompanied by licking may signify that, although the approach is rapid, attack was not intended. Further, when stags stood bush-gazing (antlers low) prior to the low-stretch run, they invariably stood parallel to the female or facing away, aspects that minimized the presentation of antlers. Slurping was first noticed on the following dates: October 7, 1957; October 8, 1958; October 7, 1959; October 9, 1960. These dates indicate that the display was stimulated approximately three days before the mating phase of the rut gets underway. Stags occasionally ran at does with their necks outstretched prior to these dates, but they did not lick.

Only three matings were recorded in which the breeding stag actually licked the external genitalia of the doe while slurping. These three does stood quietly with their tails lifted while being licked. A fourth stag was seen to lick two different females during tending activity. The captive 2-year-old stag frequently licked the does throughout the heat cycle (Fig. 11). These displays often lasted for 15-30 seconds.

Medium and some small stags slurped but this could not be termed active tending since these animals divided their attention among several does even when not bothered by a larger stag. Some smaller stags slurped the does from behind, contrary to the habit of large stags. The females always ran when so approached. Each season I have seen one or two small or medium stags which had a slurping 'habit'. These animals were constantly on the run, slurping at all the does indiscriminately. The slurping display probably undergoes a maturation process.

The captive 2½-year-old stag also showed little discretion in slurping. He slurped at both a male calf and yearling and displayed vacuum licking when he was mounted. He licked and slurped less when he was 3½ years old and 4½ years old (Tables 8 and 10). His slurping at 2½-years-of-age was correlated with his degree of stimulation which reached a high point approximately 8-14 hours after a doe entered heat (Fig. 12).

## Stag Tending

Stag tending occurred when a mature stag determined that a doe was approaching or was in heat and consistently stayed with her. Tending males aligned themselves behind or beside the female (Fig. 13). The sexual arousal of the stag and doe influenced the duration of tending; the experience of the stag may also have been a factor.

In Newfoundland it was common to see five or six 'pairs' in a herd of 50-80 animals during the peak mating days. If breeding took place in a rutting company instead of a large herd with several stags, the dominant stag divided his time between repelling stags, herding and isolating females, and serving the does. The six matings observed in this latter type of herd structure occurred when the herd was inactive and the dominant stag could devote all his time to tending a doe that was approaching heat.

A stag attempting to get in position and mount was easily distinguished in a herd. As the stag tried to mount, the doe commonly shifted a few steps and the stag then had to swing his head over her hind quarters as he tried to re-adjust his position. This head-swinging movement was repeated time and again. Even when he was in position and had left the ground with his forefeet, the doe often moved a few steps, resulting in the stag either sliding off the rear of the doe (loose mount) or failing to make contact at all. This behaviour sequence lasted. 21, 21 and 30 minutes in the three most complete observations.

TABLE 10. COMPARISON OF STAG LICKING-DISPLAYS USED IN COURTING FEMALES WITH INCREASED EXPERIENCE AT 2½ AND 3½ YEARS-OF-AGE. CF. BEHAVIOUR OF STAG AT 4½ YEARS IN WILD SHOWN IN TABLE 8.

| Age and dates of estrus | Number of displays recorded per 150 min. | |
|---|---|---|
| | Slurping | Licking genitalia |
| 2½-years-of-age | | |
| October 25, 1960 | 107 | 22 |
| October 26, 1960* | 138 | 29 |
| November 15,1960 | 29 | 8 |
| Subtotal | 274 | 59 |
| 3½-years-of-age | | |
| October 25, 1961 | 49 | 1 |
| October 27, 1961* | 13 | 13 |
| November 16,1961 | 74 | 3 |
| Subtotal | 136 | 17 |

*Not same doe in heat as October 25.

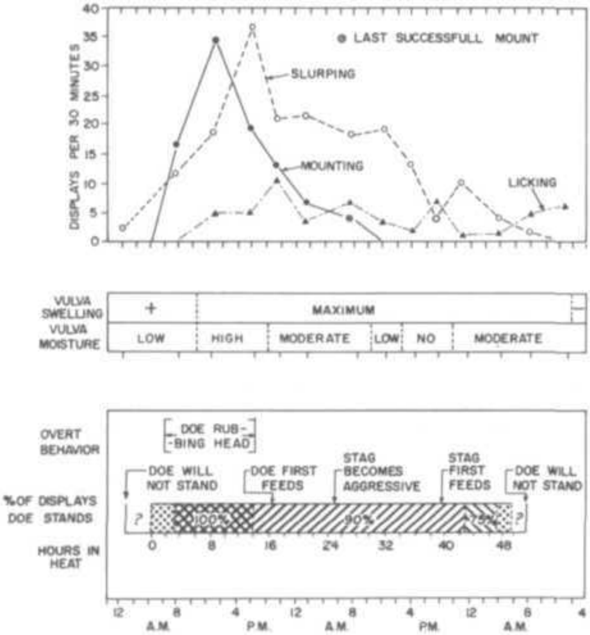


Fig. 12. Overt heat period of captive 2½-year-old doe. Lower diagram shows doe's behaviour in the ±50 hours of her heat. Middle diagram shows physiological condition of doe's external genitalia—observation times indicated by bars along the bottom line. Top graph compares the stag's behaviour during each release to him (at 4-hour intervals) with doe's heat period (bottom diagram). A successful mount implies only a cover of several seconds.

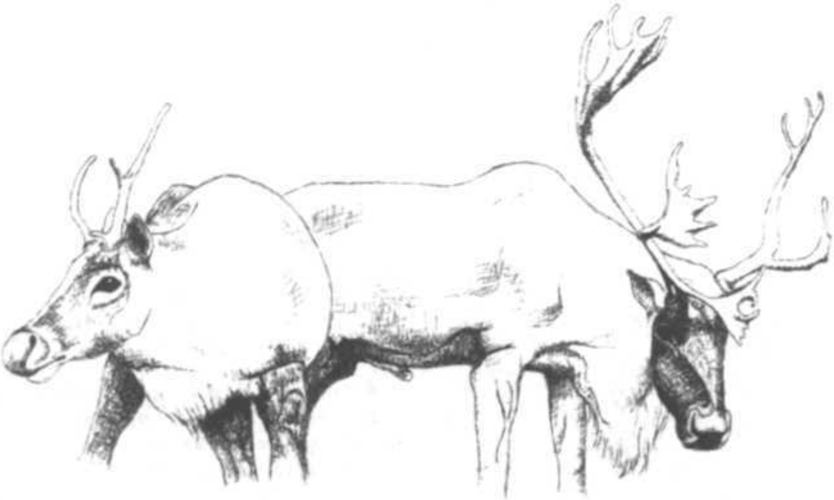


Fig. 13. Doe and tending stag (sketch by Penny L. Brown)

An average of one pre-copulatory mount for every 5 minutes of tending was recorded in 10 matings in Newfoundland. A pair was watched on October 15, 1957, in which the stag tried to mount a doe 23 times in a 2-hour restraining interval. In a similar time period in 1963 a stag attempted 19 mounts. In Quebec in 1959 only one incomplete mount was seen in 209 minutes of tending display.

Hale and Almquist (1960) have reviewed four papers that showed a definite value of pre-copulatory mounting in cattle. Restraining the breeding bulls and allowing pre-copulatory mounts increased the quantity of sperm per service from between 36-251 per cent. Cromback *et al.* (1956) in experiments with identical bulls showed that restraining and pre-copulatory mounts also ameliorated the high quality of the sperm.

## Doe precoitus behaviour

Two captive does exhibited a readiness to stand on their first association with the stag after heat had commenced. One doe's evasive movements ceased after the stag had slurped at her once; in another heat period this same doe accepted mounting after she had been stimulated by a few preliminary mounts during which she struggled. No preliminary stimulation was needed for the second doe to stand.

The early acquiescence of the penned females in 1960 was in contrast to the behaviour of 9 wild does that were bred in 1957 and 1958. The wild females were tended for an average of 30 minutes before they would stand and were bred. The slurping of the stags either coincided or assisted in bringing these wild does into heat, and they were probably served at the beginning of their psychological estrus interval.

When the doe was just about ready to stand she began rubbing her head on small bushes or trees. I recorded this for every pair that I saw at least 10 minutes prior to mating (9 matings). The head rubbing did not appear to increase stimulation in the stags; three does rubbed their heads on the hind legs of their tending stags.

The behaviour of the doe while being slurped can be described as mostly passive. She often adopted the bush-gazing posture between displays of rubbing her head. Some females that were not being served when they first came into heat followed the males; this was especially true at Mount Albert in 1959, at Brunette Island in 1962, in penned studies, and at Sandy Lake in 1964. If one member of the pair lay down the other might also, but frequently the stag remained standing. The tending stag and doe normally rested near each other. Does in heat or approaching heat frequently shifted resting locations to be near the tending stag.

Active breeding behaviour on the part of the females (other than following the male) was recorded in the field on five occasions. In one example the doe followed the stag and jabbed him on the flanks with her antlers. Each time she jabbed him he would turn and slurp at her. She would not tolerate the presence of other does in the immediate vicinity of the tending stag and was seen to threaten (head down) and to give another doe a hard push. In another observation an antlerless doe was seen following a stag. A few seconds prior to coitus she sniffed the stag's external genitalia and then a moment later she smelled his anus. One doe prodded a stag lying down and smelled his sheath when he got up.

## Coitus

The average length of the matings that I considered successful, based on the stag's thrusting behaviour and doe's pre-coitus behaviour, was 7 seconds. The longest successful mount was 15 seconds (Fig. 14). Only two stags appeared to successfully breed a doe a second time, and these covers occurred immediately following the first service. Five does fell after losing their balance due to the added weight of the stag (Table 11). Does were struck with the stag's antlers on four occasions when they would not stand. Nearly half of the does in which mating was witnessed struggled to escape the stag during coitus. These does were probably being bred at the very start of heat. We saw several examples of inappropriate mounting in the wild: doe mounting doe, males trying to mount female calves, and a male calf trying to mount a female calf. A captive yearling male mounted a male calf and the male calf mounted the male yearling seven times.

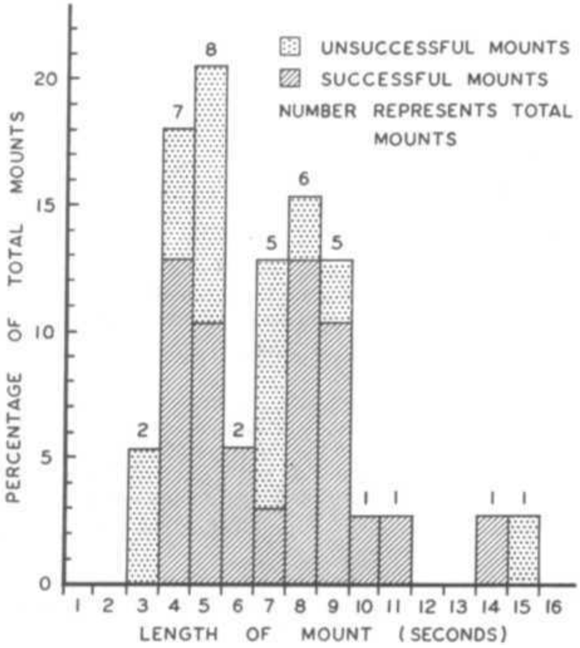


Fig. 14. Lengths of mounts in the wild

Common display sequences for the male prior to coitus were:

Bush-gaze →slurp (female runs) →pant →threat

Bush-gaze →slurp (female moves a little) →bush-gaze

Bush-gaze →slurp (female stands) →mounts →pants

The mounting of the doe often stimulated other males in the herd to increased activity. One large stag was struck broadside by another stag and knocked off. In another case a second male ran beside a couple but did not interfere.

Small stags that tried to associate with or mount a doe were usually charged and driven off, but may occasionally have had success; the most successful technique being to sniff a doe lying down and mount her when she got up. The large stags that tended the does were normally not bothered during mating.

Most of the mating occurred in the afternoon (Table 12). Most of the mating in reindeer also occurred in the afternoon (Espmark, 1964a).

Nocturnal breeding probably occurred. Panting stags passed by my tent at night on two occasions. A herd we visited at midnight on October 7 was active. Furthermore, the breeding activity of the captive animals was not curtailed by darkness.

The percentage of does that were bred in the daytime in three large herds (60-80 animals) watched for 5 or more hours was:

6 per cent in 6 hours—October 10, 1963
8 per cent in 7 hours—October 11, 1963
0 per cent in 5. 5 hours—October 12, 1963
16 per cent in 8 hours—October 13, 1958
8 per cent in 5 hours—October 14, 1958
13 per cent in 6. 5 hours—October 15, 1957
6 per cent in 6. 5 hours—October 16, 1957
6 per cent in 6 hours—October 16, 1963

TABLE 11. GENERAL REMARKS RELATIVE TO COITUS AND POST-COITION ACTIVITY

| Coitus No. | Remarks |
|---|---|
| 1 | She was walking when he mounted he had not inserted his penis when he was struck by another stag (head down) broadside and knocked off. |
| 2 | While the stag was mounted another stag came over and ran alongside the couple but did not interfere. |
| 3 | A small stag appeared to jump on doe, she either got away or he dismounted as a large stag came over; he ran and larger stag chased doe. Smaller stag returned immediately to coition spot in erection and searched spot with nose to the ground, mouth open. He then chased a stag smaller than himself. |
| 4 | Small stag mounts doe without preliminaries. She struggles very hard and he falls off. Act excites other stags. |
| 5 | A large stag mounted (14 sec.) and reached well forward causing doe to lose balance and be pulled backwards. She escapes and a few moments later he mounts again. After this copulation he laid his muzzle on her back after panting at her. She urinated after second copulation and walked stiff-legged and immediately began to feed. He was still with her 45 minutes after copulation. |
| a | The weight of the stag causes doe to fall. Upon getting up she walked away stiff-legged with her tail up. They separated. |
| 7 | The weight of the stag causes the doe to fall. She walks away stiff-legged and he follows panting still in erection. Coition was at 4: 53 p.m. At 10: 55 a.m. this stag had been defeated in hard two minute battle. |
| 8 | She walks away slowly and stiff-legged. He follows and makes a short run at a stag and then returns to doe panting. After she lies down (6 min. after coition); he also beds down near her. |
| 9 | He didn't have a secure enough grip on her to be successful. He leaves her immediately and slurps at another doe; he is in erection with second doe. |
| 10 | Small stag mounted doe, driven-off by dominant stag #1. Stag #1 follows female slurping and panting. He would stand still bush-gazing for about 1 minute, then slurp 5 seconds. Doe rubbed head on stag's neck 5 times before stag mounted. Mounted for 9 seconds at 5: 15 p.m. Mounted again 5: 20 for 7 seconds. Doe fell in waterhole and hurt one leg. He tried to mount twice more but she ran. No. I returned to herd and a small stag tried to mount. Doe walked 50 yards from herd followed by small stag and doe. Stag No. 1 ran at the three animals and they returned to herd. |
| 11 | Stag courting doe 11: 00 a.m. Stag lies down 11: 05 and female lies down beside him at 11: 12. At 12: 40 stag gets up and slurps at doe causing her to get up. He mounts 1: 05 for 15 seconds unsucessfully. Mounts again 1 : 14. They were 100 yards from herd and stag (4th in rank) kept doe from entering herd. Stag left doe after breeding and she disappeared into woods. |
| 12 | 3: 24 stag mounts doe unsuccessfully for 8 seconds. Mounts again 3 : 25 for 5 seconds. Doe and stag fall down—doe then runs into woods. Stag did not follow but started tending another doe. |
| 13 | 3 : 24 old stag slurped doe and driven off by 6th rank stag. Doe then mounted by 4th rank stag. 1st rank stag charges to drive him off; however, copulation was successful as doe walked off, humped back and tried to urinate. 1st ranking stag smelled doe but she would not let him touch her. Stag 1 returned to doe he had been courting. |
| 14 | 1st rank stag following small doe 1: 42. He courted her all afternoon and unsucessfully covered her 16 times (2: 27, 2: 29, 2: 31, 2 : 35, 2: 40 (7 seconds), 2: 47, 2: 54, 2: 59, 2: 59, 3: 02, 3: 08, 3: 12, 3 : 23, 3 : 34, 3: 41 and 3: 47 (7 seconds). He left her at 2: 34 to investigate a doe rubbing her head on tree and was followed by doe he had been courting. He left her again at 2: 41 to walk to another doe and again she followed. He then returned to her and was last seen courting her at 3: 50. |

TABLE 12. HOURLY SEQUENCE OF 32 MATINGS RECORDED.

| A.M. Time | No. of Matings | P.M. Time | No. of Matings |
|---|---|---|---|
| 7-8 | – | 12-1 | 1 |
| 8-9 | 1 | 1-2 | 3 |
| 9-10 | – | 2-3 | 5 |
| 10-11 | 3 | 3-4 | 8 |
| 11-12 | 5 | 4-5 | 5 |
|  |  | 5-6 | 1 |
| TOTAL | 9* |  | 23 |

* Caribou often not located until late in the day.

TABLE 13. HIGHLIGHTS IN THE SEXUAL BEHAVIOUR OF A CAPTIVE DOE DURING HEAT.

| Time from Start of Heat | Behaviour Description |
|---|---|
| 5 min. before heat estimated to start | Doe starts along fence. Stag rushes at her, drives her in a hard run twice around yard and back to other doe's pen. Doe walks about nervously. |
| Start of Heat | Stag slurps mildly at doe. She lowers her head and rubs it against a bush; stag ignores her. |
| 10 minutes | Stag slurps at doe again, mounts her. Doe struggles to keep her footing, but stands. (Stag had slurped 7 times first 10 minutes). |
| 14 minutes | (Man) tried to return doe to her pen. Doe did not come in for 12 minutes. During this time stag mounted her four times. Doe would rake at stag's side with antlers, rub head on bushes. |
| 7½ hours | Doe rubbing her head on bush. Doe touches stag's side with her antlers; stag slurps, mounts for 9 seconds. Dismounts, walks around doe. Doe moves herself into right position but stag does not mount. |
| 13 hours | Doe released; walked to middle of yard. Stag followed and licked at her genitals; doe stood. Doe started to feed. Stag ran at her, slurping; doe moved away. |
| 13¼ hours | Doe walks up behind stag and pokes him with her antlers. |
| 23¼ hours | Stag starts to walk away. Doe follows, touches him on rump with antlers; stag wheels on her, threatens with antlers. |
| 24 hours | Doe touches him on rump with antler; he turns, swipes at her with his antler. |
| 28 hours | Stag moves away from doe; doe follows; stag threatens with antlers; doe rubs head on-small hummock. |
| 38½ hours | Stag slurps at doe; she rubs her head against him... stag walks away, starts to feed; doe follows; stag threatens her with his antlers. .. stag roams around the yard, threatens doe with antlers when she tries to follow.. . doe licks his side... she rubs her head on poles of pen. |
| 2 hours after heat estimated to have ended | Doe released. Stag walks towards doe. She turns away. Stag starts to feed near her; she moves away. Stag threatens and drives doe down to other doe's pen. Stag slurps at doe; she ignores him. Stag slurps at doe; she keeps her foreshoulders to him; will not put herself into correct position for stag to mount. |

TABLE 14. SEXUAL BEHAVIOUR OF TWO CAPTIVE DOES AND ONE STAG* DURING A FIRST OVERT HEAT PERIOD.

| Behaviour description | Hours from commencement of hea | |
|---|---|---|
| | Doe 1 | Doe 2 |
| Doe behaviour | | |
| Stands for 100% stag displays | 0-14 | 0-13 |
| Stands for 90% stag displays | 14-42 | 13-39 |
| Stands for 75% stag displays | 42-50 | 39-50 |
| Rubs head on bushes | 0-14 | 0-28 |
| Doe first feeds | 16 | 13 |
| Stag behaviour | | |
| Most mounting attempts | 8 | 8 |
| Most slurping displays | 14 | 8 |
| Most licking | 17 | 25 |
| Stag first aggressive to doe | 21 | 30 |
| Last time doe covered | 27 | 25 |
| Stag first feeds | 39 | 39 |

*The stag was prevented from breeding the does by a belly harness.

The penned studies in 1960 provided additional information on the sexual behaviour of females throughout heat (see Table 13), since fertile matings were not permitted. Three stages of psychological heat were recognized for the first estrus period from the observations of the two captive does (Table 14; Fig. 12).

Judging from the stag's behaviour and the moisture condition of the vulva (Fig. 12) the physiological development of heat was at its highest level about 8 hours after the commencement of estrus.

The captive stag frequently tried to mount the does over their heads, at which times they would hook at him with their antlers. This behaviour continued throughout heat and was seen again in another heat 20 days later. Presumably learning is involved in mounting behaviour.

After being bred wild does often squatted and urinated, raised their tails and walked stiff-legged; servicing may have been painful. When stags tried to mount does again they normally ran from the stag.

The stags displayed successive polygamy in their breeding habits, seeking other females immediately following breeding. Three recognizable males courted three different does on two successive days. There was little evidence of polyandrous breeding. One female was mounted by the dominant stag in the herd at 5 :18 p.m.; he stayed up 4. 5 seconds; she then urinated and walked with legs spread. The second-ranked stag in the herd mounted her' at 5 : 55 p.m. for 7 seconds; again she walked with legs spread. Five other females would not stand for sexually interested stags on the day following breeding.

## DOMINANCE BETWEEN MALES AND BREEDING STATUS

It was difficult to determine a breeding hierarchy among stags in Newfoundland because the herds were larger and the unrestricted range facilitated extensive movements; seldom was it possible to recognize known stags on subsequent days.

A ranking or social order of stags was indicated by several observations. In the first example, two harems met on October 5 with Stag 41 defeating Stag 49 (see Table 4). The next day the herd was again located and large stags 62, 65 and 51 were also present. No dominance battles occurred between these five animals in the morning. Their status could have been determined before arrival. At 12: 30 p.m. a very large stag (54) joined the herd. He immediately pushed very briefly with Stag 51 who backed off. Stag 54 then advanced to meet Stag 41 who backed away. Stag 54 sttod panting and then at 12 : 45 p.m. Stag 62 advanced on No. 54. They locked antlers and fought vigorously for a few seconds until Stag 62 gave up and jumped aside. A few minutes later Stag 49 locked antlers with the new stag but he in turn was defeated. Stag 54 had established himself over four rivals in less than one hour's time. The presence of several large rivals precluded the establishment of a rutting company dominated by one stag, but a 'pecking-order' seemed evident.

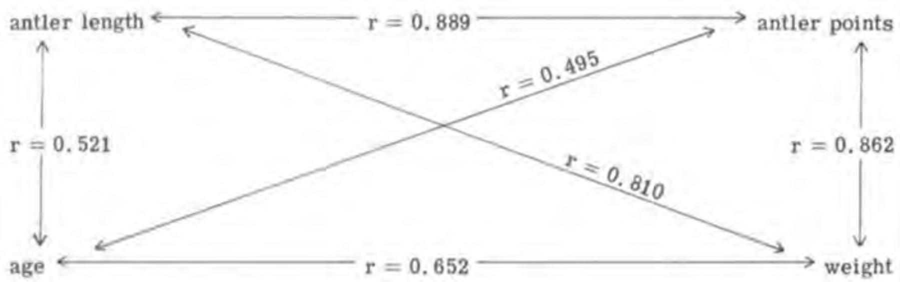
The second observation involved a herd of animals watched on October 10-12 and 16, 1963. Interactions between stags indicated that a definite social hierarchy was being enforced.

The studies at Mt. Albert, Quebec, in 1959 showed a clear dominance ranking among 26 stags (Bergerud, 1960). The large antlered animals were near the top of the hierarchy while the young and smaller antlered animals were subordinate.

### Physical Basis of Dominance

Dominance status between males should be based on physical status since fighting is very vigorous. Body weight and antler size probably reflect physical condition. A dominance ranking between five wild stags held in captivity was correlated with weight and antler length. In descending order of rank the five stags weighed 310. 300. 295 and 235 pounds.

In the wild, only stags of comparable antler sizes had dominance fights. Antlers were used for threatening. Stags may recognize the approximate status of potential rivals by their antler size. Antler size and body weight showed a closer correlation than antler length and age in 27 Newfoundland stags (below and Fig. 15).



Antler size then should be a reliable index of size and provide some advance information of the strength and possible outcome of a fight.

Males continue to increase in body size and antler size until about 6 years (Fig. 15; Table 9; and Skoog, 1968). Yearlings, 2-year-old stags and 3-year-old stags (those classified in this investigation as having small antlers) were clearly of subordinate rank to large antlered stags. These small animals did not challenge large stags to dominance fights but avoided them when threatened.

There were also older stags that had regressed antlers (Table 15). One stag with regressed antlers that I captured had only 7 points; another stag had spindly antlers with 4 points. Two animals with regressed antlers collected in 1959 were aged by

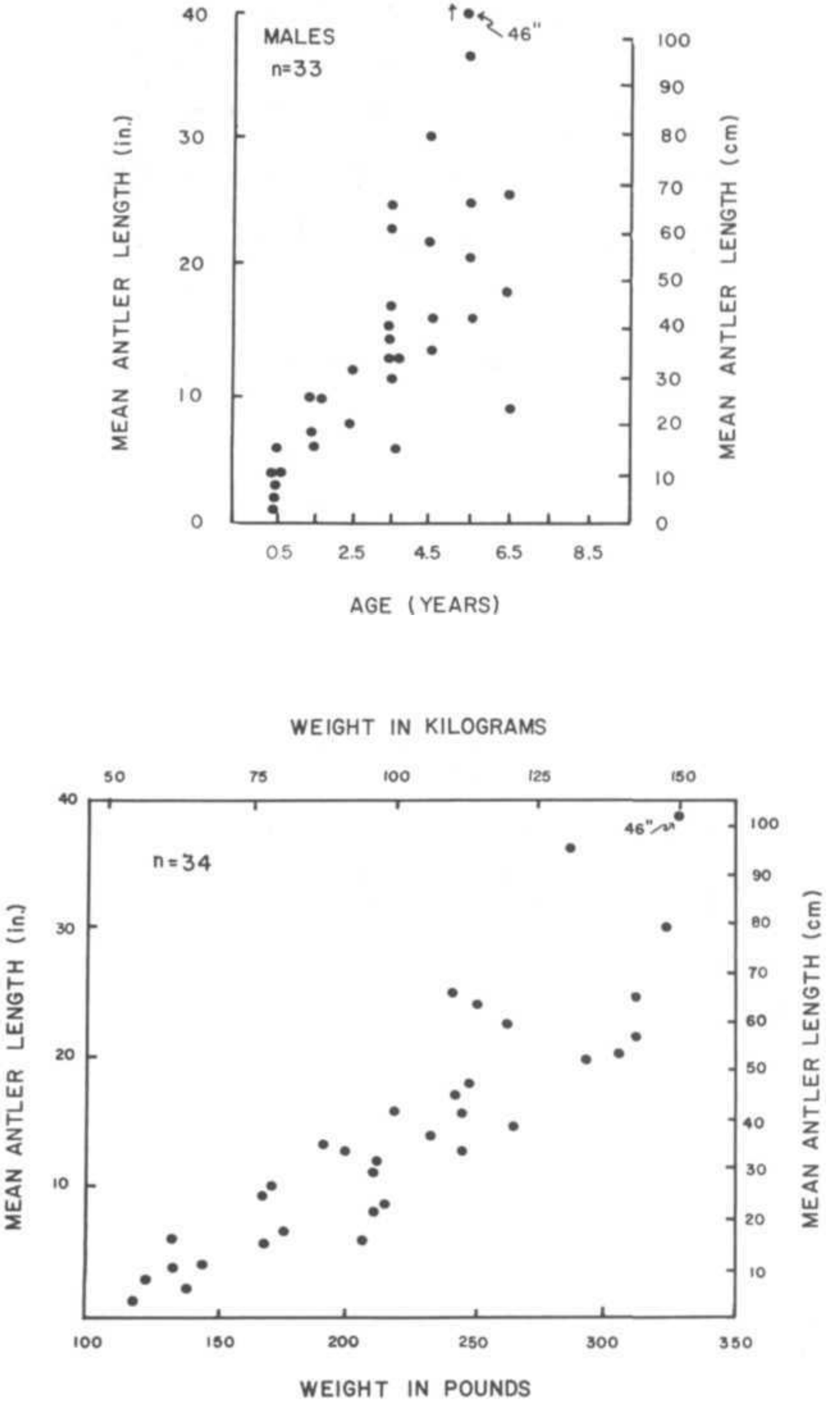


Fig. 15. Comparison of age (upper) and weight (lower) with antler length in stags

tooth wear as 7-9 years and 10+ years. Approximately 8 per cent of the males older than yearlings had regressing antlers (Table 16). Based on the age arrays of stags aged by tooth wear and annulations in an earlier study (Bergerud, 1971b), this 8 per cent of the male population would represent animals 10 years of age and older.

TABLE 15. NUMBER OF ANTLER POINTS OF STAGS COMPARED BY AGE.

| Age in years | Stags in sample | Mean No. of points |
|---|---|---|
| 1 | 14 | 5 |
| 2 | 2 | 8 |
| 3 | 7 | 15 |
| 4-6 | 11 | 24 |
| 7-9 | 7 | 17 |
| 10+ | 3 | 14 |

TABLE 16. STAG CARIBOU CLASSIFIED AT SANDY LAKE ON THE BASIS OF ANTLER SIZE AND CONDITION.

| Fall season caribou classified | Total stag caribou in sample | Percentage of stags observed based on antler size* | | | |
|---|---|---|---|---|---|
| | | Small antlered | Medium antlered | Large antlered | Regressed antlered |
| 1957 | 56 | 30 | 20 | 45 | 5 |
| 1958 | 158 | 10 | 20 | 69 | 1 |
| 1959 | 101 | 3 | 64 | 25 | 7 |
| 1960 | 49 | 39 | 31 | 16 | 14 |
| 1961 | 30 | 47 | 10 | 37 | 7 |
| 1962 | 82 | 40 | 13 | 39 | 7 |
| 1963 | 46 | 37 | 22 | 28 | 13 |
| 1964 | 16 | 12 | 20 | 62 | 6 |
| Unweighted Average | | 27 | 25 | 40 | 8 |

*The estimated age of the stags were: small, 2-3 years; medium and large 3-9 years; regressed, 10 years and older.

These older animals did not challenge large stags in fights and were usually seen alone. In 1959 seven old stags were seen all travelling alone.

The senile stags were usually not active with does and often did not even approach females. For example, on October 6, 1957, I encountered a 'senile' stag in a lichen woodland (Fig. 16). I approached the animal to within 25 feet before he even noticed me. He paused only for a moment and continued to feed. The animal moved, with what can only be described as a 'tired walk'; I could not get him to run. I followed him until he joined a doe. He walked up to her and panted softly; they fed together for a few minutes and then he left her and continued on his way. A few days later, on October 9, just prior to the commencement of breeding, a senile stag with four points was seen following a large active mating herd. The 'tired walk' of this animal just managed to

Fig. 16. A senile stag with regressing antlers.

keep him within sight of the herd. When the herd bedded down, he caught up and remained on the fringe, presumably so as not to be bothered.

### Function of Dominance Hierarchy

I believe a dominance ranking between males provides the best stud stock, through competitive selection, and reduces disturbances during breeding. It does not appear that a dominance rank results in a saving of stag energy that can be applied to greater activity in servicing the females; the energy of the stag appears to be related to the number of does to be served (Table 17). In the observations in 1959 and 1962, the does took an active part in provoking the breeding stag to greater effort. They frequently pushed the males with their antlers and attempted to smell and lick them. The dominant stag in both the 1959 and 1962 study herds showed definite signs of fatigue. The dominant stag in 1962 actually fell over backwards in attempting to mount a doe. Also in this herd two does were not served until 19 hours and 25 hours after they first showed signs of being in heat by rubbing their antlers on the stag and trailing after him.

TABLE 17. RELATIONSHIP BETWEEN SEX RATIOS AND LENGTH OF COURTSHIP (SAMPLE SIZE IN PARENTHESIS).

| Year | Herd name | Does per mature stag* | Length of courtship |
|---|---|---|---|
| 1957-58 | Sandy Lake, Nfld. | 3 | 30 min. (9) |
| 1959 | Mt. Albert. Que. | 5 | 106 min. (2) |
| 1963 | Sandy Lake. Nfld. | 5 | 147 min. (2) |
| 1962 | Brunette Island, Nfld. | 9 | 4½ + hrs. (2) |

*A stag one classified as having medium or large antlers, probably 4 to 9 years of age.

TABLE 18. COMPARISON OF THE FIGHTING FREQUENCY AND POSSIBLE MODIFYING FACTORS BETWEEN NEWFOUNDLAND AND GASPE, QUEBEC, CARIBOU HERDS.

| | | Sandy Lake-Badger, Newfoundland | | Mt. Albert Gaspe, Que. |
|---|---|---|---|---|
| | | 1957 | 1958 | 1959 |
| 1. | Extent of breeding area | Unrestricted, herd moving ¾ miles/day | Unrestricted, herd moving 1¼ miles/day | Restricted, entire area 5.5 sq.mi. |
| 2. | Possible mature stag combinations* | 435+ | 435+ | 91 |
| 3. | Sex ratio of mature stags per 100 does | 30 | 37 | 18 |
| 4. | Average number of large stags seen per day | 8 | 7 | 3 |
| 5. | Size ratio of small: medium: large stags | 1:1:2 | 1:2:7 | 1:1:1 |
| 6. | Length of breeding season (days) | 6 | 6 | 19 |
| 7. | Dominance fights seen per day (fights and days recorded) | 1.2 (6/5) | 1.4 (14/10) | 0.2 (3/19) |

* [N(N-1)]/Z

The role of a dominance status in reducing disturbance during breeding is illustrated by comparing the fighting frequency between stags in Newfoundland with fighting between stags at Mt. Albert, Quebec (Table 18). In Newfoundland there were many more large stags of similar physical status than at Mt. Albert, Quebec. This difference resulted because few calves had survived in Newfoundland from the 1954-1956 cohorts (Bergerud, 1971b); hence fewer young animals. Also in Newfoundland the area covered by the herds was greater than Mt. Albert, hence stags encountered each other less frequently. The dominance hierarchy between 26 stags at Mt. Albert, Quebec, was clear-cut (Bergerud, 1960). The dominance status between individuals of similar size in Newfoundland was less clear. Fighting was considerably more intense in Newfoundland than at Mt. Albert (Tables 16 vs. 19). Medium-antlered stags were able to breed some females, especially in 1963 and 1964, when the percentage of stags in the population had been reduced by stag-only legal hunting (Bergerud, 1971c). Young small-antlered stags (2 and 3-year-olds) and senile stags (10 to 14 years) bred few females (Table 19).

Young stags were physiologically capable of breeding females. A captive yearling male successfully bred a female. The captive 2½-year-old stag was very active mounting females although he was clearly very tired when two females were in heat simultaneously (Table 20). Young stags in the wild were prevented from breeding, since they were not always dominant over older females and their subordinate status in the male hierarchy usually prevented them from associating with females. In the few instances that they did mount females they were invariably driven off by a large stag (see Table 11).

It is not clear if the senile stags would have bred females in the absence of mature stags 4 to 9 years of age. The two senile stags collected had mature spermatozoa in the epididymis. Incidentally, neither stag smelled musky even though both were collected at the peak of breeding activity. Old stags had little interest in females, and even without competition they probably would not have served females.

TABLE 19. COMPARISON OF THE SIZE OF STAG ANTLERS AND SUCCESS IN BREEDING IN NEWFOUNDLAND BETWEEN THE YEARS 1957-1962 (APPROX 1 ♂♂:2 ♀♀) AND 1963-1964 (APPROX. 1 ♂♂: 3 ♀♀).

| Year and size of stag's antlers | Number of observations (Covers)* | | |
|---|---|---|---|
| | Successfully breeds doe | Unsuccessful in breeding | Success unknown |
| 1957 to 1962 | | | |
| Small | – | 3 | 1 |
| Medium | – | – | 1 |
| Large | 24 | 2 | – |
| Senile | – | – | – |
| 1963 and 1964 | | | |
| Small | – | 3 | 1 |
| Medium | 2 | – | 1 |
| Large | 3 | 5 | 3 |
| Senile | – | – | – |

*Mounted for at least 4 seconds.

TABLE 20. COMPARISON OF THE BEHAVIOUR OF A CAPTIVE 2½-YEAR-OLD STAG WITH THE NUMBER OF CONTACTS WITH TWO DOES IN SIMULTANEOUS HEAT AND WITH ONE DOE IN HEAT.

| Order of* Experimental Releases (Contacts) | Two Does in Heat | | | One Doe in Heat | | |
|---|---|---|---|---|---|---|
| | Total Mounts Tried | Per cent Successful† | Average Length Mount‡ | Total Mounts Tried | Per cent Successful† | Average Length Mount‡ |
| 1 | 27 | 81 | 5.3 | – | – | – |
| 2 | 65 | 54 | 4.5 | 2 | 0 | – |
| 3 | 35 | 71 | 3.5 | 7 | 29 | 3.5 |
| 4 | 13 | 31 | 3.3 | 27 | 56 | 7.7 |
| 5 | 25 | 64 | 3.6 | 20 | 60 | 4.4 |
| 6 | 5 | 100 | 3.5 | 17 | 41 | 5.3 |
| 7 | 5 | 0 | – | 14 | 64 | 7.8 |
| 3 | 1 | 0 | – | 15 | 47 | 5.7 |
| 9 | – | – | – | 11 | 55 | 6.2 |
| 10 | – | – | – | 6 | 17 | 3.0 |
| 11 | – | – | – | 5 | 40 | 3.5 |
| Totals and Means | 176 | 60 | 4.4 | 124 | 49 | 6.4 |

*does released every 4 hours, does continued to stand until the 12th release
† i.e. stag covered does (he was prevented from breeding by harness)
‡ time in seconds (mean length of copulations seen in wild which were considered successful was 7 seconds)

TABLE 21. COMPARISON OF THE SOCIAL RANKING OF STAGS AND SUCCESSFUL BREEDING FREQUENCY IN NEWFOUNDLAND, 1963.

| Social Ranking of Stags (descending order) | Days Stag Observed | Females Bred |
|---|---|---|
| 1 Large Stag 1 | 4 | 4 |
| 2 Large Stag 6 | 3 | – |
| 3 Large Stag 5 | 1 | – |
| 4 Large Stag 2 | 4 | 1 |
| 5 Large Stag 10 | 1 | – |
| 6 Medium Stag 3 | 3 | 1 |
| 7 Medium Stag 4 | 3 | 1 |
| 8 Medium Stag 7 | 2 | – |
| 9 Medium Stag 8 | 2 | – |
| 10 Old Stag 11 | 1 | – |

The rutting study in 1963 showed that success in breeding females was a function of dominance status (Table 21). The success of stags breeding at Mt. Albert, Quebec in 1959 was also correlated with dominance status. The dominant stag on the mountain performed two of three matings observed. His tending and slurping behaviour indicated that he bred additional females (Bergerud, 1960).

The considerable difference in the size of males and females is indirect evidence that physical size is important for the Darwinian fitness of males. A large male frequently weighed 375 pounds whereas females averaged 234 pounds (Table 9). Presumably, the greater size in males has been selected for in threatening and dominance fighting. Large animals were more successful than smaller animals in these competitions and in the subsequent siring of young.

It is relevant to note that coitus is extremely strenuous for females. They often fell, seemed to get hurt, and seldom would stand a second time. Competition between males favoured increase in size, but this trend could not go too far or females would not be successfully bred. The size difference between males and females may be a factor in the brief coitus. It is difficult to imagine how the time interval could be successfully shortened further to accommodate larger males.

## DISCUSSION

### Differences in the survival of males vs. females

In Newfoundland male caribou have a lower survival rate than females: the mean age of males was 3. 0 years and of females 4. 7 years. In a sample of 42 males there was only one male older than 6. 5 years whereas in 99 females there were 17 females older than 6. 5 years (Bergerud, 1971b). The tertiary sex ratio of caribou in Newfoundland and elsewhere in North America shows a predominance of females (Table 22). The secondary sex ratio shows slightly more males (Kelsall, 1968; Skoog, 1968; Bergerud, 1971b). The alteration of these ratios clearly indicates males die at greater rates than females in all populations.

There are many cause-and-effect hypotheses to explain the increased mortality of males in mammals. The most commonly mentioned are: (1) genetic-sex-linked mortality in the XY sex; (2) increased predation of males since they are more bold

TABLE 22. THE TERTIARY SEX RATIO IN THE GENUS RANGIFER IN NORTH AMERICA FOR ANIMALS 2 YEARS AND OLDER.

| Name of Herd and Geographical Location | Per cent Males | Source of Information |
|---|---|---|
| Arctic Herd, Alaska | 42 | Lent 1965 |
| Forty Mile Herd, Alaska | 40 | Skoog 1968 |
| Nelchina Herd, Alaska | 35 | Skoog 1968 |
| St. Matthew Island Herd, Alaska | 41 | Klein 1968 |
| Mt. Albert Herd, Quebec | 36 | Bergerud 1971b |
| Mealy Mt. Herd, Labrador | 40 | Bergerud 1967 |
| Avalon Penninsula Herd, Nfld. | 40 | Bergerud 1971b |
| Interior Herd, Nfld. | 32 | Bergerud 1971b |
| N.W.T. Herd, Canada | 34 | Kelsall 1968 |

and independent than females; and (3) greater energy demands for males, hence increased susceptibility to starvation.

In cause-and-effect arguments one can recognize four possibilities in a 2 x 2 contingency table (after Chitty, 1967):

| | | **Supposed Cause** | |
|---|---|---|---|
| | | Present | Absent |
| Supposed | Present | A | B |
| Effect | Absent | C | D |

Correlation arguments are possible if both the cause and effect are present. However, for a supposed cause to be both necessary and sufficient, one must provide evidence of *not* finding incidences of (1) the cause absent but effect present (B)—cause not necessary, and (2) the cause present but effect absent (C)—cause not sufficient.

The first hypothesis to explain increased mortality of males on the basis of sex-linked mortality in the XY sex does rot seem to meet the requirement of a sufficient cause. Apparently in the wildebeest (*Connochaetes taurinus*) there are more males than females (Talbot and Talbot, 1963). In moose (*Alces americana*) the sex ratio of adults is likely balanced (Pimlott, 1959).

The second hypothesis that males are more prone to predation does not seem to be a cause that is necessary when applied to ungulates. There are several studies of ungulates in North America that show a preponderance of females in populations with little or no predation.

The third hypothesis that the physiological and energy requirements are greater for males than females, leading to increased starvation of males (cf. Flook, 1970), also does not qualify as a necessary cause when extrapolated to all ungulates. There are many ungulate species living in moderate climates where starvation has not been reported but where the sex ratio favours females (cf. Schaller, 1967).

Another theory for the shorter life span of males could be based on the productive probability distribution of Medawar (1952). Williams (1966:266) explains the distribution: 'Any variation that appears before sexual maturity will play a role in determining the entire population. By contrast, variation in fitness that appears only at an age to which almost no individuals survive will play little in determining the extent to which individuals reproduce. Selection may therefore produce slight increases in fitness in youth, even if they produce markedly deleterious effects later on.'

Medawar's (1952) model for senescence indicates that the force of natural selection weakens with increasing age because the older age classes are less frequent. The accumulation of deleterious characteristics would be inversely proportional to an animal's contribution to future generations. In caribou, the selective value of natural selection would decline more rapidly in males than in females since social competition prevents older males from breeding but is not similarly restrictive to females. Maximum genetic fitness for males may occur as early as 5 or 6 years of age (body growth completed by that time). Females in Newfoundland continue to bear young until perhaps 17-years-of-age.

In summary then, this hypothesis would suggest that the increased mortality of males is simply due to the fact that males age more rapidly than females; this is because maximum genetic fitness in males occurs at an earlier age than in females.

We have little information on how to judge senescence. In caribou the antlers of males commonly regressed in animals 10+ years of age (see Table 16), but not in females of a similar age (Fig. 17). Older males also seemed listless, but this was not noted in females. Recently Lowe (1969) and Flook (1970) have reported that the teeth of elk (*Cervus* spp.) abated more rapidly in males than in females, which is consistent with this hypothesis.

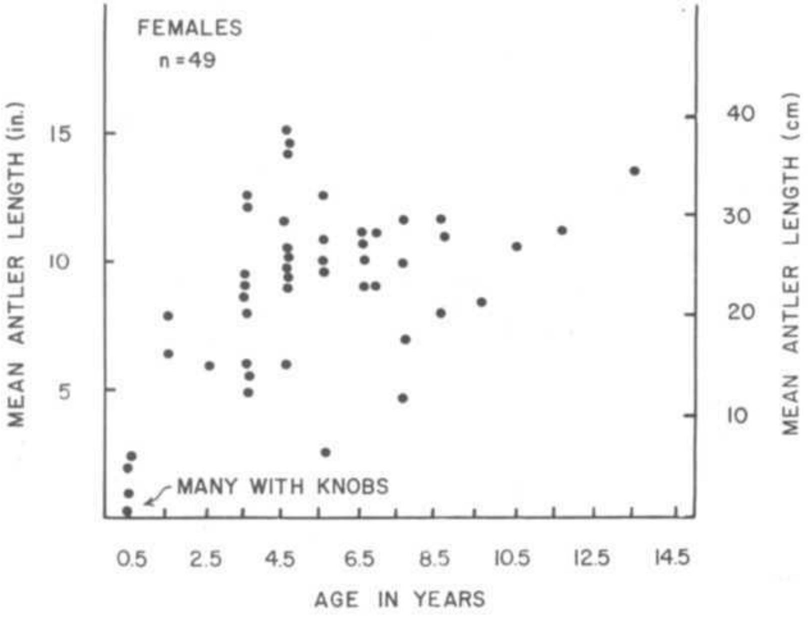


Fig. 17. Comparison of age and antler length in females

This hypothesis will fail as a universal generality for ungulate species where the female rears the young, if the sex ratio favours females yet the frequency of breeding is not altered between females vs. males with advancing age—cause not necessary. Again the hypothesized cause will not qualify as sufficient in polygynous species that have equal numbers of males and females but in which older males are prevented from breeding while females continue to bear and raise young beyond the common breeding age of males.

### Behavioural Differences in Males and Females

Stag caribou are more solitary, bold and less wary than does. These differences likely contribute to the Darwinian fitness of each sex: the more wary and gregarious female in her role of successfully rearing young, the more bold and solitary male in locating females, competing for them and courting them.

Many times we disturbed tending pairs. The females became alert, often took flight. The males hardly reacted, but the perseverance of males meant that a female in estrus would not get separated from the courting male, and courtship would commence again when the female became quiet.

Travelling stags were likely successful with females. They ranged widely, alone, searching for females. They advertised their presence by panting and were bold in investigatory behaviour. These mannerisms would enhance contacts with females.

### Management Considerations

As a planned management program the proportion of males in the Newfoundland population was reduced by legal hunting of stags only from 1957 to 1967 (Bergerud, 1971c). The decline in the ratio between mature males (4 to 9 years) and females was from 1 : 3 to 1 : 5. This change may have accounted for: (1) an increase in the size of aggregation in October (Bergerud, 1972); (2) an increase in the percentages of medium-size stags that bred does (see Table 20): and (3) a longer courtship interval (see Table 18). There was no decrease in pregnancy percentages (Bergerud, 1971b) or in the does that conceived in a second heat period.

When, on Brunette Island in 1962, the sex ratio was 1 mature stag and 9 does, the stag appeared tired and required approximately half a day to breed a female. If the sex ratio were 1 : 12 or more, it might not be possible for the mature stags to breed all the females in the short 6-7 day rutting season. Many small stags might not be able to dominate females and contribute to stud stock.

A few calves are born in Newfoundland from does who conceive in a second estrus (Bergerud, 1961). These calves may be at a survival disadvantage since they are born only a few days before flies become bothersome. Doe-calf bands are disrupted by the appearance of flies and does might not stand as often for nursing when bothered by insects.

A sex ratio of about 1 : 2 seems to be a species characteristic for caribou. This ratio provides for extensive competition among males which results in the most vigorous males breeding the females. *A priori we* can argue that this is the optimum sex ratio for caribou and one to be sought in management programs if the quality of the stock is a primary consideration.

## ACKNOWLEDGEMENTS

I would like to acknowledge my gratitude to the Wildlife Management officers of Newfoundland who tramped the barrens with me: Stephen T. Hall, Michael J. Nolan, Bruce R. Porter, H. Lloyd Russell, Samuel Kelly and Heman Whalen. Those were golden days. Dr. W. O. Pruitt kindly reviewed the 1964 draft of this paper.

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Paper No. 21

# Social Organization in Male Groups of White-tailed Deer

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## ABSTRACT

During a 15-month study on the Rob and Bessie Welder Wildlife Refuge in San Patricio County, Texas, in 1969 and 1970, information was gathered on the composition and organization of male groups of white-tailed deer (*Odocoileus virginianus* L.). Males in the study area seemed to display 4 types of gross association patterns. Each of these was associated with a particular type of social behavior. Immature males are part of the family groups of their mothers. Males in their first year of separation from their family groups seem not to form permanent attachments, but associate with a variety of groups. Mature males form the stable segment of the all male groups, seeming to form true social bonds with other mature males in these groups. Some very large, mature bucks seem to become independent of the male groups and may begin to associate with a variety of groups. Male groups were seen to vary in size from 2 to 17 individuals, the modal figure being 3. These groups seem to have a stable core membership of 2 to 4 mature males and a variable number of smaller males. Two groups which lent themselves to extensive observation were found to be organized in the form of linear dominance hierarchy among the core animals, while no clear order could be seen in the subdominant floaters in these groups. The frequency of agonistic encounters was seen to be lower in those groups with social organization (including all male groups) and the proportion of the more severe agonistic encounters was smaller. Prior to the rut, the dominance relationships are extended beyond the male groups in the push fighting which occurs then. This extension seems to result in a reduction of the frequency of overt fighting behaviour which occurs during the breeding season.

## INTRODUCTION

During the 15-month period of 1969 and 1970, I gathered data on the behavior of free-ranging male white-tailed deer (*Odocoileus virginianus* L.) on the Rob and Bessie Welder Wildlife Refuge in San Patricio County, Texas. This study combined the techniques of radiotracking and visual observation to gather data on a variety of behavioral events. Although the study focused on the observation of certain marked animals, a great deal of information was gathered on the behavior of groups of deer, as well. The Welder Refuge is located in an area of the lower Gulf Coast of Texas known as the Coastal Bend. The immediate area in which the refuge lies is a transitional one where the Gulf Coastal Prairies and Marshes interdigitate with the South Texas Plains (Box and Chamrad, 1966). As a result, the refuge contains 4 major soil types and 16 distinct vegetation types which offer a variety of habitat conditions. The terrain is relatively flat with the only relief being provided by the valleys of the Aransas River (which forms the northern boundary of the refuge) and Moody Creek (a tributary of the Aransas). Deer densities on the study area during the study period ranged from one per 4. 5 acres on the riparian sands to one per 7 acres on the clay slopes. Observation of the external appearance of the animals as well as the results of periodic collections of deer by refuge personnel and personnel from the Department of Veterinary Science at the University of Wisconsin, indicated that the health of the study animals was excellent throughout the course of the study.

For this study, the radiotracking system of Inglis, Sittler and Kirby (1968) was used. Animals were captured with the aid of a Cap-Chur gun (Palmer Chemical and Equipment Company, Douglasville, Georgia) and succinocholine chloride muscle relaxant. Observations of study animals were made with the aid of a 20x spotting scope, a 20-45x variable spotting scope, and 7 × 50 and 7 ×35 binoculars. Marked animals accounted for a substantial portion of the observations, particularly during the breeding season. For these, the marked animals were located with the aid of a portable receiver and loop antenna, and observations were then made from a pole tower (erected for that purpose; Michael, 1963), a vehicle, or on foot, as the circumstances dictated. In addition, observations on unmarked animals and naturally marked animals were recorded in an attempt to determine whether the behavior of the marked animals were typical of the population as a whole. These observations were made primarily from pole towers, but a number of observations on naturally marked animals and particular groups of animals were made from vehicles or on foot.

## GROSS BEHAVIOR PATTERNS

Males on the study area were seen to join family groups, breeding groups, and all male groups (all of which seemed to be characterized by definite social ordering), as well as a variety of aggregations which lacked apparent social order. The all male groups seem to fit the description of 'fraternal groups' described by Linsdale and Tomich (1953) for mule deer. Such groups have been frequently described in white-tailed deer throughout their range (Hawkins and Klimstra, 1970; Thomas, Robinson and Marburger, 1965; and Severinghaus and Cheatum, 1956). Michael (1966) reported the existence of such groups on the Welder Refuge during seasons other than the rut, and believed that these groups were organized in the form of a dominance hierarchy.

Males on the refuge seemed to display 4 distinct types of gross association patterns, each linked with a characteristic form of social behavior. Immature males, up to the summer they are one year old (and possibly up to the summer they are 2 years old, in some instances), are a part of the family groups of their mothers. The home range approximates that of the mother, and the associates of such males are usually maternally related to them. Males which are in the first year of separation from their maternal family groups (and possibly during the second year of separation, in some individuals) become 'subdominant floaters'. These animals associate with a variety of groups during this time, both mixed groups (containing males and females) and all male groups. However, such associations are characteristically transitory.

Those members of the all male groups which comprise the core membership are usually mature males. These animals provide the real stability in such groups and the basis of that stability seems to be the formation of social bonds between the core members. My data suggest that the core membership of stable all male groups is most often composed of 2 to 4 animals. However, the strongest attachments seem to be formed between pairs of males, even in those groups where the core membership is composed of 3 or 4 animals. These core animals are characterized by small home ranges and regular habits. Aggression within these stable groups is low in frequency and intensity, and is lowest among the core animals themselves. Although these groups break up during the breeding season, data gathered during this study suggest that the core members may reassociate following the breeding season.

The fourth type of gross behavior pattern seen is that of the 'dominant floater'. These are typically large, mature bucks which show high social ranking in aggregations of various sorts. However, these animals do not seem to form permanent or prolonged associations during the course of the year. They may be seen associating with all sorts of groups of deer, including mixed groups, all male groups, and groups of does. These associations are usually of short duration. The home range of a dominant floater is usually quite large.

## ALL MALE GROUPS

Although the bucks on the Welder Refuge may be seen associating with does at any time of the year, the most typical association is that of the all male group or fraternal group. This sort of association is typical of all times of the year except the breeding season. During the rut, these all male groups may be seen occasionally, but they are

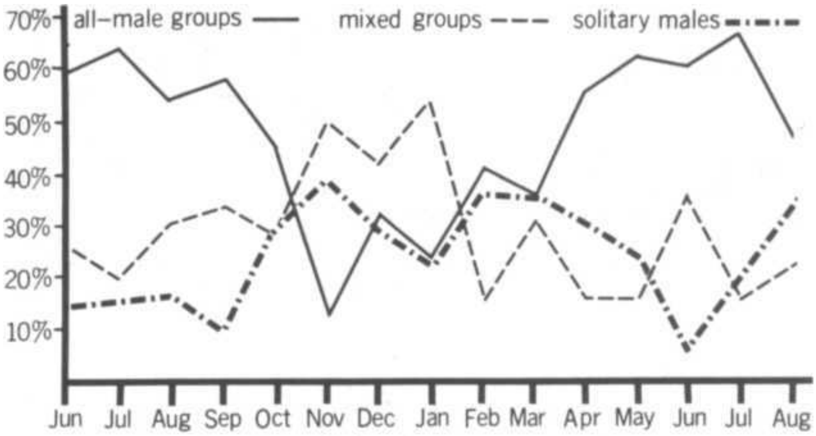

Fig. 1. Relative frequency of all male groups, mixed groups (males and females), and solitary males observed throughout the 15-month study period, June, 1969, through August, 1970.

TABLE 1. COMPOSITION OF LARGE BUCK GROUP OBSERVED IN THE ROOKE BEND AREA, JUNE 24, 1969 THROUGH SEPTEMBER 2, 1969 (EXPRESSED IN TERMS OF THE NUMBER OF INDIVIDUALS OF EACH ANTLER CONFIGURATION OBSERVED ON EACH DATE).

| Antler Class Date | 6-6 pts. | 6-5 pts. | 5-5 pts. | 5-4 pts. | 4-4 pts. | 4-3 pts. | 3-3 pts. | 3-2 pts. | 2-2 pts. | 2-1 pts. |
|---|---|---|---|---|---|---|---|---|---|---|
| 6-24-69 | 1 | | 2 | 1 | 3 | 1 | 3 | 1 | 3 | |
| 6-30-69 | 1 | | 2 | 1 | 3 | 1 | 2 | 1 | 3 | 1 |
| 7-1-69 | 1 | | 2 | 1 | 3 | 1 | 2 | 1 | 3 | 1 |
| 7-17-69 | 1 | | 2 | 1 | 3 | 1 | 2 | 1 | 3 | 1 |
| 7-19-69 | 1 | | 2 | 1 | 3 | 1 | 2 | 1 | 4 | 1 |
| 7-27-69 | 1 | | 2 | 1 | 3 | 1 | 2 | 1 | 4 | |
| 7-28-69 | 1 | | 2 | 1 | 3 | 1 | 2 | 1 | 4 | |
| 8-5-69 | 1 | 1 | 2 | 1 | 4 | 1 | 2 | 1 | 4 | |
| 8-10-69 | 1 | 1 | 2 | 1 | 4 | 1 | 2 | | 4 | |
| 8-16-69 | 1 | | 2 | 1 | 4 | 1 | 2 | | 4 | |
| 9-2-69 | 1 | | 2 | 1 | 4 | 1 | | | 4 | |

quite unstable at this time and are likely to be transitory in nature. Bucks are usually seen associating with does and/or fawns during this period, or else moving about singly. Additionally, solitary males may be seen at any time of the year, but usually not with the frequency seen during the breeding season (Fig. 1).

Fraternal groups of males were seen to vary in size from 2 to as many as 17 individuals, but the modal figure was 3. The larger groups (7 animals or more) seemed to be relatively unstable and may have been composed of several fraternal groups combined. One such group was observed in the Rooke Bend area of the refuge. On 14 occasions between June 24, 1969, and September 6, 1969, the composition of this group was recorded, and they were observed for relatively long periods during the day. During this period, the size of this group varied between 15 and 17 animals. The group

TABLE 2. COMPOSITION OF BUCK GROUP IN LAGARTO TANK-GAS WELL ANTENNA AREA, JUNE 3, 1969, THROUGH SEPTEMBER 14, 1969 (EXPRESSED IN TERMS OF THE NUMBER OF INDIVIDUALS OF EACH ANTLER CONFIGURATION OBSERVED ON EACH DATE).

| Antler Class<br>Date | 5-4 pts. | 4-4 pts. | 4-3 pts. | 4-2 pts. | 4-1 pts. | 3-2 pts. | 2-2 pts. |
|---|---|---|---|---|---|---|---|
| 6-3-69 | 1 | 1 | 1 | | 2* | 1 | 2 |
| 6-5-69 | 1 | 1 | 1 | | 2* | 1 | 1 |
| 6-11-69 | 1 | 1 | 1 | 1 | 2* | 1 | |
| 6-14-69 | 1 | 1 | 1 | 1 | 2* | 3 | |
| 6-18-69 | 1 | 1 | 2 | 1 | 2* | 3 | 1 |
| 6-19-69 | 1 | 1 | 1 | 1 | 2* | 3 | |
| 6-25-69 | 1 | 1 | 2 | | 2* | 1 | 1 |
| 6-29-69 | 1 | 1 | 2 | 1 | 2* | 1 | |
| 7-3-69 | 1 | 1 | 2 | 1 | 2* | 1 | |
| 7-4-69 | 1 | 1 | 2 | 1 | 2* | 1 | 1 |
| 7-6-69 | 1 | 1 | | 1 | 2* | 1 | 1 |
| 7-8-69 | | 1 | 1 | | 2* | 1 | 2 |
| 7-9-69 | 1 | 1 | 1 | | 2* | | 2 |
| 7-10-69 | 1 | 1 | | | 2* | | 3 |
| 7-11-69 | 1 | 1 | | 1 | 2* | | 3 |
| 7-14-69 | 1 | 1 | 1 | 1 | 1* | | 3 |
| 7-15-69 | 1 | 1 | 1 | 1 | 1* | | 3 |
| 7-16-69 | 1 | 1 | 1 | 1 | 2* | | 1 |
| 7-17-69 | 1 | 1 | | | 2* | 2 | 1 |
| 7-25-69 | 1 | 1 | | | 2* | 1 | 2 |
| 7-28-69 | 1 | 1 | | 1 | 2* | 2 | 1 |
| 8-1-69 | 1 | 1 | 1 | 1 | 2* | | 2 |
| 8-2-69 | 1 | 1 | 1 | 1 | 2* | | 2 |
| 8-14-69 | 1 | 1 | 2 | 1 | 2* | | |
| 8-16-69 | 1 | 1 | 1 | 1 | 2* | 1 | 1 |
| 8-17-69 | 1 | 1 | 1 | 1 | 2* | 1 | 1 |
| 8-19-69 | 1 | 1 | 1 | 1 | 1* | 1 | 1 |
| 8-20-69 | 1 | 1 | 1 | 1 | 2* | | 2 |
| 8-21-69 | 1 | 1 | 1 | 1 | 2* | | 2 |
| 8-25-69 | 1 | 1 | 1 | 1 | 2* | | 2 |
| 9-4-69 | 1 | 1 | 1 | 1 | 2* | | 1 |
| 9-5-69 | 1 | 1 | 1 | 1 | 2* | | 1 |
| 9-7-69 | 1 | 1 | | | 2* | 1 | 2 |
| 9-14-69 | 1 | 1 | 1 | | 2* | | 2 |

* naturally marked

fed and bedded together during this time, often mixing with other groups of deer on the sand flat in the area (where large feeding aggregations are common in the summer). However, when the animals sought cover during the day, these animals retreated to a fringe of mesquite trees to the southwest of the feeding area, while most of the other animals in the feeding aggregations sought out clumps of huisache and motts of trees to the north along the Aransas River. It was possible to identify only 2 members of this group, but the relatively consistent composition of the group with regard to antler conformation suggests that there was considerable stability during the 2. 5-month period (Table 1). One other relatively large all male group was observed frequently on the study area. This group ranged north of the Lagarto Tank and the size of this group varied between 7 and 11 animals. Thirty-four sightings were recorded during the period from June 3, 1969, through September 14, 1969. Again, none of the animals in this group was marked and only 2 deer were positively identifiable by means of natural markings. However, tabulations of antler configuration suggest that this group was composed of a stable nucleus of 4 animals plus 3 to 7 floaters (Table 2).

Two other groups which seem to be more typical of the all male groups seen on the refuge provided most of the data which suggests how these all male groups are structured and how they function. Both of these groups had rather limited ranges in the area of the sand flat south of the Venado Bend of the Aransas River. Both could be observed easily throughout the day and the observer could readily learn to recognize individual members of the groups. As a result, a great deal of information was collected on the composition, social interactions, and movements of these groups. The first of these groups was termed the 'Turkey-trap group'. This group was first recorded on June 28. 1969. and by July 30. 1969. the individuals forming the nucleus of the group could be positively identified each time. From July 30, 1969, through November 6. 1969, this group most often consisted of 6 members (Fig. 2). The 3 'core animals' were seen on every occasion on which the individuals were positively identified. These core animals were all large adults. The less dominant floaters were smaller adults with relatively small antlers. These less dominant animals could not always be positively identified and I am reasonably certain that the same 3 animals did not associate with the group during the entire 3-month period. Varying numbers of these less dominant animals associated with the group during this time, as individuals periodically left and rejoined the group. As can be seen from Fig. 2. the group was organized in a straight line dominance hierarchy among the core animals. This ranking was established from information collected during 41 hours of observation from July 30 through November 6. during which 112 dominant-submissive interactions were recorded. Thirty-one of these dominant-submissive interactions were between pairs of core animals. All of the floaters were subdominant to any of the core animals in any social encounter.

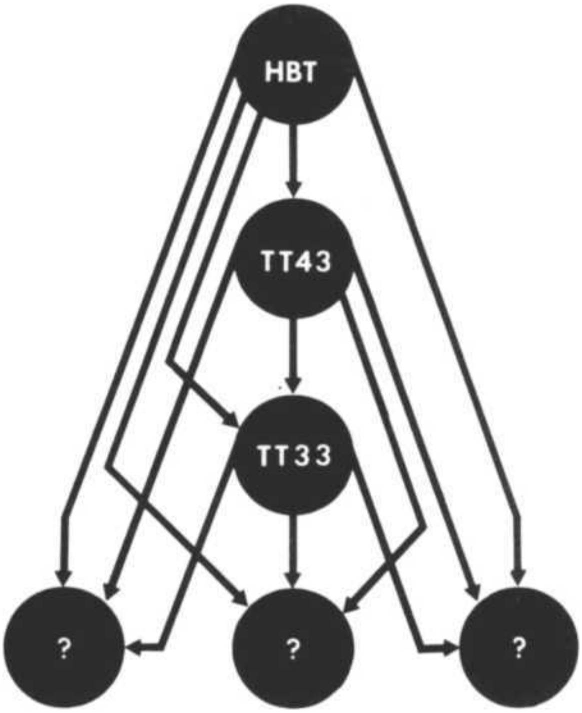

**Fig.** 2. Dominance order for the Turkey-trap group f(.r the period of July 30. 1969, through November 6. 1969.

Despite the fact that 28 of the dominant-submissive encounters recorded during this period were between pairs of floaters, no stable hierarchy could be discerned in this segment of the group. It is my feeling that these animals **were** not consistent in their dominance relationships. In addition, the problems of identification and changing composition among this segment may have tended to conceal any order which may have existed in their social interactions. By contrast, the stability of the social order observed among the core animals was without exception. Of the 31 interactions recorded for pairs of core animals, 27 involved low-intensity threats. Of the 4 higher intensity threats recorded, 3 involved antler-threats directed at less dominant animals which had replied to lower intensity threats with a threatening display of their own. All these three instances occurred in the 15-day period preceding the breakup of the group on November 6. During this period, all of the animals in the group had polished antlers and swollen necks and were exhibiting increasing aggressiveness as the beginning of the rut approached.

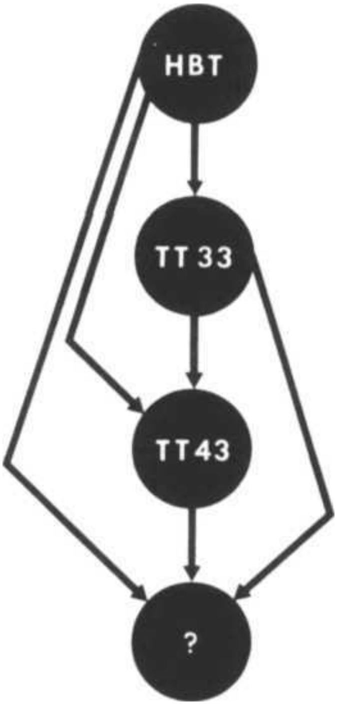

Fig. 3. Dominance order for the Turkey-trap group for the period of December 10, 1969, through December 19, 1969.

On November 6, the Turkey-trap group broke up and deer on the study area began to show overt signs of rutting activity. However, by December 10. rutting activity was infrequent. This period coincided with a period of extremely mild weather in which the days were warm and sunny (high temperatures in the high 70s and low 80s) and the nights were only moderately cool. On December 10 I found that the core animals of the Turkey-trap group had once again begun to associate with one another. This situation prevailed until December 29, when the arrival of a pronounced cold front coincided with another burst of rutting activity. During the intervening 19 days, I compiled slightly over 17 hours of observations on the Turkey-trap group. During this period. 29 dominant-submissive interactions were recorded and I observed 11 pushing contests. During this same period, the ranking among the core animals of the hierarchy had shifted (Fig. 3). HBT was still the dominant animal in the group, but TT33 had replaced TT43 as the second-ranking animal. This reversal was confirmed by the outcomes of 4 dominant-submissive interactions between these 2 animals during this period, and by the results of 2 push fights involving this pair of animals. The 2 deer were very similar in body size (it would have been quite difficult for me to judge which of the 2 was the larger with any degree of certainty) and the conformation of their antlers was very similar.

By January 3, 1970, HBT and TT33 had begun to reassociate in the same area as before, along with 2 smaller floaters. Once again, it was impossible to rank the floaters with respect to one another in the hierarchy. Six hours of observation between January 3 and January 14 yielded records of 9 dominant-submissive interactions and resulted in the ranking shown in Fig. 4. On January 14. HBT lost his antlers and there was a reversal of his dominance relationship with TT33. which now became the dominant animal. Shortly after that, TT33 also lost his antlers and groups of antlerless bucks became common on the study area, making my identifications of individuals which were not marked somewhat doubtful.

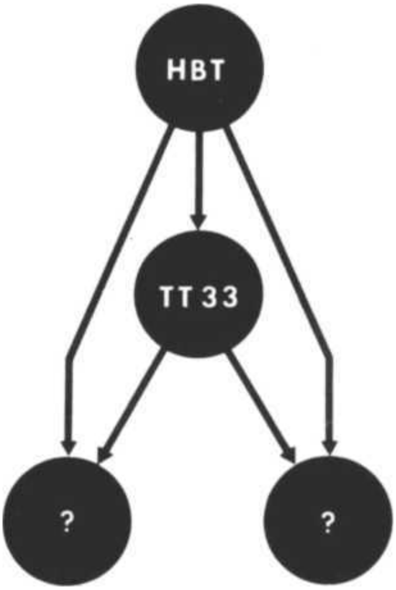

Fig. 4. Dominance order for the Turkey-trap group for the period of January 3. 1970. through January 14, 1970.

The Venado group ranged in much the same area that the Turkey-trap group had used, but spent their days along the Aransas River in the area known as Eagle Bend. Like the Turkey-trap group, the social ordering in the Venado Group took the form of a linear dominance hierarchy. But unlike the Turkey-trap group, the composition of the whole group, not just the core members, was very stable. The alpha animal was a large-bodied buck with 10-point antlers (V44). V33L was a slightly smaller animal with larger than average 8 point antlers. V33S was a medium-sized male, also with 8-point antlers. V32 was also medium-sized, but his antlers (although very thick and heavy) were small, with 3 points on one side and a fork on the other. Between May 15, 1970. and June 10. 1970, I recorded slightly over 11 hours of observation on this group. During this time, only 9 dominant-submissive interactions were recorded. 6 of which involved V44 as the dominant animal. The. order is represented in Fig. 5.

On June 8, 1970, a marked animal which had been marked with a numbered cattle collar was recaptured and fitted with a radio collar, becoming Deer No. 672 in the radio collar series. This animal was also a large 10-point buck. On June 10. this animal joined the Venado group and was integrated into the group at, or near, the top of the hierarchy. Between June 10 and August 20. I recorded a total of almost 51 hours of observation time devoted to the Venado group. I recorded 77 dominant-submissive

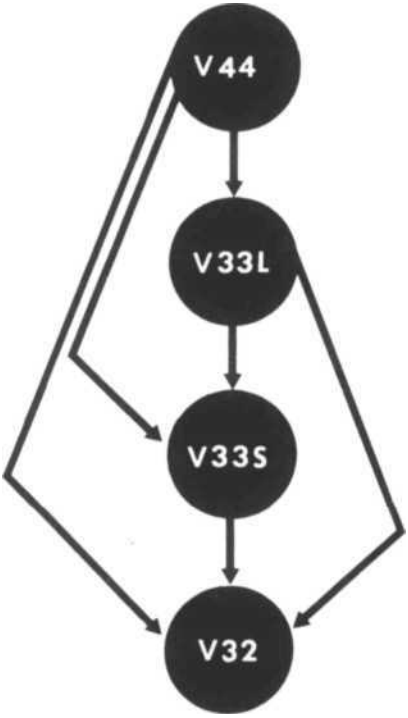

Fig. 5. Dominance order of the Venado group for the period of May 15, 1970, through June 10, 1970.

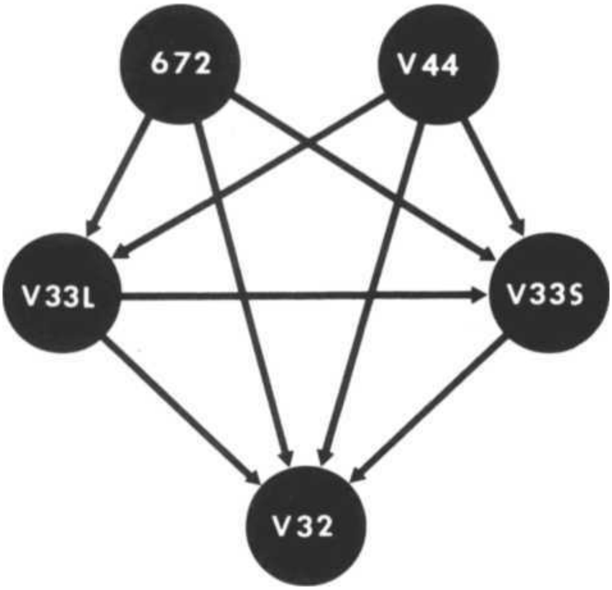

Fig. 6. Dominance order for the Venado group for the period of June 10, 1970, through August 20, 1970.

interactions. Of these 77, 50 were interactions involving a pair of animals within the group. As a result of these observations, I constructed the ranking seen in Fig. 6. During this entire period, I failed to observe a single dominant-submissive encounter between 672 and V44. In addition, I could detect nothing in the feeding or movement patterns which would give me a clue as to which of these animals might be dominant to the other. Thus, the illustration of the ranking shown in Fig. 6 reveals a linear ranking, with codominant animals at the top which show no interaction between them.

Thomas, Robinson and Marburger (1965) described the aggressive behaviors observed in white-tailed deer on the Edwards Plateau of Texas. These are virtually identical to the agonistic behavior seen in white-tails on the study area on the Welder Refuge. The dominance hierarchies in the fraternal groups result from an almost continuous series of such encounters. The frequency of these encounters is typically lower within the fraternal groups (and within the family groups, as well) than within those aggregations which lack social order. Additionally, the proportion of the more aggressive behaviors is smaller within those groups which exhibit social ordering. The distribution of social encounters within a fraternal group may be seen in Fig. 7. The largest proportion of the dominant-submissive encounters occurred between a core animal and a floater. These encounters primarily involved the enforcement of the privileges of dominance in such matters as obtaining desired food items, the selection of bedding sites, right-of-way, and the enforcement of a larger individual distance. The small number of encounters involving nonmembers probably results from the small amount of time that the group spent in the larger feeding aggregations while under observation. The immediate advantages of social order must be rooted in the lowered levels of intraspecific strife within those groups which have social order. The result seems to be a savings in terms of energy expended in intraspecific aggression.

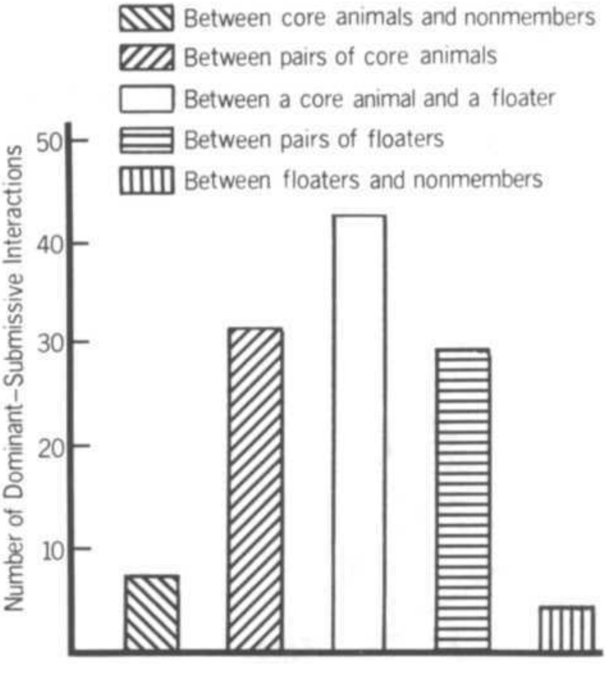

Fig. 7. Distribution of dominant-submissive social interactions (excluding push fights) involving the Turkey-trap group, July 30, 1969, through November 6, 1969.

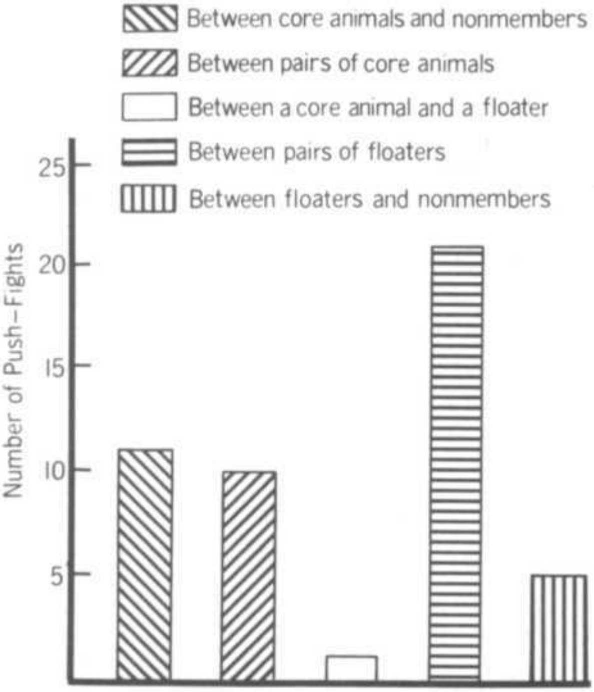

Fig. 8. Distribution of push fights involving members of the Turkey-trap group, September 24, 1969, through November 6, 1969.

Additional benefits seem to accrue when the levels of aggression begin to rise as the breeding season approaches in the fall. The distribution of push fights for the same fraternal group may be seen in Fig. 8. Push fights were usually confined to deer of similar body and antler size within the group. As can be seen, the greatest proportion of push fights involve a nonmember as one of the participants. Such a circumstance seems to reduce the chance for injury due to a mismatch of contestants, and reduces significantly the amount of energy that must be expended in establishing dominance within the group at that time. Thus, just prior to the rut, the greatest proportion of energy seemed to be expended in establishing dominance with males external to the Venado group. This expenditure of energy in establishing dominance order outside the group prior to the breeding season has as its reward the lower probability of a hostile fight erupting between 2 males during the rut. During the breeding season, high individual levels of aggression increase the likelihood of serious injury during such a fight. Thus, when 2 individuals meet during the breeding season, the issue of dominance likely has already been settled prior to that time. Given recognition of individuals, the 'possession' of a receptive female may be resolved through the expression of previously established dominance relationships by means of threats and displays without resorting to overt fighting.

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**Paper No. 22**

# Marking Behavior and its Social Function in White-tailed Deer

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## ABSTRACT

The existence of either sign post marking or of 'territorial' behaviour in white-tailed deer has not been generally recognized or accepted. Breeding season activities suggestive of these behavior patterns were investigated in a number of populations in forested areas of the south-eastern United States. Intensive studies of 14 bucks by radio-tracking, direct observation of animals conditioned for reduced flight distances, and by use of hounds to test objects for scent were made on two study areas. 135 instances of antler rubbing and 32 of scraping behavior were observed. The relationships among these and other behavior patterns including branch marking, urination, scenting, vocalization, movements, home range and social relationships are described. Rubs and scrapes were marked with visual and olfactory signals. Rubs apparently expressed dominance during the breeding season whereas scrapes facilitated communication with does, although both types of signposts probably also had other functions. Urination on tarsal glands and resulting scent trails may have functioned to attract does and intimidate bucks. Our observations suggest that in some situations, bucks defend areas and utilize signpost marking and displays to delineate these areas. Three types of defended areas are postulated.

## INTRODUCTION

Visual, olfactory, tactile and auditory stimuli form the basis for communication in mammals. Sign posts are semi-permanent signals, involving visual or olfactory stimuli or both, that are made a part of the environment (Bourlière, 1954; Graf, 1956). In studying marking behavior of Roosevelt elk (*Cervus canadensis roosevelti*) and black-tailed deer (*Odocoileus hemionus columbianus*), Graf (1956) concluded that one method of marking sign posts was by rubbing objects with the antlers. From this work with Roosevelt elk, Graf (1956) suggested that sign post behavior might be related to some form of territoriality in deer.

Although numerous authors (e.g. Trippensee, 1948; Severinghaus and Cheatum, 1956; Erickson *et al.*, 1961; Harlow and Jones, 1965) have discussed antler rubbing in white-tailed deer (*Odocoileus virginianus*), and pawing behavior in rutting white-tailed bucks has been mentioned by Pruitt (1954) and Teer *et al.* (1965), the possible sign post function of these activities has not been emphasized. A summary of the social behavior of the North American cervids during the reproductive period was reported by De Vos *et al.* (1967) but made no reference to sign post communications in white-tailed deer. In contrast, recent popular articles written by hunters have regarded certain 'signs' observed in the woods during the rut as having communicative functions.

The objectives of this study were to describe white-tailed deer activities which are suggestive of sign post marking behavior, and to analyze the functions of these and associated activities in relation to communication and social organization during the mating season.

## DESCRIPTION OF STUDY AREAS

The two primary study areas were located in north central and south Georgia habitats and differed ecologically. The north central area was near Athens (Clarke County) which lies within the Piedmont Upland portion of the Piedmont Province (Fenneman, 1938). The habitat includes pine (*Pinus* spp.) and pine-hardwood forest types interspersed with permanent pastures and cultivated areas. Observations of recognizable deer suggested a relatively low population density of four to six deer per square mile on the area. Hunting pressure was light, with hunting prohibited on University of Georgia owned lands interspersed throughout the area.

The south Georgia study area was centered on and around Jones Island in the Okefenokee National Wildlife Refuge. Physiographically this area is included with the Sunderland Terrace portion of the Coastal Plain Province (Fenneman, 1938). The swamp habitat is composed of prairies, bogs, islands and open water. On the higher portions of the islands, pine and oak (*Quercus* spp.) predominate. The deer population density on the Okefenokee study area was considerably higher than that on the Athens study area. There was no hunting season within the refuge and the aquatic nature of the habitat caused deer to congregate on the islands. In addition to work on the major study areas, surveys and descriptions of sign made by deer in a variety of other habitats and geographical regions in Georgia and adjacent states provided supporting information.

## MATERIALS AND METHODS

Fourteen individually recognizable bucks were observed for 382 hours (264 during rutting season). Five were equipped with radio transmitters to facilitate locating them and periodic radio contact was maintained for up to 11 months. Although does were not radio-equipped or individually marked, many were observed interacting with the bucks. Movement patterns were determined by radio-tracking and more detailed behavioral information by direct observation of free-ranging animals, preconditioned for a reduced flight distance (Marchinton, 1969). This method allows an investigator to radio-locate subjects and to approach close enough to make detailed observations of behavior in natural environments.

Three bucks, preconditioned in pens, were radio-equipped and released on the Athens study area. One animal (Athens 1) was released in mid-January and the other two in late September, 1968. The behavior of these animals was studied primarily during November and December, 1968, therefore the bucks had from 2 to 10 months to adapt to the habitat conditions and become integrated into the social organization. A group of wild deer that had been fed daily to allow park visitors to see them and as a result had lost much of their fear of man was studied on the Okefenokee area. Two of these deer were captured with a syringe gun and radio-equipped in October, 1969. Flight distances varied with individual deer and density of the cover. Generally the investigator attempted to maintain a distance of 11 to 15 yards from the animal. Observations of deer that were more difficult to approach were made from portable tree stands. The animals were often observed continuously throughout the daylight hours but relatively few night observations were made. Social ranking of the bucks on both study areas was ascertained by observation of approximately 300 agressive-submissive interactions as described by Collias (1950) and by Thomas *et al.* (1965). These interactions most often involved threat displays with no physical contact. Physical condition of study animals was assessed in the field using criteria described by Riney (1960).

Approximately 350 hours were spent locating and studying field signs (i.e. rubs and scrapes). Trained hounds were used to test for scent left on trees or branches. The dogs were presented several specimens. Some of these were known to have been either rubbed with antlers or 'mouthed' by deer during behavior patterns suggesting an olfactory communicative function and others had not. If the dogs were able to detect scent, it was evident by their behavior while smelling a specimen.

## RESULTS AND DISCUSSION

### Antler Rubbing Behavior

Rubbing was observed primarily in the morning and evening, and only immediately prior to and during the breeding season. It was usually done by lone animals although the dominant individuals sometimes rubbed when confronted by another buck. In rubbing, an animal typically stood with antlers against a tree or shrub and pushed up, down or sideways (Fig. 1A). The time spent making a rub averaged approximately 15 seconds; however, there was considerable variation. It was common for an animal to pause for short periods while rubbing and to carefully sniff and lick the portion of the tree which was being rubbed.

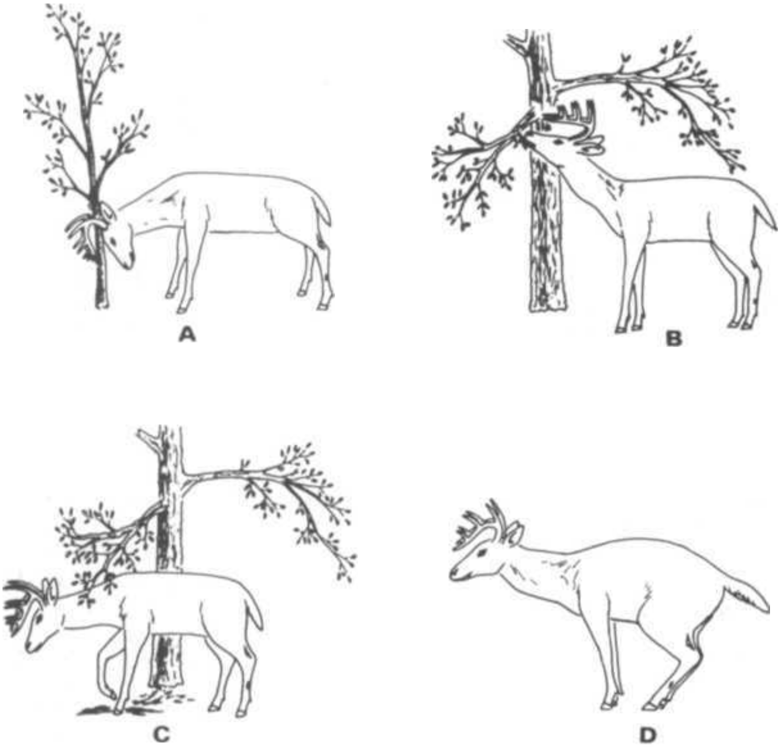

Fig. 1. Postures assumed by study animals during activities suggestive of sign post behaviour—(A) antler rubbing, (B) marking branch and foliage, (C) pawing under marked branch, (D) urinating on tarsal glands.

Rubbing usually removed or frayed the bark but the extent to which trees or shrubs were visibly marked depended upon how vigorously they were rubbed. Eastern red cedar (*Juniperus virginiana*), winged sumac (*Rhus copallina*), sourwood (*Oxydendrum arboreum*), sassafras (*Sassafras albidum*), short leaf pine (*P. echinata*) and long leaf pine (*P. palustris*) were most often rubbed. The plants selected for rubbing ranged from ½ to 4 inches in diameter with the average being about 1 inch. A trained hound could detect deer scent on these trees and shrubs several days after they had been rubbed and signs of rubbing remained visible for at least several months.

## Scraping Behavior

Behavior involving pawing the ground has been referred to as scraping (Teer *et al.* 1965). Thirty-two instances of scraping behavior in five different bucks were observed. These were mature animals and three of them (Athens 1, Okefenokee 1 and Okefenokee 6) were known to be dominant within the areas where they made scrapes. Observations of the other two animals were inadequate to determine if they were the dominant bucks within their areas.

The usual prelude to scraping behavior was for an animal to urinate on the tarsal glands (described later) and then begin walking slowly through the woods following old roads or other trails. As the animal proceeded he occasionally stopped to 'mark' a low hanging branch by nuzzling, licking and pulling on the branch with his mouth (Fig. 1B) and sometimes by raking it with his antlers. The branches marked were generally about antler height when the buck was walking in a normal head up position. On a few occasions, however, the branches were much higher and it was necessary for the animal to stand on his hind legs to reach them with his mouth. In every observation, after a branch was marked the buck pawed back leaves or litter directly under the branch (Fig. 1C). Two to five strokes were made alternately with each front foot. The scraped area was typically 1 to 2 square feet in size. After pawing, the animals usually urinated either in or behind the scraped area.

The scrapes and marked branches were often visible to the observers at considerable distances. In addition to the visible markings, scent left on the branches could be detected by hounds for at least 4 days. When the animal urinated at the scrape, an odor was present that was readily detectable by human observers for several hours.

Tracks of the bucks which made the scrapes were usually left in the bare soil, but on later examination we often found tracks of smaller deer. Although the authors did not. personally observe does visiting scrapes, reports by hunters and other field observers in and around the study areas indicated that does frequently approached scrapes and urinated in them. The bucks under observation periodically returned to the scrapes and sometimes reworked them following the same pattern described above. On seven occasions upon returning, a buck encountered a doe's scent trail at a scrape. In each case the buck began making grunting sounds and moved off at a fast walk with his nose near the ground. The doe was generally within two hundred yards of the scrape and was always quickly located by the buck. In most cases the buck and doe separated after a brief association. If the doe was nearing estrus, however, the buck stayed with her, often trotting or running after her until she would stand for mounting. One such 'chase' continued for three days. Copulation was observed twice on the third day at a location 1.1 miles from the scrape where the doe's trail was initially encountered.

In two instances, one of us when standing within five feet of a scrape was threatened by a radio-equipped buck. The buck displayed the 'ear drop' and 'hard look' threat postures described by Thomas *et al.* (1965), until the observer moved away from the scrape. Small bucks appeared uneasy when near scrapes, and a young buck was observed to rapidly leave the vicinity of a scrape made by a dominant buck, when the latter approached. Subordinate bucks did not behave this way in the presence of a dominant unless they were near a scrape or a doe in estrus. A notable exception was a very small spike buck, often seen with a dominant animal, which approached a scrape made by the dominant and mouthed the branch even though the dominant animal was only 30 yards away and in plain view.

Pawing by bucks at the base of trees which had been rubbed, or where neither rubbing nor branch marking had occurred was observed 72 times. Bucks rarely urinated near pawed areas of this type. These and other deviations were not considered to be scrapes for the following reasons: (1) all pawing variations observed were made by Athens 1 and 78 percent occurred during a period of only 3 days early in the rutting season; (2) they were generally hastily made and the pawed areas that resulted were usually small and hardly noticeable; and (3) the pawed areas were not periodically revisited.

## Urinating on Tarsal Glands

A behavior pattern which we referred to as 'scenting' was often associated with rubbing and scraping. It involved an animal urinating on the tarsal glands while rubbing them together (Fig. 1D), and resulted in a scent trail being left during the animal's subsequent movements. This urination posture, previously described by Haugen (1959), differs from that during normal urination, as in the latter the hind legs are well apart. Although normal urine had an odor barely detectable by the investigators, urine passed over the tarsal glands had a much stronger odor. After urinating on the tarsal glands, the animal usually licked the inside of his hind legs, including the glands. He then began walking and rarely stopped to feed. As he walked, we could detect a very pungent odor even at distances of 100 yards or more behind the animal. In most cases scenting was observed late in the afternoon and was followed by increased movement and by rubbing and scraping. However, penned deer even with antlers in velvet were induced to urinate on the tarsal glands in an apparent threat or displaced fear response to harassment by dogs.

### Associated Vocalization

The grunting sound previously referred to was heard only during the rutting season and in every case when a buck was with or trailing does. Another type of vocalization used by dominant male animals when associated with females in estrus was heard on 34 occasions. This was a rapid sneeze-like sound produced by releasing air through the nostrils. The sound was directed towards bucks that tried to approach the doe and was often accompanied by antler rubbing apparently as a threat display.

### Spatial and Temporal Distribution

All activities suggestive of marking behavior that we observed occurred immediately before and during the breeding season. Rubs made by individual bucks, although in several parts of the home range, tended to have clumped distributions (Fig. 2). Scrapes were made in conspicuous places such as the intersection of trails, near roadbeds and along the edges of openings but their locations generally coincided with areas where there was a high density of rubs (Fig. 2). Rubbing was most intense prior to the peak of the breeding season while scraping activity coincided more closely with breeding activity. Most feeding and bedding occurred during the morning and early afternoon whereas marking behavior usually was in late afternoon. Movements of study animals between areas where intensive marking activity was observed were rapid and occurred primarily at night. Radio tracking data obtained before the rutting season indicated that centers of activity during these times were often not the same as during the rut.

### Communicative Significance

Antler rubbing in white-tailed deer has in the past generally been thought to have one of two functions, i.e. removal of velvet or combat practice. Graf (1956), however, concluded that antler rubbing does not occur for the sole purpose of removing velvet, although in some cases there may be removal of velvet incidental to rubbing antlers for other purposes. de Vos (1967) observed the same tree being rubbed by white-tailed deer in successive years and suggested that rubs might serve to mark the boundary of a territory. Schaller (1967) studying the chital (*Axis axis*), suggested that the act of rubbing trees and shrubs may be a means of releasing energy through redirected aggression. Graf (1956) states that there is more significance in these acts than the immediate fulfillment of the need for something upon which an animal can vent his surplus energy. Prior (1968), discussing fraying (antler rubbing) in roe deer (*Capreolus capreolus*), dismisses the displacement activity explanation and regards fraying as a display of strength and threat. He also noted extreme fraying damage to trees near the territorial boundary when there was intense competition from other large bucks near that boundary.

On several occasions in our study, rubs were made when a dominant buck encountered other male deer. These rubs were accompanied by snorts, and by intimidating postures similar to those described in black-tailed deer by Cowan and Geist (1961), and in white-tailed deer by Thomas *et al.* (1965). It is our impression that such rubs served as visual expression of dominance. Rubs made when an animal was not in the presence of other deer probably serve a similar purpose, but through olfactory as well as visual signals. Rubbing activity of this latter type was concentrated in relatively well defined areas within the home range. Possible territorial implications of this distribution will be discussed later.

The significance of pawing by white-tailed deer during the rutting season has not been established in the literature. An explanation presented by Severinghaus and Cheatum (1956) suggests that if one buck in in the 'territory' of another, he may stamp and paw the ground and thrash the brush with his antlers. They further state that this stamping and pawing may result in numerous torn-up places on a ridge, all attributable to the activities of one rampaging buck. They do not suggest any sign post significance for these pawed areas. The behavior they described seems comparable with what we have termed scraping behavior and pawing variations, although in the present study such activities occurred within the animals' home ranges and coincided with areas in which intensive rubbing occurred.

Branches that were marked over a scrape were identifiable by both visual and olfactory signals. This was probably also true for the scrape itself. Schaller (1967),

Fig. 2. Spatial distribution of rubs and scrapes Athens 1 was observed making between October 14 and December 5, 1968. Home range boundaries are based on radio and visual locations between January 17 and December 5, 1968.

studying deer in India, suggested that secretions from the interdigital gland are added to the soil when pawing. The interdigital gland may be a source of odor in white-tailed deer also. Urination in or near the scraped area provides another scent that may serve as a means of communication. The scrape apparently represents a complex sign post consisting of the visual stimuli presented by the scraped area and the overhanging branch, combined with a complex of olfactory signals on the branch and on the bared soil.

Does were known to approach scrapes and urinate in them, and in the present study a buck often detected the scent of a doe at a scrape and easily located her by following what seemed to be a very well defined scent trail. This evidence together with the observations that a buck made scrapes only during the breeding season, often urinated in the scrapes and periodically returned to check them, strongly suggests that they are sign posts, and that one of their functions is to facilitate locating animals of the opposite sex.

Haugen (1959) discussing the function of urinating on the hind legs stated, 'Is it to mark territory to warn other bucks to stay away or is it to add "irresistable" lure to does or both?' Linsdale and Tomich (1953) observed mule deer (*Odocoileus hemionus*) releasing urine over the tarsal glands while rubbing the hind legs together and also noted that the animals licked the tarsal glands after this action. They suggested that this behavior in rutting bucks clearly is an act of threat towards other males.

Espmark (1964) and Lent (1965) observed similar urinating behavior among rutting male reindeer (*Rangifer tarandus*) which they called trampling. Espmark (1964) noted that this behavior occurs frequently when a bull hears or sees another bull of similar size and age; however, he also stated that there were 'undefined' occasions when this behavior was observed. He concluded that it was a form of territory marking. He suggested that the bull may mark himself as the center of his moving territory and also mentioned the possibility that the characteristic odor of the markings may attract cows.

The scenting observed in our study apparently involved an activation of the tarsal glands which produced a strong, far-reaching odor. The odor may intimidate other bucks as suggested for mule deer by Linsdale and Tomich (1953), but the scent trail is probably also important in aiding does to locate scrapes. In addition, licking the tarsal glands may permit the transfer of scent from the tarsal glands to the trees that are rubbed and then licked and to overhanging branches that are mouthed.

White-tailed deer have a wide variety of vocal expressions (Seton 1929). Of the sounds recorded during the present study, the grunt and rapid sneeze-like sound were often emitted in conjunction with sign post behavior. Linsdale and Tomich (1953) reported mule deer bucks uttering growling or rumbling grunts when chasing does. During the present study grunting was heard only when a buck approached a scrape which had been visited by a doe or was trailing and otherwise associating with does. Dixon (1934) suggested that grunting in mule deer discourages pugnacious competition between males. In white-tails, at least, it may also be a form of communication with does.

The vocalization described as a rapid sneeze-like sound was heard only when a male was with a female in estrus and other bucks intruded. It apparently acts as a warning to keep other bucks away from a female. It was used in conjunction with the visual threat displays described by Thomas *et al.* (1965) and with rubbing. Cowan and Geist (1961) reported similar behavior in captive mule deer but called it a snort which they described as a prolonged 5-10 second, sibilant expulsion of air through the constricted nostrils, causing them to vibrate. Bromley (1969) described a vocalization made by territorial pronghorns (*Antilocapra americana*) which apparently closely resembles the sneeze-like sound of white-tailed deer.

In summary, the data obtained in the present study suggest that vocalizations, displays, and sign posts which communicate a threat in the animal's absence, may all be important to a male white-tailed deer maintaining a dominant position in a given area during the rutting season. Sign posts not only play a part in relating warnings but also in providing communication between the sexes to increase the probability of males locating females for mating.

## Relationships to Social Organization

Collias (1950) stated that there was a definite dominance hierarchy in white-tailed deer based on frequent aggressive-submissive interactions of all the individuals. Severinghaus and Cheatum (1956) suggested a social organization that involved the temporary dominance of bucks within their 'territories'. A number of investigators, however, have noted that male white-tailed deer occupied the same range or were even observed together during the rutting season (e.g. Skinner, 1929; Illige, 1951; Teer *et al.* 1965; Downing *et al.,* 1969). Observations such as these have led to the general conclusion that white-tailed deer are not territorial, at least not in the traditional sense.

Although dominance hierarchies are undoubtedly basic to the social organization of white-tailed deer, our observations indicate that in some forested areas, particularly where deer populations are low, dominant white-tailed bucks have behavior patterns which are suggestive of territoriality. These behavior patterns will require further study to be fully understood, but involve sign post marking and related behavior which apparently identify areas of dominance and sexual activity too large to otherwise defend. The system provides for efficient communication between sexes during the reproductive season and acts to reduce conflict between males. At least three types of defense against conspecifics are suggested—one geography-oriented, and the other two object-oriented.

(1) 'Dominance areas' involving sizable portions of the home range are marked by intensive rubbing early in the rutting season. There may be several such areas within the range of a mature buck (see Fig. 2). In these areas the buck asserts his dominance by the ritualistic display of rubbing and by the visual and olfactory sign posts (rubs) which result. It is our impression that physical combat is common during the period when dominance is being established. The buck, however, does not physically defend these dominance areas against males as long as the latter maintain subordinate postures. As a result the presence of subordinate bucks within these areas is common. Observations suggested that an animal dominant in one area may act as a subordinate in the dominance areas marked by other bucks.

(2) The individual scrapes are sometimes physically defended against other bucks, including subordinates. Therefore, within a 'dominance area' are interspersed many small, more strongly defended intolerance zones immediately around the scrapes. Since the scrapes serve as a means of communication between sexes, the physical defense of the scrapes probably results in females being more accessible to the dominant buck.

(3) Finally, the space immediately surrounding a female in estrus is an intolerance zone which moves with the female. A dominant buck defends this area by intimidating displays including rubbing, sneeze-like vocalization and lastly by physical combat. The potential for conflict is considerably because does apparently do not respect dominance area boundaries. As a result a dominant buck may accompany a doe which is in estrus out of his dominance area, and into that of another buck. A situation like this was observed in our study when Athens 1 followed a doe into the range of Athens 4. Although Athens 1 copulated with the doe twice the dispute was finally settled by physical combat which resulted in Athens 1 returning to his own range.

Eaton (1970) in studying the cheetah (*Acinonyx jubatus*) defined territoriality as any behavior associated with defense of a space in the home range. Although behavior we observed in dominant bucks broadly qualifies as territorial according to this definition, it is quite unlike the behavior reported for territorial ungulates such as the Uganda kob (Buechner, 1961). The male kob will not follow a female across the territorial boundary and can be considered a social castrate out of its territory. This is not the case in white-tails. Although most white-tailed does may be initially contacted within a dominance area, the buck will follow does out of this area if necessary to breed them. Also in white-tailed bucks evidence of 'territorial' behavior seems to break down at higher population levels and in a given area the extent to which it is manifested may be related to the population structure and density. Rubs and scrapes were observed in all areas supporting deer populations; however, cursory examinations revealed no defensive behavior in many populations. At high population levels and during the non-reproductive season spatially oriented defense by bucks is apparently replaced, for the most part, by a simple dominance hierarchy.

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Paper No. 23

# Mating Activity and the Social Significance of Rams in a Feral Sheep Community

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## ABSTRACT

An account is given of the mating activities of feral Soay sheep on the island of Hirta, Scotland, and of the developmental and social contexts of male behaviour.

A phase of agonistic interaction between rams follows the breakdown of their social grouping in October and tends to precede the main peak of overt oestrus occurring in mid November. The nudging display is the chief behaviour involved in short-term encounters, when a dominant-subordinate relationship may be demonstrated. With various other behaviours nudging contributes to long term interactions ('blocking'), apparently indecisive attempts to define rank. Males tend to interact with others of similar age and size. An imperfectly linear social hierarchy is developed.

Rams contact ewes in the 'flehmen-urination' sequence. Copulation is preceded by a modified nudging display and usually occurs while the ram 'tends' the ewe during oestrus. Males high in the social hierarchy establish more 'tending bonds' than those lower in the scale. The latter also make relatively more of these associations late in oestrus. Some rams achieve up to 30 conceptions in a season, but the majority few or none. Estimated age class fecundity patterns for the two sexes are compared.

Male lambs exhibit nudging in a single context, as a preliminary to mounting. The display differentiates ontogenetically so as to appear in two apparently separate contexts among adults and is interpreted as an assertion of dominance. Male lambs of the year participate in the rut.

It is possible to trace the sequential position of particular ovulations in the polyoestrous cycle throughout the population. The majority of ewes conceive in their first overt oestrus, which corresponds to at least the second ovulation of the season. Ewes from the same social group tend to come on heat together.

Males exhibit a higher mortality rate than females, reflecting reduction in grazing time during the rut and differential winter weight loss. Life table statistics are complex and separate tables can be prepared for each cohort. There is a relation between population density and the scale of mortality but for males, especially, it is not necessarily a close one, though rams are generally more density sensitive than ewes.

## 1. INTRODUCTION

For at least 300 years and perhaps for the last 1, 000 years, sheep have existed in a feral state on Soay (244 acres), a small island of the St. Kilda group 45 miles from the Outer Hebrides off the West coast of Scotland. The history of this Neolithic stock, their introduction to the neighbouring island of Hirta, methods of marking and ageing, and the nature of the study area, sited on the Village Glen or Hirta, are discussed by Boyd, Doney, Gunn and Jewell (1964). Social organisation has been surveyed by Grubb and Jewell (1966), who have demonstrated the existence of two kinds of social unit. In the 'ewe home range group' are females, lambs and young rams up to 3 years of age.

Older males leave the ewe group and associate in 'ram home range groups'. Some aspects of the behaviour of Soay rams are usefully discussed in relation to their juvenile background within the ewe group.

## 2. SOCIALISATION OF LAMBS—A BACKGROUND TO ADULT BEHAVIOUR

The young lamb makes contact first with its dam and later with other adult sheep, whose aggressive responses to its approach tend to reinforce the bond with the parent, but also may promote experience of fellow group-members. During the first twenty days of life, when much time is spent resting, occasional contact with other lambs is also made. At this stage, the lamb's exploratory behaviour involves approaching and nosing objects and mouthing vegetation, stones and other materials. This develops into intensive grazing when the lamb is about three weeks old. At the same time, contacts with other lambs become more frequent. Lambs from a single ewe group gather daily into play assemblages in which behaviour shifts from communal exploration and grazing to sequences of greater activity. Here the lamb shows spurts of galloping or sessions of butting, mounting and pushing. Intention butting or nodding of the head may be exhibited towards companions, often combined with variously executed rearing or leaping. Lambs do not rear to butt but it is possible that the jump threat and the jump into the clash of certain wild sheep (Geist, 1968) derives ontogenetically from movements of this type. Mounting and pelvic thrusts are shown chiefly by males thus providing one of the earliest indications of a behavioural differences between the sexes (Table 1).

TABLE 1. NUMBERS OF OCCASIONS IN WHICH MOUNTING WAS OBSERVED IN LAMBS

(Data collected spring 1966)

| | | Sex of mounting | |
|---|---|---|---|
| | | Lamb | |
| | | ♂ | ♀ |
| Sex of | ♂ | 101 | 14 |
| mounted lamb | ♀ | 78 | 16 |
| | Total | 179 | 30 |

In a minority of cases (31 out of 179 observed) mounting is preceded by a sequence of 'nudging', (a 'twist' frequently accompanied by a 'kick' or 'laufschlag') but only in the males. The twist is silent and made without lip or tongue movements or penis erection.

The behaviour of the two sexes is evidently not as fully differentiated as in adulthood, for female lambs do mount. (Mounting by adult females is rare). Similarly the male lamb does not apparently differentiate between male and female in his agonistic/sexual approach, as he will do when adult.

Mounting and nudging are nevertheless shown chiefly by males, especially the largest individuals, and it appears reasonable to suggest that functionally these activities and the other contacts made between lambs are part of a social and environmental exploration through which there is an early determination of rank among group-members (see Geist, 1971). This may be the basis for the apparently lesser degree of agonistic behaviour shown towards familiars as opposed to strangers among older rams. Much lamb activity can be envisaged as an ontogenic stage in behaviour and since individual behaviour patterns (mounting, nudging, butting) are modified in form, function and context on attaining adulthood, these can be regarded individually as stages in a developmental sequence.

'Play' activities decline during the summer, though lambs continue to associate while grazing. Suckling continues into the early rut, but by this time the horns of male lambs are stout and 'masculine', and they are heavier than ewe lambs. Their subsequent behaviour during the rut is very similar to that of the adult rams. After the completion of the rut, ram lambs return to the ewe groups and if they survive heavy winter mortality, consort with their peers more closely than do females of the same age (more than 50 per cent of associations against less than 30 per cent respectively). These associations, often developed in the lamb play-group, are the basis for new ram home range groups, though, again because of high male mortality, these may not be maintained long enough to establish a distinct home range and become independent of the ewe group. Single young rams sometimes stay with the ewe group until two to three years of age, but then usually join up with older males.

## 3. RUTTING ACTIVITY

The rut begins gradually in early October. Nosing of the ewes with 'flehmen' becomes more frequent, especially at the beginning or end of the day, and at first leads to a gradual departure from the regular grazing cycle and an alteration or expansion of the home range. As a number of ewes come on heat, each ram tends to wander quite independently, losing any set pattern in his daily circuit of movement.

The changes that occur in the dispersal of the ram groups can be envisaged as the formation of a single 'society' out of both the several ram home-range groups and the ram-lambs and yearlings (1. 5 year olds) from the ewe-groups. In a ram group, the members keep together, apart from other rams, and are probably fully familiar with one another. The loose society formed for the rut contrasts with such a closed organisation. Rams no longer stay together for any length of time, most other males encountered are strangers, no social grouping is recognisable and the complement of males in any area is continually changing.

Numerous confrontations are made between rams in the early rut. Displays of 'nudging' are commonly observed and these may develop into long engagements ('blocking') sometimes involving fighting ('clashing'). In late October, the first ewes are on heat, and agonistic behaviour shows a decline as the peak of oestrus is reached towards mid November (Fig. 1). At this time up to 10 per cent of the adult ewes (those over one year old) are in oestrus together.

While the dispersal of rams anticipates the rut, their reassembly into home range groups begins even before every ewe has been served, though some males may remain away from their home ground until the following spring. Ram lambs are comparatively late in leaving the ewe groups to commence their rutting wandering and at the end of the season complete their return promptly.

The time spent in grazing by all males, young and fully adult, declines quite strikingly over the rut (Fig. 2). In late September, both sexes spend ninety per cent of the daylight hours in grazing but though this level is maintained by females right through until the following April, the figure drops to 20 per cent among males by mid November. There is a. recovery before mating has been fully completed, perhaps in response to weight loss experienced in the rut.

## 4. PERIODICITY OF OESTRUS

The social grouping of the females is not affected by rutting activity, but the frequency distribution of their oestrus periods determines the pattern of the rut. Behavioural oestrus can be recorded when rams persistently associate with a ewe or show overt sexual behaviour towards her (repeated nudging, chasing, mounting and copulation). In 1966, rams showed interest in 68 adult ewes for one day only, in 63 for two days and in 27 for three or four days. Of 26 lambs seen to come on heat, only one was followed by rams for more than one day, so oestrus is evidently much shorter in these young individuals.

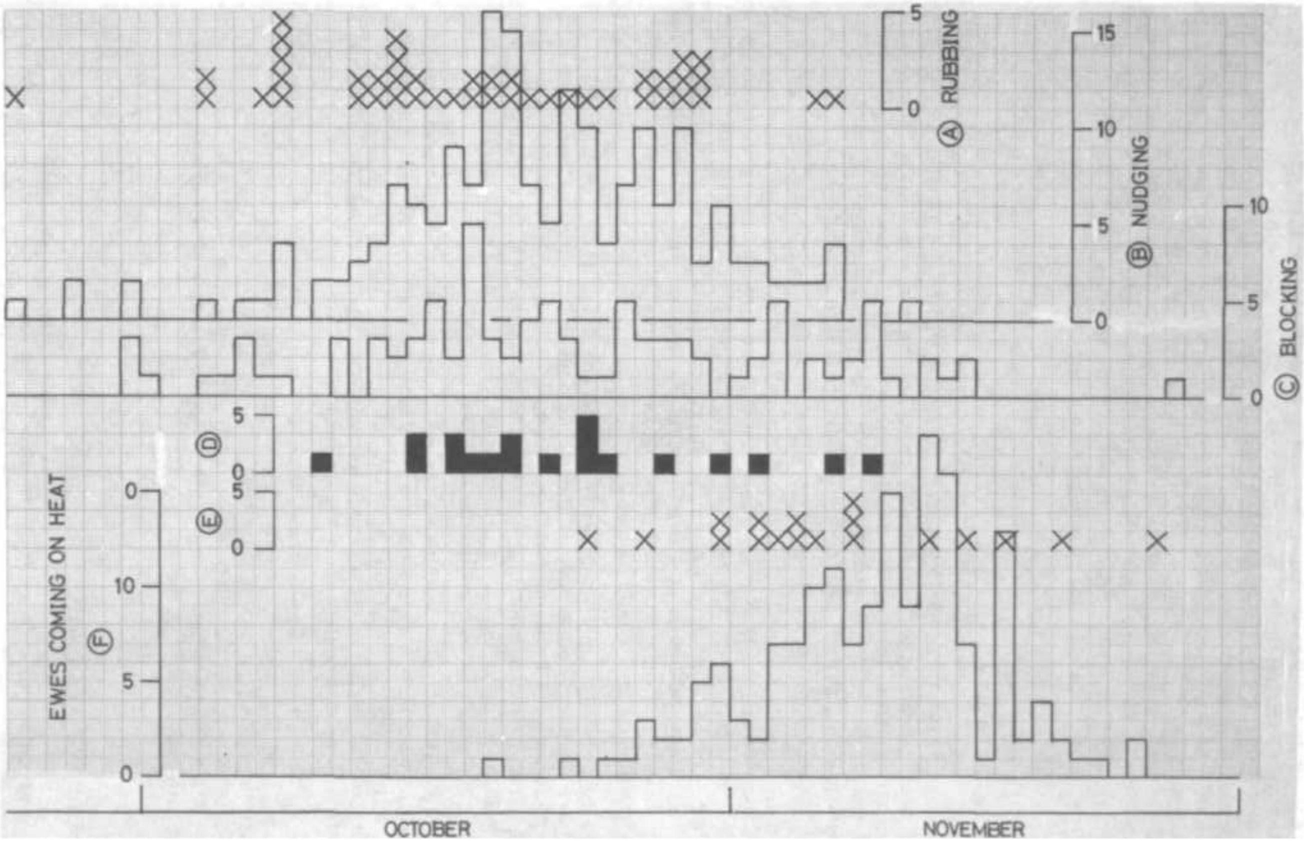

Fig. 1. Frequency distribution of observations during the rut on Hirta in 1966:

(A) numbers of encounters between rams involving rubbing; (B) numbers of encounters between rams involving nudging outside the contexts of blocking or tending; (C) numbers of blocking contests; (D) dates of onset of 'first observed oestrus'; (E) dates of onset of 'second observed oestrus'; (F) dates of onset of 'sole observed' oestrus.

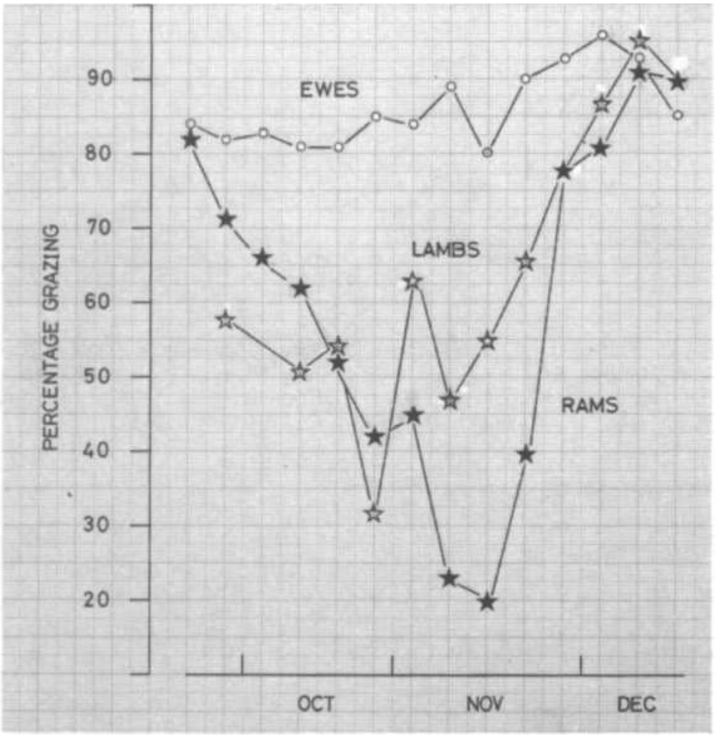

Fig. 2. Records of grazing activity during the rutting season for (a) ewes, (b) ram lambs, and (c) older males. Each point represents the mean number of each sex observed grazing at half hour intervals over one day expressed as a percentage of the mean of the total numbers seen at those intervals. Observations were made at weekly intervals.

Most ewes come on heat only once during the mating season but a proportion do so twice (19 out of 162 ewes in 1966) and a few on more occasions. Interoestrus ranges from 10 to 18 days (mean of 15). Three chief categories of oestrus can be recognised:-

(a) first oestrus and

(b) second oestrus, of ewes that come on heat twice, and

(c) the sole observed oestrus of ewes, and lambs, which come on heat only once during the season.

Oestrous periods of the (b) class have a distribution which is only significantly different from the distribution of the (c) class above the 10 per cent level (Student's t = 1. 54 with 161 degrees of freedom; Table 2). The mean date for class (c) is thus separated by one interoestrous period from the mean date for class (a). The standard deviation of class (c) oestrous dates is however only half the interoestrous period, so that the distribution of these and of class (a) oestrous dates are fairly discrete. It seems reasonable to infer that ewes which show heat once only have a 'silent heat' or undetected ovulation at the time the others first exhibit overt oestrus. The result is that the equivalent stages in the polyoestrous cycle can be distinguished throughout the population.

TABLE 2. DISTRIBUTION OF DATES OF THREE CATEGORIES OF OESTRUS.

(Data collected autumn 1966)

| Category of oestrus | Number in sample | Mean date (expressed as nth day of year) |
|---|---|---|
| (a) first observed | 19 | 298 ±7.5 |
| (b) second observed | 19 | 314 ±7.6 |
| (c) sole observed | 144 | 333 ± 6.1 |

Although 'sole observed' oestrous dates, class (c), have a restricted distribution, these dates are even more closely aggregated for ewes from a single home range group (Fig. 3). There is a very highly significant difference between different home range groups in the mean day of oestrus, (F ratio = 10.04, P = 0.001).

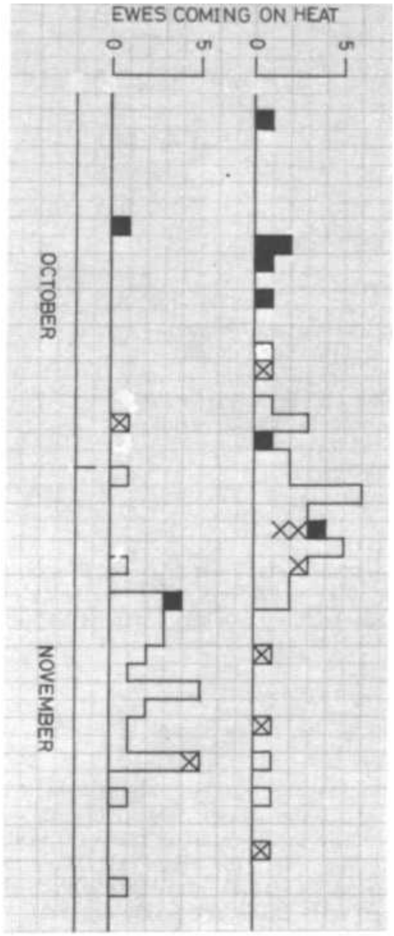

Fig. 3. Frequency distribution of dates of onset of oestrus in two adjacent ewe home range groups in 1966. Symbols as in figure 1.

The gestation period is 151. 2 ± 1. 34 days (n = 162) so that the distribution of births accurately mirrors the distribution of conceptions. When the dates of conceptions are compared with the distribution of oestrous dates, it becomes clear that the oestrus in which conception occurs usually corresponds to the second identifiable ovulation in the series but in 10 per cent of cases (out of a total of 491 births) is known or inferred to have been the first or third. This implies that the distribution of birth dates is polymodal, and though the modes are usually hard to detect, they were demonstrated by probability paper analysis for birth dates in 1966, two modes being clearly evident and separated by 16 days, approximately one interoestrous period (Grubb, 1968).

## 5. AGONISTIC AND AMICABLE BEHAVIOUR PATTERNS OF RAMS

### (a) Nudging

During the rut encounters between single rams become frequent once the ram groups disperse. Brief encounters involve certain mutual or reciprocated displays, rubbing, horning of vegetation, or clashing. Within the first category are two behaviours, the twist (a turn of the head about its longitudinal axis) and the kick or laufschlag (a forward poking movement of the foreleg) which have already been described by Geist (1968) for mountain sheep (*Ovis canadensis*). In the Soay these displays contribute to a series of activities which for the moment I assume reflect a scale of increasing intensity. At one end of the scale, there are movements of the tongue (empty licking) combined with a growling vocalisation (rutting call), made when one ram meets another. To this behaviour, more an excited state than a display, a twist may be added, and in a fuller display this is accompanied by a kick and partial erection of the penis, with rapidly repeated kicking in the most intense version. There is a close relation between kick and twist, for a kick with the left leg is accompanied by a clockwise twist and vice versa. As the kick is rarely shown without the twist, I refer to displays of this type as 'nudging', following a usage by Banks (1964) and to avoid coining a new phrase. Although a nudging display is usually directed towards an opponent, mutual displays occur in a variety of positions, for instance with the two rams standing in parallel (head-to-head or nose-to-tail) or in tandem (nose-to-tail).

A ram which retreats from a nudging display is usually smaller than the displaying male. Ram lambs never nudge larger, older males, and yearling rams (1. 5-year-olds) hardly ever do so. Out of about 50 older rams present in the rut of 1966, only one was nudged or butted by yearlings, and this was a particularly small 2. 5-year-old. Size disparities are evident among mature rams in cases where a younger ram nudges an older one. Among rams of similar size, the relationship is not so clear. Some consistently nudged other individuals, but there are also many reciprocated displays.

TABLE 3. NUMBERS OF ENCOUNTERS INVOLVING NUDGING OBSERVED IN 1966 IN RELATION TO THE AGE CLASSES OF RAMS INVOLVED.

| | | Approx. age in years of displaying ram | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 0.5 | 1.5 | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 |
| Approx age of recipients of display | 0.5 | 51 | 1 | 2 | 3 | 1 | 4 | | |
| | 1.5 | | 48 | 4 | 8 | 1 | 9 | 2 | |
| | 2.5 | | 3 | 11 | 15 | 3 | 10 | 2 | 1 |
| | 3.5 | | | 12 | 13 | 10 | 18 | | 3 |
| | 4.5 | | | 2 | 10 | 1 | 9 | 2 | |
| | 5.5 | | | 1 | 6 | 4 | 80 | 14 | 6 |
| | 6.5 | | | | | 3 | 14 | | |
| | 7.5 | | | | 2 | 1 | 3 | 2 | |

TABLE 4. THE NUMBER OF ENCOUNTERS INVOLVING NUDGING IN RELATION TO AGE DIFFERENCES BETWEEN THE RAMS

(Data from 1966)

| | Number of years by which nudging ram differs in age from recipient of display | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | –5 | –4 | –3 | –2 | –1 | 0 | +1 | +2 | +3 | +4 | +5 | +6 |
| Number of encounters | 0 | 2 | 2 | 14 | 31 | 217 | 53 | 39 | 14 | 15 | 7 | 0 |

The numbers of interactions involving nudging vary with the abundance of animals in each age class (Table 3) and with the relative age of participants. Over 50 per cent of nudging encounters are between animals of the same age and there are successively less between animals separated in age by one, two or more years (Table 4). Size is related to age, and it is reasonable to infer that rams are more likely to display to others of similar size, results which are close to those of Geist (1968) and Schaller and Mirza (this volume, Paper 13). Nudging may be an assertion of dominance, or an attempt at such when the relative status of two individuals is not established.

### (b) Submissive posture

A ram may respond to nudging by reciproacating the display or by walking away. In the latter case a well defined avoidance-posture is shown, with the neck extended, a little above the line of the back, and the head tilted upwards. It is taken to be a submissive action, but is only manifested by a few individuals.

### (c) Clashing

Soay rams do not jump into the clash, which resembles that of the mouflon (Pfeffer, 1967) and is frequently, but not invariably, shown in a 'blocking' sequence. Rams march backwards before clashing and a ram may solicit a clash by stepping backwards in front of another, without necessarily eliciting a response.

### (d) Horning of vegetation

A solitary ram, or two rams together, may rub their horns in vegetation by rapidly moving the lowered head from side to side, sometimes erecting the penis at the same time. Horning appears to combine elements of autoeroticism and redirected aggression.

### (3) Nosing

Young rams (1. 5-year-olds) sometimes nose the groin or penis sheath of elder strangers, apparently an investigatory behaviour shown with a low level of fear.

### (f) Rubbing

Another non-aggressive activity is for one ram to rub his throat and face over the horns of another who receives the attention by yielding slightly or by nudging. Of 40 cases observed in 1966 only two involved reciprocated activity. 6 concerned old rams rubbing younger ones, 14 involved rams of the same age and the majority, 29, involved young rams rubbing older ones (Table 5). In nearly all cases the ram performing the rubbing was the smaller individual. I suggest that rubbing is a submissive gesture shown with a low level of fear. Geist (1968, 1971) notes that rubbing is performed by subordinates.

TABLE 5. THE NUMBER OF ENCOUNTERS INVOLVING RUBBING IN RELATION TO AGE DIFFERENCE BETWEEN RAMS

| | Number of years by which rubbing ram differs in age from recipient | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | –6 | –5 | –4 | –3 | –2 | –1 | 0 | +1 | +2 | +3 | +4 | +5 |
| Number of encounters | 1 | 0 | 2 | 4 | 13 | 9 | 14 | 4 | 1 | 1 | 0 | 0 |

### (g) Blocking

A short exchange of nudging between rams can develop into much more complex sequences of behaviour. A pair of rams take up a 'reverse-parallel' position, standing side by side, nose to tail. Various activities are exhibited in this position and the animals return to it if a new one is temporarily adopted while they participate in some other behaviour. It is convenient to have a term for these long engagements, which can last for as long as a day or more, and I refer to them as 'blocking'. Principal kinds of behaviour shown in blocking, usually by both rams simultaneously, are as follows:

- (1) Reverse parallel position:
  - (a) standing with head lowered to ground
  - (b) standing with head raised, sometimes making cud chewing movements
  - (c) circling
  - (d) striking opponent on rump with sideways thrust of horns
  - (e) standing, pushing on opponent's rump
  - (f) grazing
  - (g) urinating, then nosing own urine, and flehmen
  - (h) nudging
  - (i) horning of vegetation
- (2) Parallel, head to head position
  - (a) standing and pushing shoulder to shoulder
  - (b) circling, pushing shoulder to shoulder
  - (c) nudging (sometimes combined with the above)
  - (d) trotting, pushing shoulder to shoulder, sometimes with horns interlocked
  - (e) trotting separated and with head lowered
- (3) Clashing.

Blocking appears to be the development of an inconclusive encounter, in which tactical manoeuvering rather than retreat is shown in response to aggressive displays and assaults. In some cases, a bout of clashing or sideways butting in a 'reverse parallel' position leads to blocking being terminated with the retreat of one participant, and in other cases it is evident that the contestants are not quite evenly matched. Nevertheless, only rams of about the same size engage in blocking, so that in most cases they are of about the same age (Table 6). In other words, only very evenly matched rams have difficulty in determining their relative rank. Geist (1966a, b, 1971) notes that strangers approaching bands of rams receive most attention from individuals of the same horn-size class.

TABLE 6.

Age class distribution of 'blocking' rams, from data collected in 1966. The figures indicate the numbers of pairs of different age class composition involved.

| | | Age of (senior) combatant in years | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 0.5 | 1.5 | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 |
| Age class of (junior) combatant | 0.5 | 22 | | | | | | | |
| | 1.5 | | 20 | 3 | | | | | |
| | 2.5 | | | 4 | 5 | 1 | 3 | | |
| | 3.5 | | | | 4 | 5 | 1 | | 3 |
| | 4.5 | | | | | | 3 | 1 | |
| | 5.5 | | | | | | 11 | 2 | 3 |

### (h) Familiarity and agonistic interaction

Rams remain relatively tolerant of their group-mates during the rut. Blocking usually involves unfamiliar adversaries. Of 56 examples observed in 1966, where the participants were known individuals, only two concerned animals from the same social group. The same situation was seen in ram lambs, for of 22 cases of blocking in lambs 16 involved animals from different ewe home range groups and in the other six cases, one or both were not certainly identified.

### (i) Social hierarchy

In many encounters between males during the rut, the role of dominant and of subordinate can be distinguished. When this is not the case the animals involved are often strangers and they spend much time and energy in an apparent attempt to discover each other's rank. Such a situation is most likely to arise with evenly matched animals and in general rams are more likely to react aggressively to near equals.

The resulting social hierarchy is an imperfectly linear one. The hierarchical pattern is not completely known, for many individuals are not seen to interact and, as several encounters between the same individuals are equivocal, relative rank may not always be determined. From all observations of encounters in 1966, a linear hierarchy was drawn up, though the position of some individuals had to be decided a little arbitrarily. The sequence was later used for comparison with individual mating success.

## 6. CONTACT BETWEEN RAM AND EWE

In the 'flehmen-urination' sequence a ram approached a ewe and if she does not trot away, noses her tail or vulva. She then squats and urinates and he, after nosing the urine, raises his head with the lips drawn back in the 'flehmen-face'. Such tests for oestrus (Fraser, 1968) are shown early in the season, when the rams are first recovering from weight loss in winter, but they become part of a systematic search for oestrous ewes during the rut. If an oestrous ewe is located, several rams may join in chasing her as she attempts to avoid them. The leading ram trots in a 'low-stretch' position (head and neck extended in line with the back), occasionally 'twisting' his head to right or left or stopping to turn on the other males with a full nudging display (twist plus kick). Sometimes he may butt the smaller individuals, and may even clash with another large male.

Such chases usually occur in the early stages of the rut and later it is possible for the larger males to establish a 'tending bond' with a ewe, in which he remains close to her for the whole of the oestrous period.

Ram lambs are very persistent in approaching the consort pair, but the tending ram will chase and butt them. Other approaching males are greeted with a violent nudging display. A dominant ram displaces a subordinate tending a ewe merely by nudging at him. The new arrival immediately approaches the ewe and nudges, standing beside and a little behind her. When she is receptive, little nudging is shown before she allows mounting but at other times he may make over 100 nudging movements before the ewe stands for him. One to four mounts with thrusts (rarely up to 15) occur before ejaculation is achieved. The act of nudging may include twist and kick but is variable, both within a single sequence and between individuals. It may for instance take the form of a twist with a forward step or flexure of the foreleg; or a series of backward and forward steps without any head movements. The precise form of these variants and their hesitant nature is interpreted as an incorporation of intention-mounting movements into the behaviour.

The oestrous ewe overtly ignores the tending ram but association with him is a positive action, as she temporarily stops following her group-mates. Untended oestrous ewes may associate with consort-pairs but are ignored, and are then approached by other rams.

The tending ram appears to exhibit a cycle of sexual activity. Mating is attempted when he first approaches the oestrous ewe and in one 8 hour period of tending, the dominant ram in the study area then mated regularly at hourly intervals. On another day the same ram tended a series of 6 ewes and mating was then attempted on 13 occasions in 8 hours, so the pattern may be more complicated.

Ewes are less ready to stand for mating late during oestrus and try to evade the tending ram. This change in behaviour can be noted even within one day. Rams nudge more and mount more frequently before achieving ejaculation later in the oestrous cycle of the ewe and they show less continuous interest in ewes late in oestrus. As a result a ewe may be mated more often by more rams later in oestrus. For instance, one ewe was mated 15 times by nine rams on her second day.

In 1966, the numbers of ewes tended on their first and second days of oestrus were noted for each ram in the Village Glen by closely checking all the sheep three or more times daily. As copulation is usually achieved only after the formation of a tending bond, the numbers of bonds established by rams is an indication of success in mating. Records for individual rams are illustrated in Fig. 4 in the order of rank of the rams, information being derived quite separately from the results of agonistic encounters. It is apparent that rams of higher rank form more tending bonds than those lower in the scale, and hence are responsible for more conceptions.

The stronger rams associate less with ewes on their second or later days of oestrus than do subordinate rams. For instance, the alpha dominant was seen with 34 ewes on their first day, and with only seven on their second day of oestrus. A younger

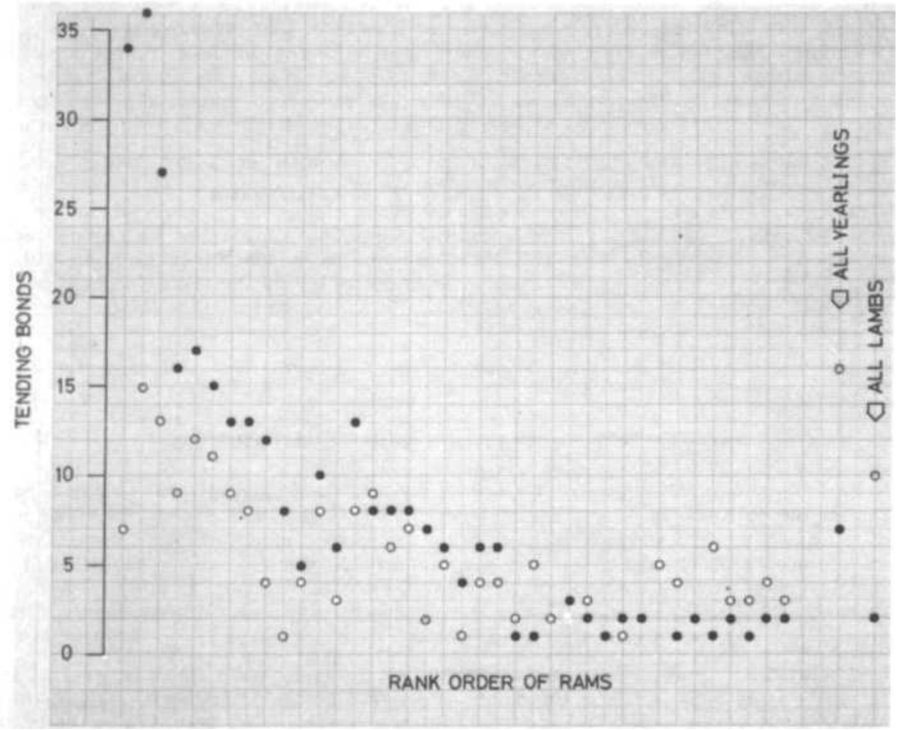

Fig. 4. Numbers of tending bonds established by rams in 1966 arranged in the order of their social rank as determined in agonistic encounters for the day of onset of oestrus in ewes (•) and the second day of oestrus (o). Data are lumped together for the first (lamb) and second age classes.

animal, 4. 5-years-old, was seen with 7 and 9 ewes respectively. The three rams of highest rank each tended twice as many or more ewes as those next in rank and accounted for nearly 30 per cent of the 304 associations recorded in 1966. 38 adult rams and many yearlings and ram lambs accounted for the ather associations. Records of mating activity during the 1966 season are most complete for the dominant rams. Conceptions could be achieved by such individuals at the rate of one per day. The alpha dominant made his 34 observed bonds with ewes over a 38 day period. The lower mating success of subordinate rams is less reliably assessed. These males are forced to wander more and allowed to tend ewes for shorter periods, so that their mating activity can be less accurately interpreted from regular daily observations. On many days their contact with ewes is minimal. For instance, within a 10 hour period a 4. 5-year-old ram made several circuits of the Village Glen, investigated ewes 95 times and showed flehmen 44 times. A ram lamb during a 8. 5 hour period approached ewes on 81 occasions and showed flehmen 18 times. Neither remained with a ewe for more than a few minutes though the first was displaced twice from oestrous ewes by older rams.

## 7. RAM LAMBS AND THE MATING SEASON

Ram lambs are especially agile in mounting a moving ewe and can trot in a mounted position, attempting copulatory thrusts when she pauses. Mounting from the side is sometimes seen and though this is only in situations where another male is correctly mounted, adult rams are never seen mounting incorrectly, no matter how highly motivated. Ram lambs sometimes persist in pursuing ewes that are not on heat or start chasing a ewe in which adult rams have lost interest — that is, whose oestrous period is waning. Clashing between adults seems to provoke ram lambs to mount one of the contestants and exhibit pelvic thrusting. On a few occasions ram lambs form tending bonds with ewes, but it is not known whether they ever successfully achieve conception. Park-reared Soay lambs will fertilise ewes (Jewell, personal communication).

The status of ram lambs before the rut is varied. Sometimes a ewe treated to a sexual approach rounds on the lamb and butts him, but in other cases she responds by urinating. During the rut, ewes usually react to lambs as they do to adult males but there are exceptions. In one case an oestrous ewe was approached by a small lamb and she turned and faced it each time it attempted to approach from behind. In the end the two butted and pushed at each other. It is possible that the lamb was not large enough to dominate the ewe but was so sexually motivated that it persisted in approaching her even when attacked.

## 8. SEXUAL AND AGONISTIC BEHAVIOUR-SOME COMPARISONS

Nudging is shown in the apparently separate contexts of agonistic and sexual behaviour. During the ontogeny of sheep it is apparent that these two categories of behaviour differentiate from a single kind, namely the nudge with mount of the two month old ram lamb (Table 7). The nudging display is here incomplete and the sequence of appearance of further elements is not related either to the sequence in which they are shown by the adult ram or to the variation of the display with different levels of intensity.

Following the summer lull in social interaction between lambs, there is a return of activity during the rut, and at this time differences between nudging in male-male and male-female contexts become apparent. In the former, higher levels of intensity are reached than in the latter context. The position of the nudging ram relative to the oestrous ewe is much more rigid than in male-male contexts, for he displays only from behind the female. There is further differentiation of nudging in different contexts among older males. Ram lambs may attempt mounting with little preliminary solicitation of the ewe but among mature rams, the nudging of an oestrous ewe always preceded copulation. It becomes a cautious and delicate manoeuvre often combined

TABLE 7

Ontogenic differentiation of behaviour patterns involving nudging and mounting.

(1) Ram lambs (first two months): nudging display incomplete (no empty licking, rutting call, penis erection) and in essentially a single context; mounting in a 'non-sexual' context.

(2) Ram lambs (next six months): nudging display now complete (rutting call, empty licking, twist, kick; and penis erection?); mounting of adult ewes may occur.

(3) Ram lambs (first rutting season): nudging now shown in two distinct contexts with different associated behaviour; mounting of oestrous ewes shown in definitely sexual context; mounting of clashing or blocking males also occurs.

(4) Younger rams (1. 5 to 4. 5-years-old): the same, but mounting almost completely confined to sexual contexts; mounting of other rams may occur, but rare.

(5) Older rams: the same, but nudging may form part of a 'mixed' display, in sexual contexts only; mounting of other rams never shown apparently.

TABLE 8

Estimates of the numbers of litters conceived in 1966 in the Village Glen or born there in 1967

| | litters conceived | | |
|---|---|---|---|
| litter | rams | ewes | litters born to ewes |
| size: | | | |
| 0 | approx. 100 | 61 | 26 |
| 1 | 17 | 197 | 157 |
| 2 | 6 | 21 | 15 |
| 3 | 2 | | |
| 4 | 1 | | |
| 5 | 2 | | |
| 6 | 3 | | |
| 7 | 3 | | |
| 8 | 1 | | |
| 9 | | | |
| 10 | | | |
| 11 | 1 | | |
| 12 | | | |
| 13 | 1 | | |
| 14 | 2 | | |
| 15 | | | |
| 16 | 2 | | |
| 17 | 1 | | |
| 18 | 1 | | |
| 19 | | | |
| . | | | |
| . | | | |
| . | | | |
| 29 | 1 | | |
| . | | | |
| . | | | |
| . | | | |
| 36 | 1 | | |
| . | | | |
| . | | | |
| . | | | |
| 40 | 1 | | |

with mounting intention movements, perhaps the result of negative reinforcement by past failures to achieve intromission and ejaculation with indiscriminant mounting.

It seems that with greater experience rams distinguish the different contexts to which agonistic or sexual behaviour is appropriate. There are also cases when rams are confused as to the context of nudging—a ram nudges another from behind and then mounts, his orientation facilitating the action. Such exceptional behaviour is seen only in young rams (less than 4 years of age). In many other situations clear distinction is made between 'courting nudging' and 'aggressive nudging', as when a ram 'twists' while following an oestrous ewe in a low stretch position and intermittently turns on other pursuers with a high intensity nudging display.

## 9. LITTER SIZE

The reproductive potential of the two sexes can be compared by estimating litter size and age-class fecundity. 'Litter size' commonly means the number of offspring resulting from one birth and the sole impregnation of one male. As sheep are polygynous, several 'ewe litters' may be sired by a single ram and represent a 'ram litter'. The number of lambs sired in the study area in 1966 can be inferred from the numbers of lambs born in the following spring. The assumption is made that the

TABLE 9

Estimates of age specific fecundity tabulated against generalised survival data based on all available records of individual life histories on Hirta, assuming initially the birth of 1,000 ewe lambs and 1,000 ram lambs.

| Age class | Numbers of ewes or rams | Mean fecundity or mean number of ewes tended | Percentage contribution to total conceptions |
|---|---|---|---|
| | | Ewes | |
| 1 | 695 | 0.40 | 10 |
| 2 | 388 | 0.82 | 11 |
| 3 | 339 | 0.96 | 11 |
| 4 | 317 | 1.08 | 12 |
| 5 | 295 | 1.09 | 11 |
| 6 | 278 | 1.12 | 11 |
| 7 | 254 | 1.12 | 10 |
| 8 | 225 | 1.12 | 9 |
| 9 | 187 | 1.12 | 7 |
| 10 | 124 | 1.12 | 4 |
| 11 | 45 | 1.12 | 1 |
| 12 | 16 | 1.12 | 1 |
| 13 | 6 | 1.12 | 1 |
| 14 | 2 | 1.12 | 1 |
| | | Rams | |
| 1 | 695 | 0.03 | 2 |
| 2 | 290 | 0.3 | 7 |
| 3 | 193 | 1.4 | 23 |
| 4 | 131 | 1.9 | 21 |
| 5 | 83 | 4.0 | 28 |
| 6 | 51 | 13.5 | 59 |
| 7 | 29 | 6.7 | 29 |
| 8 | 16 | 6.0 | 8 |
| 9 | 5 | 6.0 | 3 |
| 10 | 3 | 6.0 | 2 |

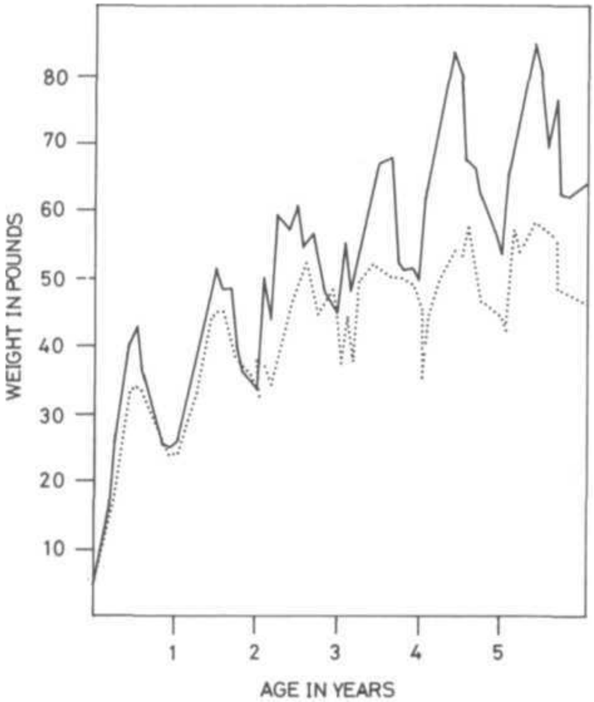

Fig. 5. Growth curves based on monthly means of weights of live known-age animals recorded in 1964 and 1965, for males and females.

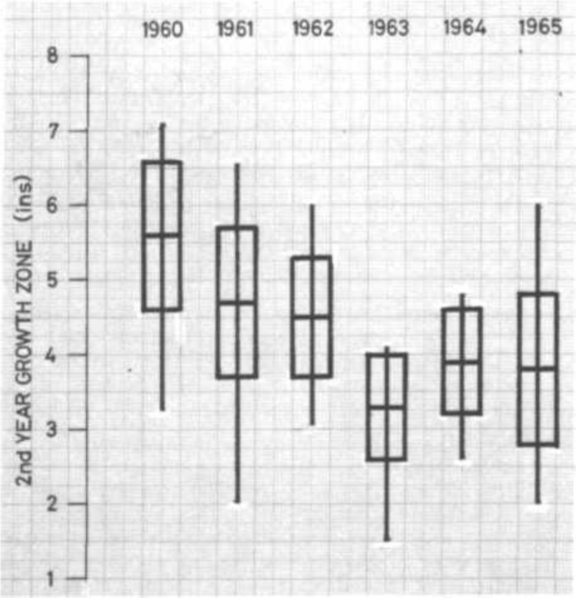

Fig. 6. Annual variation in the growth of the horn in the second summer of life among Soay rams. Measurements are of the greatest length of the growth increment, and mean, range and standard deviation are indicated.

fecundity of ewes which died during the winter of 1966 was the same as that of the ones which survived. The numbers of those conceptions per ram is taken to be directly proportional to the numbers of tending bonds observed. It is felt that any inevitably speculative correction of the figures provides no increase of accuracy. The results (Table 8) emphasise that the majority of males sire no offspring and of the remainder about a third sire only one.

A very few individuals sire as many as 20 or more lambs. In contrast, most females conceive and a small proportion produce twins. The life-time fecundity of individuals would show a greater variation, especially among rams and it is possible that a few males achieve 20 to 30 conceptions several years running.

## 10. COMPARATIVE AGE CLASS FECUNDITY

Age specific fecundity of ewes on Hirta is known with some accuracy from three years' records of over 500 births to known-age ewes. For the males it is estimated from the 1966 records of tending bonds. For a theoretical population, whose mortality pattern is provided by a composite life table, based on data for over 800 known-age animals (Grubb, 1968), estimated age specific fecundities are given in Table 9. The results are only a very rough guide but they demonstrate the different fecundity patterns in the two sexes. In ewes, age specific fecundity is largely a function of the size of the age class, while in rams it is much more dependent on age. The real differential in age-specific fecundity is probably not as exaggerated as the figures suggest, for they are based on only one set of records in which three individual rams of the same age dominated mating activity.

## 11. RUTTING AND MORTALITY

Reduced grazing time and increased energy expenditure during the rut lead to a greater winter weight-loss among rams than among ewes (Fig. 5). This is associated with a sex differential in mortality rate primarily reflected in the sex-ratio. In the Village Glen population there were between 2.8 and 3.6 ewes per ram in 1964-1966 (excluding lambs) and the figure rose to 8.0 after a population crash in 1967.

Levels of mortality and presumably of mean weight loss appear to have some relation to growth rate in the subsequent summer. Annual growth increments of the horns, which presumably reflect general growth patterns, show significant differences from year to year (Fig. 6), at least in some cases reflecting changes in population density.

At any one time age structure of the Village Glen subpopulation is irregular, that is there are not necessarily successively fewer individuals in successively older age classes. It is not possible therefore to construct 'horizontal' or time specific life tables. Although a generalised life table can be drawn up (See Table 9) it is more informative to prepare separate life tables for each cohort or year class (Table 10).

The irregular age distribution reflects the cycle of abundance in the population, for it is the result of a greater density-sensitivity in mortality among the lamb and yearling classes and a less variable mortality among older animals. The neonatal death rate is of equal severity in the two sexes and at this stage differentials in mortality are related not to sex but to dam age, birth weight, weight of dam and size of litter (Grubb, 1968). First winter mortality is of greater magnitude and is always higher in males than in females. These two early phases of mortality are quite distinct in character and in timing, and produce a kink in the mortality curve (Fig. 7; cf. Caughley, 1966).

Among older males, mortality rate exhibits a higher but more erratic sensitivity to population density than is evident among females (Table 10).

TABLE 10

Relation between sex, age, population size and scale of mortality (expressed to the nearest one percent) for sheep in the Village Glen from 1961-1967. Data available for rams in 1961-1963 are less reliable than those for ewes, explaining the apparent sex differential in neonatal mortality for 1962.

| | Year in which post winter mortality occurs | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1967 | 1966 | 1965 | 1964 | 1963 | 1962 | 1961 |
| Age in years at which mortality occurs | age-class percentage mortality, females | | | | | | |
| 0 | 45 | 32 | 20 | 53 | 31 | 11 | 10 |
| 1 | 79 | 47 | 32 | 63 | 31 | 8 | 0 |
| 2 | 10 | 4 | 9 | 22 | 12 | 14 | 9 |
| 3 | 4 | 0 | 3 | 14 | 8 | 0 | 19 |
| 4 | 0 | 3 | 0 | 27 | 0 | 8 | |
| 5 | 24 | 3 | 0 | 10 | 0 | | |
| 6 | 13 | 0 | 0 | 0 | | | |
| 7 | 37 | 33 | 8 | | | | |
| 8 | 67 | 9 | | | | | |
| 9 | 60 | | | | | | |
| | age-class percentage mortality, males | | | | | | |
| 0 | 45 | 36 | 20 | 48 | 28 | (35?) | 10 |
| 1 | 94 | 64 | 86 | 80 | 49 | 15 | 10 |
| 2 | 59 | 0 | 23 | 44 | 30 | 17 | |
| 3 | 50 | 30 | 21 | 57 | 40 | | |
| 4 | 86 | 55 | 26 | 11 | | | |
| 5 | 100 | 24 | 25 | | | | |
| 6 | 67 | 33 | | | | | |
| 7 | 100 | | | | | | |
| | Village Glen population size in previous season | | | | | | |
| | 404 | 392 | 317 | 425 | 392 | 313 | 174 |

## 12. DISCUSSION

Agonistic interaction between males has the same adaptive value in Soay and mountain sheep (Geist, 1971). A social hierarchy develops which establishes the freedom of the male to tend and inseminate females. Soay sheep nevertheless differ in behaviour from these wild relatives, reflecting their more primitive status as descendents of wild mouflon. The twist and kick are closely associated; there is a submissive posture; contestants step back before clashing and do not rise into a bipedal position; the *threat jump* and *present* are not shown; and during *dominance fights* (blocking) a reverse-parallel position is taken up and the opponents butt each other in the rump, recalling the fighting techniques of rupicaprines (Geist, 1971).

In the absence of horn displays (*low stretch* and *present*) and with the relative weakness of the clash, social rank in Soay rams is evidently determined less exclusively by the appearance of the horns and by the blows which they actually deliver. The nudge, in which mane and ruff as well as horns are displayed; wrestling during blocking, when

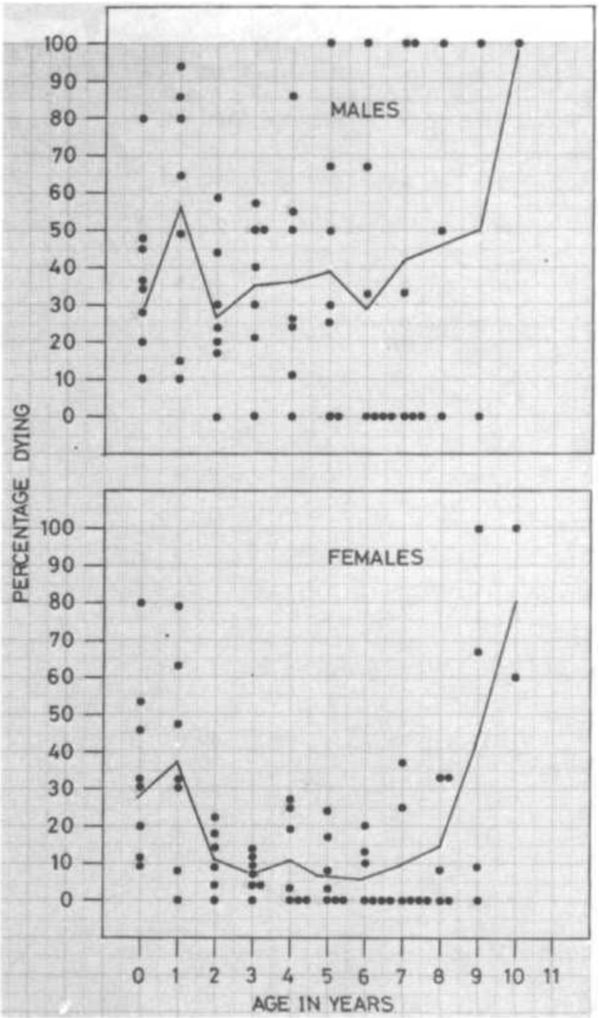

Fig. 7. Mortality curves for males and females, composed by plotting the mean percentage of animals dying in each class in different years against the time when mortality occurs, taking the date of birth as '0' years. The scatter of values is also indicated for comparison. The difference in mortality rate between '0' and 1 year old animals represents the kink in the mortality curve.

relative strength can be evaluated, play a significant role. The Soay lamb partly foreshadows evolutionary advances in behaviour shown by adult mountain sheep, for it exhibits a threat jump and does not discriminate between the sexes when mounting or nudging. To increase the force of the clash and for the subordinate male to be treated more as if it were an oestrous female, there is in mountain sheep an extension into adulthood of what used to be juvenile behaviour patterns (see Geist, 1968, 1971).

Pfeffer (1967) records male mouflon mounting other rams and Schaller and Mirza (this Volume, Paper 13) note the same in urial, as well as low stretch used towards other males. Perhaps the behaviour of the Soay has in fact been modified significantly following domestication. There is not yet enough information to be certain of this. It is somewhat inappropriate to regard the Soay sheep as a domestic animal, however, for this feral stock is closer to the wild mouflon in proportions, general form and growth rate (see Pfeffer, 1967). Sexual maturity is admittedly relatively precocious (cf. Mottl in Pfeffer, 1967, p. 151). We may explain this in terms of unconscious or weakly directed selection by Neolithic pastoralists and natural selection over perhaps a millenium on St Kilda. probably reflecting special aspects of population dynamics under these conditions.

Although the decline in intake of nutrients over the season on Hirta has still to be fully reported, annual starvation doubtless reflects the restricted growth period of fodder plants and the absence of alternative winter grazing grounds. While ensuing mortality mainly affects lambs from the previous spring, and males of all ages (see Table 10), *adult* females have a mortality pattern not unlike that given for bighorn rams by Geist (1971, p. 295). Ultimately the differential in mortality between the sexes (see Table 9) must be explained by the independence of male ruminants from rearing their offspring. Selection then favours a much higher optimum litter size (see Lack, 1948) than in the females, as well as all the behavioural and physical devices which maximise reproductive output. In the Soay sheep these involve extreme physical exertion and reduced feeding during the rut. Resulting energy loss cannot be restored adequately by winter grazing. Under such conditions males are likely to have a higher mortality rate (see also Cowan, 1950,Taber and Dasmann, 1954 and Flook, 1970) though this is not selectively disadvantageous as long as lifetime reproductive output is not critically reduced in all individuals.

One would expect selection against sexual precocity in males, however, for the heaviest losses are among the ram lambs, indicative of their apparently futile participation in the rut. Subsequent life expectancy is still so low (> 3 years) that males which mature early may nevertheless have a higher probability of siring many offspring in a lifetime than those who take longer to mature, even though these latter have a higher life expectancy. More records of rutting on Hirta are needed before this suggestion can be critically evaluated. If lambs are small, growth rates reduced and survival rates high, then quite different patterns of selection may come into operation, as noted by Geist (1971) in comparing ibex and mountain sheep.

Annual winter mortality on Hirta increases as the population enlarges until natality (which is declining) no longer compensates for it, and there is a drop in numbers. Survival rates increase in the next season and the population builds up again (see Table 10; and also Marburger and Thomas, 1965, for a similar case). While the effect of population density on fodder supply probably accounts for this controlled situation, many factors are involved in the relationship and precise scales of mortality cannot be predicted from one year to the next. The crash in 1960 for instance was particularly severe (Boyd *et al.*, 1964), delaying subsequent recovery of numbers. Population quality (Geist, 1971) apparently declined during this phase though not on the scale illustrated by Geist or Nievergelt (1966). It may in turn have had an effect on the date of lambing.

Even though this is usually very constant (mean date of births between April 12th and 20th for 3 years of accurate data), sheep do have means whereby they could alter the date of overt oestrous (section 5). It would be attractive to believe that higher quality animals are served early by showing overt heat at what is usually a 'silent' oestrus (see Perry, 1971) in the population. This may enhance the survival rate of offspring by lengthening their effective growth period in the first year. Speculation along these lines receives a little support from P. Jewell's ms. notes. He found that lambing in 1963 was approximately one inter-oestrus early. Quality of sheep in the previous year must have been good, for the year-old ewes successfully reared lambs and in turn they must have weathered the winter well, a reflection of reduced population density after 1960. A crash of less severity in 1964 did not precipitate a similar chain of events.

It is hoped that such complications of what at first might seem a simple population control mechanism receive more attention in future. This preliminary account has treated the Soay as a primitive sheep compared with the wild American species. But domestication may have introduced new adaptations that can only be evaluated by critical comparisons with wild mouflon.

## ACKNOWLEDGEMENTS

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**Paper No. 24**

# The Social Behavior of the Vicuna

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## ABSTRACT

Vicuna (*Vicugna vicugna*) behavioral ecology and social organization was studied at the Pampa Galeras National Vicuna Reserve in southern Peru. With its specialized territorial system, it is one of the few ungulates to defend a year-round feeding territory and a separate sleeping territory. Within their socially isolated territories, a family group feeds, sleeps, reproduces and raises its young. Non-territorial males gather into all male groups and are prevented from utilizing occupied and preferred habitat by resident territorial males. The territorial male's role in the system is strategic: he not only determines the location, limits, and size of his territory, but he regulates the number of animals within his family group by accepting or rejecting outsiders and expelling juvenile members.

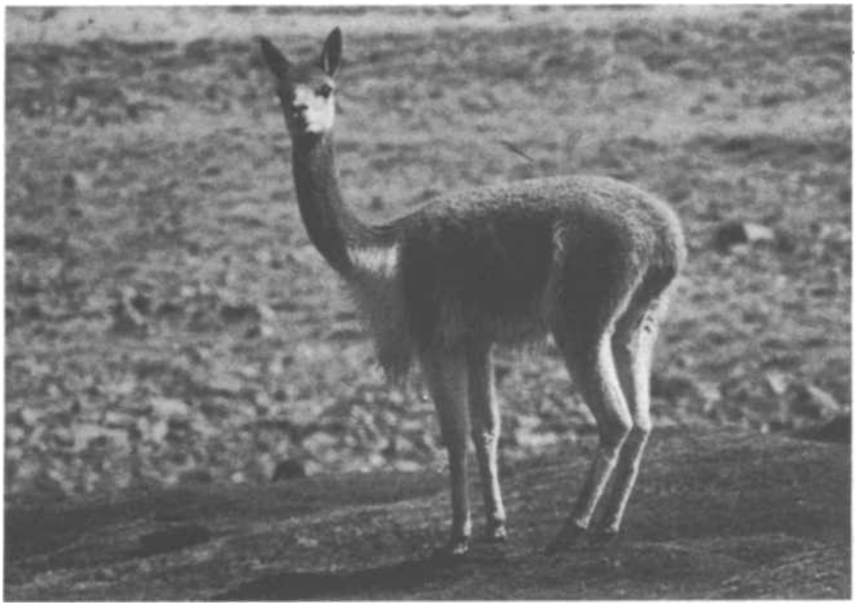

Fig. 1. Portrait of a vicuna
(Photo by W. L. Franklin)

## INTRODUCTION

The approach to the biological study of animal behavior has been expanded over the past few years to include the question of how an animal's behavior is interrelated to its environment. This field of behavioral ecology is concerned with two general problems: (1) what effect the environment has had on shaping the animal's behavior and social organization; and (2) how the animal's social organization effects the animal's utilization of its environment.

The social organization of a species refers to the system by which the individuals in a population are organized. Are they solitary? In permanent or temporary groups or herds? What is the age structure and sex composition of the social groups? Do they live in home ranges or in defended territories? Are there social rankings within groups? Beyond a description of an animal's social system, behavioral ecology examines the mechanisms that maintain the system as well as the adaptive values and advantages of that system that have enabled the species to succeed in its environment. So the door swings in two directions: a species' social organization determines how the members in a population are distributed in and use their environment, and how the environment has influenced the type of social organization that envolved there.

Of what value is behavioral ecology to the management and conservation of the endangered vicuna (*Vicugna vicugna*) ? Scott (1968) stated that until we have a general picture of an animal's social behavior and organization, we lack a firm foundation for experimental work. More recently Geist (1971) emphasized that a knowledge of an ungulate's total biology is essential if we are to manage and conserve it in the wild state. In light of the vicuna's unique social organization of year-round territoriality, a basic understanding of its ecology and behavioral ecology are important for future management planning.

A field study on vicuna was conducted at the Pampa Galeras National Vicuna Reserve in southern Peru from May 1967 to June 1971. This paper will summarize basic features of vicuna social organization and behavioral ecology. Prior to the present investigation, the only other systematic study of the vicuna was by Koford (1957). The present study has been supported by the Conservation Foundation, World Wildlife Fund, Peruvian Ministry of Agriculture and Utah State University.

## STUDY AREA AND METHODS

In 1966 Peru established the Pampa Galeras National Vicuna Reserve, 450 km (280 miles) south of Lima, in the Department of Ayacucho between Nazca and Puquio. The reserve was urgently needed since the vicuna had experienced a 98 per cent decrease in total (world) population size during the previous 20 years. In the early 1950's there was an estimated 400, 000 vicuna in the Andes (Koford, 1957). Due to illegal hunting for their valuable wool, numbers had been reduced to less than 10, 000 by the late sixties (Grimwood, 1968). The vicuna was declared rare and endangered by IUCN in 1968 (Franklin, 1969a).

Pampa Galeras' contribution to the initial recovery of an endangered and rapidly declining population has been paramount. Within the limits of the 6, 500 hectare (16, 062 acres) reserve, the numbers of vicuna have increased at an annual average rate of 16 per cent with a total increase of 50 per cent (814 to 1217) from 1967 to 1971.

Located at 4, 000 meters (13, 120 feet) above sea level, Pampa Galeras is an alpine short grassland whose treeless landscape is characterized by broad open valleys, interspersed by flat wide ridges. There are basically two climatological periods: a summer-rainy-season from November through April when plant growth occurs, and a cold-dry-season from May until October.

A 5 km (3.1 miles) straight portion of a road on the northern limits of the reserve served as a base line for a grid. Rock piles spaced 200 meters apart formed a rectangular grid 4. 4 × 3.0 km (2.73 × 1. 9 miles). The 1, 525 hectare (3, 768 acre) study area included a large valley, the slopes on each side, and one of the adjacent flattened ridges. A map of the area made it possible to record a vicuna group's location within 20 meters by using the grid co-ordinates. Observations were made from huts built on high vantage points around the valley.

## GENERAL ECOLOGY

Vicuna graze almost exclusively on perennial short grasses and forbs. Although other members of the camel family may go for periods without water, vicuna must water once to twice daily during the dry season. Open water is needed less frequently when forage is green.

Some females breed as yearlings (one-year-olds), but most females breed as two-year-olds and give birth to their first offspring as three-year-olds. Gestation is approximately 11 months and only one offspring is born. The parturition-breeding season occurs during February, March and April when forage is abundant and temperatures are favorable. The puma (*Felis concolor*) and the Andean fox (*Dusicyon culpaeus*) are predators of the vicuna.

Forage productivity is low and preferred habitat types are limited in this high altitude environment, factors which are suspected to have greatly influenced the envolution of the vicuna's unusual social system.

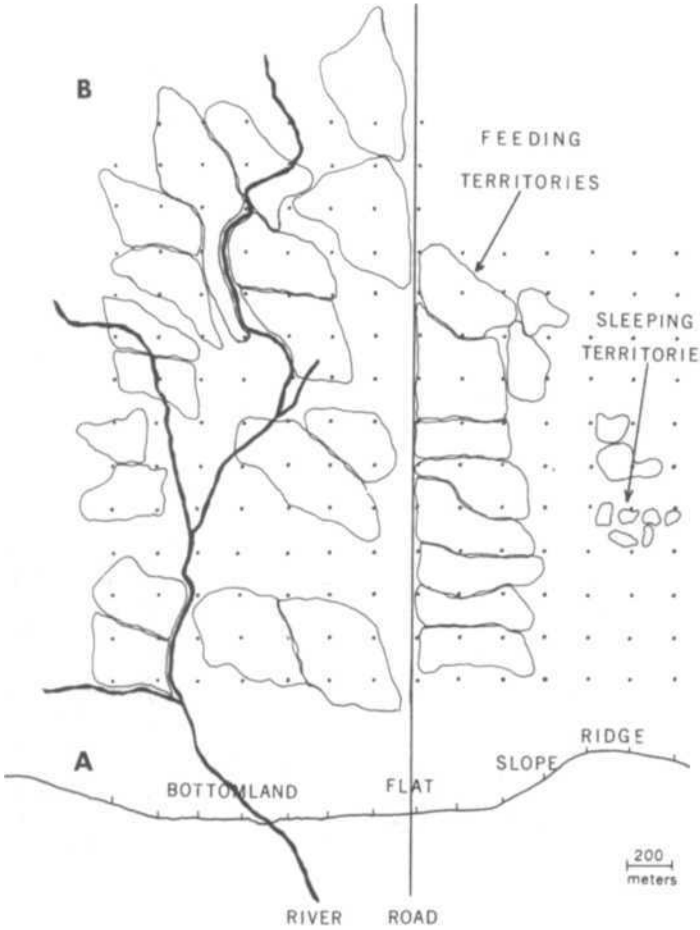

Fig. 2. (A) Lateral view of study area's topography, Cupitay Valley, Pampa Galeras National Vicuna Reserve, Peru. (B) Schematic illustration of vicuna family group feeding and sleeping territories.

## SOCIAL ORGANIZATION

The vicuna population consisted of five principal types of social groups.

(1) *Permanent Territorial Family Groups* (*PTFGs*) occupied the preferred habitat types that were found on the slopes, flats and bottomlands (Fig. 2A). A PTFG was composed of one adult male and females with and without crias. (The Spanish term 'cria' here refers to baby vicuna less than one-year-old). Their territory consisted of two parts: a feeding territory where the group spent most of the day, and a sleeping territory located on higher terrain where the vicuna spent the night. The feeding and sleeping territory were connected by an undefended neutral corridor. Territories were exclusively occupied by the resident family group and defended by the adult male against all intruding outside vicuna. Territorial boundaries were discrete and well defined. The size and shape of feeding territories occasionally changed slightly from one season to the next but remained in the same basic location for the entire year. The PTFG's feeding territory included permanent water. The family group was a stable unit with essentially the same adult females remaining throughout the year.

(2) *Marginal Territorial Family Groups* (*MTFGs*) were found on secondary habitat surrounding the better areas occupied by the PTFGs. The size, shape and location of their feeding territories were less consistent and more susceptible to change than the territories of the PTFGs. The feeding territory was less likely to include a permanent open source of water (spring or stream). As a result, marginal groups had to make brief daily movements (usually no more than two km) out of their territory during the dry season. Compared to PTFGs, marginal groups began making daily watering movements earlier in the dry season, were on the move more, and spent less time in their feeding territories. PTFGs and MTFGs commonly ranged in size from five to ten animals. For example, a group of seven might include one adult male, three adult females, one yearling female, and two crias.

(3) *Mobile Family Groups* (*MFGs*) consisted of two to five animals and often included yearling females. For example, a group of four might have included one adult male, one adult female and two yearling females. Mobile family groups appeared only to be a temporary group of females associated with a male that was without an established territory. When they entered unfamiliar zones and inadvertently trespassed onto terrain already occupied by PTFGs and MTFGs, they were promptly attacked and forced out by the resident territorial males.

(4) *Male Groups* (*MGs*) were composed of non-territorial all-male groups. They varied in size from two to 100 animals, but more often had only 15 to 25. They were not tolerated on occupied habitat and were quickly chased out by territorial males. Consequently, male groups lived in unoccupied and non-preferred habitat types. Because of the frequent attacks upon them by territorial males, male groups moved long distances in search of areas to feed undisturbed. Male group size fluctuated often due to subgroups leaving and joining.

(5) *Solo Males* (*SMs*) were sexually and physically mature individuals that had left their all-male groups and were ready to establish a territory of their own. Solo males did much wandering while looking for suitable unoccupied or poorly defended sites to set up their territories. They were usually aggressive to established males that attempted to force them out of the territorial zones. Old or injured males no longer able to hold a territory were also occasionally seen by themselves; they were not considered part of this category because of their small numbers and lack of social involvement with the remainder of the population.

## TERRITORIALITY

The territorial system formed the foundation of how the vicuna population was organized and made use of its environment. Essentially all adult females were found in family groups with territorial males. Those that became attached to a male without a territory remained only temporarily until accepted into an established territorial family group.

Many of the vicuna's vital life functions took place within the socially isolated territory free from intraspecific interference. The family group fed, reproduced, and raised its young in the feeding territory, while they passed their nights in the sleeping territory. The feeding territory played the important role of providing the reproductive units of the population, the adult females, a secure and favorable site to successfully raise their young. (Hereafter, the term territory will refer to the feeding territory. Sleeping territories will be referred to as such.)

## DAILY CYCLE

The members of a permanent territorial family group began to move around about half an hour before sunrise. Each animal defecated and began to feed immediately after rising. Within an hour after sunrise, the male led the group in its downhill walk from the sleeping to the feeding territory. Groups with territories on the slopes and upper flat, sleep about one kilometer (0. 6 mile) away on the ridge. Groups feeding on the bottomland and lower flat slept on the ridge 1. 8 kilometers (1.1 miles) away (Fig. 1B), although during the warm season they would occasionally choose to sleep only 200 meters uphill on the upper flat. On the ridge, the small sleeping territories of some eight to ten groups clustered together to form a compact sleeping ground. Klingel (1967) reports that family bands of plains zebra (*Equus quagga*) also gather at night on a common sleeping ground.

When groups moved through the unoccupied neutral zones between the sleeping and feeding territories, group males tolerated the closeness of other family groups. It was not uncommon to see several groups temporarily feeding next to each other on the way to their feeding territories. On one occasion, five groups totaling 42 animals were within 50 to 200 meters of each other on an area of only two hectares (5. 0 acres).

After a group arrived on its territory, the integrity or exclusiveness of the area was maintained by the male, who actively defended it against trespassing groups. In the late afternoon before darkness, family groups made the reverse movement uphill back to their sleeping territory.

## TERRITORY SIZE AND ANIMAL DENSITY

Territories for six PTFGs during April, May and June 1969 ranged from 7 to 30 hectares and averaged 17 hectares (17-74, 42 acres). Corridors ranged from 2 to 59 hectares and averaged 19 hectares (5-146, 47 acres). The size of a group's feeding territory from one month to the next was more constant than the size of its corridor.

Roads, streams and dry creek beds sometimes acted as obvious physical borders between territories, as Koford (1957) also found during his study. But more commonly boundaries were well defined strips or even 'lines' that separated territories. It was not uncommon to see two neighboring territorial males only two to three meters apart, each within his own respective territory, giving threat displays to the other. If one crossed over into the other's territory, he was promptly chased back to his own.

The surface area of territories was compared to the average number of animals using each territory for April, May and June 1969. The mean number of hectares per animal unit for eight groups was 3. 4 and ranged from 1. 0 to 7.3 hectares (8.4, 2. 5-18.0 acres per animal unit). In order to equate juveniles to older animals, an 'animal unit' was considered equal to four crias, since the weight of two to four month old crias during that time of year was one-fourth that of the adults. An animal one-year-old or older was treated as one animal unit.

During the same three-month period, variations in the size of the feeding territories appeared to be related to changes in group size. For group 207 the territory expanded from 22 to 30 hectares (54-74 acres) at the same time that the group increased in size from 8. 7 to 12. 2 animal units. The result was a constant area for each animal unit. For groups 211 and 213 the surface area per animal unit, the number of animal units, and the size of the territory all remained about the same. A decrease in territory size for groups 208 and 212 was proportionally greater than the decrease in group size, resulting in a decrease of surface area per animal unit. Group 214's territory size remained about the same, but had an increase in group size that caused a decrease in the surface area per animal unit.

## TERRITORIAL DEFENSE AND INTERGROUP ENCOUNTERS

The territorial male defended his territory against all intruding family groups, male groups and solo males. When an unattached female (one without a family group and not accompanied by an adult male) attempted to enter a male's territory and his family group, the male either permitted her to remain or he expelled her from his group and territory.

The male defended his territory by aggressive display, threatening charges and chases; only occasional body contact was made with an intruder. The resident male initiated and dominated intergroup aggressive encounters. This was an all-or-none type of territorial defense: winning all inside the territory, while losing all outside. Males were most active defending their territories in the morning. Of all the intergroup encounters observed during April, May and June 1969, 80 per cent occurred before 1300. In April the peak of defense was between 0800 and 0900, shifting to later in the morning between 1000 and 1100 for May and June.

Of the intergroup encounters observed in April, 1969, 72 per cent were among the family groups established on the study area (PTFGs and MTFGs); 26 per cent were between these family groups and outside family groups trying to enter the area; and 2 per cent between male groups. By June the percentage of encounters between locally established groups had decreased to 34 per cent, while the proportion of encounters directed toward outside family and male groups increased to 46 per cent and 20 per cent respectively. The increase was correlated with the onset of the dry season in May. The outside groups were most likely marginal territorial groups without access to water that had to pass through territories of locally established groups during their search for water. Outside groups were also attempting to encroach upon the resources found within the territories of the local PTFGs.

The relative involvement of territorial males in intergroup encounters differed greatly. To compare this difference, Daily Intergroup Encounter Rates were calculated by dividing the number of encounters seen during the month with the number of hours observed. The Initiator Rate (IR) was the average number of times per day a male initiated and won an encounter, while the Recipient Rate (RR) measured the average number of times per day the group was the recipient and subordinate member of an encounter. A high RR indicated a group was leaving its own territory and trespassing onto others. By contrast, groups with a low RR were staying within their own territory. When IRs and RRs were numerically listed, groups tended to be in similar order from one month to the next. The average IR-RR for all groups was 1. 2-0. 5 in April, 2. 1-1. 0 in May and 1. 4-0. 5 in June. The May increase again reflected the transition period between the availability of green and dry forage.

Males that initiated and dominated encounters the most, also maintained a constant relationship between the size of their territory and family group. Males who initiated the least encounters and who were often subordinate to other males, experienced a decrease in the available area per animal unit within their territory. It appeared that some males, such as 207, 211 and 213, were more successful at maintaining the integrity of their territories, and perhaps a better balance between the number of animal units and resources within the feeding territory.

## ESTABLISHMENT OF TERRITORIES

The most common way non-territorial single males became territorial was by taking over a suitable unoccupied site or an abandoned territory. Non-territorial males looking for a favorable site to establish themselves on, were constantly on the move in search of locations poorly defended or not already occupied. Of all the social groups in the population, such males offered the greatest threat to established territorial males. They might permanently encroach upon a portion of a male's territory, or even displace him and his family group from their territory. As a result, mature males seeking a territorial site were quickly confronted and attacked by the local territory owners. The high mobility of a male seeking a territory was adaptive for testing and finding a site where he might become established.

If a male discovered a likely location and was not driven away by the neighboring territorial males, he would remain. At first he spent most of his time feeding or resting, and was only occasionally involved in boundary conflicts with neighboring males. Perhaps this was a low profile phase of habituating his presence to the adjacent territorial males. Gradually the newcomer became more involved in aggressive encounters while testing and probing and learning the limits of the unoccupied or poorly defended site. When he had firmly established himself as resident, he would then attempt to secure females for a family group. Females were gotten from non-neighboring groups moving through the area, yearling females without a family group, or an occasional wandering unattached adult female. Once females were obtained, the male temporarily turned his attention toward keeping the new members in his territory and was less preoccupied with border defense. Females who attempted to leave the territory were promptly forced back to the group by the male. He was now a territorial male with a family group.

## EXPULSION OF JUVENILES FROM THE FAMILY GROUP

During my August 1968 census of the 6,500 hectare (16,000 acre) reserve, the average number of juveniles per 100 non-juvenile females was 48, although it was as low as 35 : 100 in one valley and as high as 70 : 100 in another. In the study area during September 1968, the ratio was 86 : 100, the unusually high ratio at least in part reflecting the more intensive observations made in the study area. By February 1969, the ratio dropped to 23 :100 and ultimately to 7 : 100 in March when the crias were about one-year-old, indicating a severe loss of juveniles.

One explanation stems from the behavior of the territorial male. Beginning in July, the territorial males became increasingly aggressive towards the juvenile males in their groups. Over the next few months they would expel each of the male crias, but only after several unsuccessful attempts. The mothers of the juvenile males vehemently defended their young from the attacking adult males. If the male was persistently aggressive while the female remained protective of the young male, she might try to leave the group with her juvenile male. The male would force the female or the pair back to the group in such a case. Maternal protection appeared to play the role of preventing the premature expulsion of juvenile males from the family group in these instances. As male juveniles became older, protection by the mothers waned and the adult male's antagonism took its affect, until the young male was permanently forced to leave the group.

After the young males had been pushed out, only the juvenile females remained in their family groups. As the March birth season approached, the adult male and the mother of a juvenile female become more and more aggressive toward her female juvenile. The juvenile female was at the bottom of the family hierarchy (the male being the alpha individual). Thus she was the recipient of frequent threats from group members, especially the adult male and her mother. The juvenile female commonly goes into submissive crouches in response to threats from her parents, and may inhibit attacks in this way. Ultimately the male harshly attacks and drives her from the territory. The expulsion of the juvenile females occurs only once and is final.

The hierarchy within the family group functions to prevent unwanted animals from joining the group, but it also functions to expel unwanted juvenile males and females.

## DEFECATION-URINATION

Many ungulates defecate and urinate at random where ever they may be. Vicuna differ by eliminating only on regularly used dung piles, a behavior that has both social and environmental significance.

All members of the family group defecate and urinate in their sleeping territory, feeding territory, when they move between their territories, and in unoccupied zones of neutrality while moving between their territory and watering site. Both males and females go through basically the same preliminary behaviors of smelling the dung pile, kneading with the forefeet, and making a quarter turn and positioning before defecating and/or urinating.

Within the feeding territories the density of dung piles was five per hectare, and seven per hectare in the sleeping territories. The amount of dung in a pile differed greatly between the two territories. The mean dry weight of a dung pile in the sleeping area was 24 kilograms (54 lbs), as against 6 kg (14 lbs) in the feeding territories.

Males usually performed a defecation-urination display on the way to, at the end of, or while returning from an intergroup encounter. They went through the same sequence of ritualized preliminary behaviors given above, including positionings, but did not necessarily defecate or urinate during each display. My observations on territorial male vicuna agree with Ralls's (1971) statement that mammalian marking displays increase when dominant to and intolerant of conspecifics. Vicuna males may also be reinforcing territorial boundaries since such displays tended to be toward the periphery of the feeding territory.

In this high Andean altiplano environment visual landmarks are scarce, so scent marks are an obvious alternative. However, dung piles did not succeed in keeping outside groups out during the absence of the owner. Male groups and non-neighboring family groups would flagrantly enter and remain to feed in a territory if the resident group was absent. In contrast, neighboring groups learned through numerous conflicts where territorial boundaries lay and remained in their own territory even in their neighbors' absence.

If dung piles do not communicate that an area is already occupied and are ineffective at preventing outside groups from using the site when the owner is temporarily absent, what adaptive value do they serve ? The traditional explanation for scent marking a territory since Hediger's (1949) classical work on territorial marking, has been generally and simply that it is a system for keeping *outsiders out.* This could be operating in part, but the vicuna scent-marking by defecation and urination may well be operating more to keep *insiders in.* Hediger (1949) implied that some odor signs might also serve for an animal's own orientation.

Dung piling by female and juvenile members of the family group appeared to function for their own orientation (Franklin, 1971) to help them stay within their own territory. When a group strayed beyond their own territorial limits into another male's territory, it was the *adult female members* that were attacked and chased out by the resident male. On one occasion adjacent family groups were feeding and moving in the direction of each other and the mutual boundary that separated their territories. The members of each group before coming to their common border, stopped to smell, urinate and defecate on a dung pile just inside their own respective territory, as if verifying where they were. Right after, each group advanced a few more meters apart, separated only by the imaginary boundary between them. If one group crossed over the line, they were promptly pushed back to their own side by the other group's male.

When a group moved over a regularly used route through a neutral or unoccupied area, for example between their territory and the river, members frequently stopped to defecate and urinate. Animals always smelled the excrement as they paused on a dung pile, but they sometimes failed to complete the behaviorial sequence. The impression was they were checking or verifying their location. If the dung pile was one they had passed before en route to the river they would smell familiar odors of their own group, otherwise, only unfamiliar scents would be present. Surrounding their regular route of movement were a number of territories from which they would be chased if accidently trespassed onto.

In Pampa Galeras the slopes and flats have an obvious downhill alternating pattern of wide-dark strips and narrow-light strips. The sparsely vegetated darker strips are dominated by surface rocks, while the intermediate light-colored areas are rock-less and densely covered with small perennial forbs and grasses. Numerous dung piles are scattered throughout the densely vegetated strips. Evidence indicates that greater soil development on the heavily vegetated strips is due to long term deposition and subsequent downhill washing of the excrement by rain. The fertilizing effects of the excrement and urination can especially be seen downhill from dung piles during the beginning of the summer rainy season.

An obvious contribution of this excrement influenced vegetation (E.I.V.) was its higher production of a preferred forage type. E.I.V.'s annual productivity was three times that of the adjacent rock covered type.

Thus, dung-piling for the vicuna appeared to serve a short term primary function of marking territories, especially for intragroup orientation, but also, over the long term, a secondary side-effect of causing favorable environmental changes in the vicuna's habitat.

## THE ADAPTIVENESS OF THE SYSTEM AND THE ROLE OF THE TERRITORIAL MALE

Essentially all life processes of the vicuna family take place within its sleeping and feeding territories. The isolation and spacing of a year-round territorial system guarantees the family group a secure place to carry out these life processes. The fact that territoriality is year-round, suggests that the commodities being defended are only enough to confer advantages upon those individuals who take the time and energy to maintain their exclusive use of an area for the entire year. Intensive competition for preferred defendable areas and the time-energy costs required to become successfully territorial may have also made it more economical to establish a territory once and maintain it perennially than to repeat the establishing process each year.

For a year-round feeding territorial system to be adaptive, it must somehow limit animal density and maintain the number of animals near the carrying capacity of the territory. Being selectively advantageous for a territorial male to pass on a large number of offspring, one might expect him to secure as many females for his family group as possible. But the opposite negative force of greater competition for available food would cause a reduction of reproduction and survival of group members. Some balance must be achieved between group size and territorial resources for maximum reproductive success.

The territorial males' role in achieving this balance appears to be paramount. Although habitat resources probably dictate group size within the feeding territory, they do not regulate it: the territorial male does. His individuality, pugnacity or even 'perceptiveness' ultimately determines the boundaries and size of his territory and the number of adult females within his group. In addition, the territorial male aggressively disperses the juvenile members from his group. Some males are obviously more successful at being territorial than others. Yet, behavioral regulation of family group size by the territorial male is a central factor in the social organization and behavioral ecology of vicuna.

## PRELIMINARY RESULTS APPLICABLE TO PRACTICAL MANAGEMENT

Full protection of the vicuna is clearly the best management at this stage. This approach was not necessarily fully realized before, since range deterioration had been suspected as a possible co-factor responsible for the sharp decline in vicuna numbers over the past twenty years. Although domestic animals are abundant at Pampa Galeras, vicuna have increased by over 50 per cent during the past four years. This points out two important factors: (1) effective protection against hunters appears to have been a key factor that enabled numbers to increase; and (2) population recovery is possible in the face of common use with the domestic stock.

Vicuna got along with alpaca and llama herds in the same area. Sheep caused some disturbance since they were normally accompanied by herders and dogs. Even when vicuna were displaced from their territory by herders it was only temporary. The vicuna group escaped a few hundred meters up the nearest slope while the sheep grazed through the area, and returned to their territory soon after the sheep had moved on.

It is not practical to manipulate range at this stage because of high costs and questionable results. Qualitative observations indicate sheep have the greatest overlap of use with vicuna, llama the least, and alpaca intermediate. Limiting domestic stock, especially sheep, is a management tool useful only in areas where vicuna restoration has high land use priority, such as in wildlife reserves. Control, even by the government, over private stock on community owned lands is unrealistic.

Another lesson learned from Pampa Galeras, supporting the thesis that the best management strategy is well-protected areas, is that as vicuna density increases, animals will disperse and repopulate the surrounding unoccupied vicuna habitat.

As discussed earlier, the basic social unit in a population of vicuna is the family group: the territorial male, his adult females, and their offspring less than one-year-old (crias). A typical group composition would be one male, three females, and two crias. In future management programs when vicuna restoration can be speeded by reintroducing animals into former parts of their range, best results will be obtained when complete family groups are captured and transplated as intact units.

The excess non-territorial males represent a harvestable surplus; as live captures for sale to zoos or for breeding alpaca-vicuna hybrids. The ratio of territorial to non-territorial males that could be removed annually without endangering population growth, will be discussed further in a later publication.

The average *annual increase* of vicuna numbers within the Pampa Galeras Reserve in the past four years has been *thirteen per cent,* but the theoretical increase is much higher. At the beginning of the summer birth season, 90 per cent of the females two-years-old and older were pregnant (Franklin, 1969b). Six months later only 50 per cent of these females had crias at their sides, or 40 per cent of the new born died during their first six months of life. Exposure to cold and wet weather at birth resulting in early death is not the expected cause since nearly 90 per cent of the births recorded were during the morning hours when temperatures were warm. The timing of this adaptation of morning birth is critical since altiplano storms begin daily around noon.

It appears that Andean foxes prey on both adult and baby vicuna. Vicunas attack members of the dog family by 'group mobbing', much like the treatment dogs receive from North American elk (*Cervus canadensis*). But the full significance of predation on baby vicuna and of the extent to which it contributes to this 40 per cent mortality, needs further examination.

If the causes of juvenile mortality are correctable through management, then the rate of vicuna restoration could be speeded up.

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**Paper No. 25**

# The Social Behaviour of Coke's Hartebeest
## (*Alcelaphus buselaphus cokei*)

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## ABSTRACTS

The social ethology of Coke's Hartebeest, a medium-sized Alcelaphine, was studied in Nairobi National Park, Kenya. The study area within the Park was 30 $km^2$ in size and contained four small short grass plains, 13.1 $km^2$ of *Acacia drepanolobium* scrubland on medium-length grassland, and 6. 6 $km^2$ of steep valley slopes bearing tall coarse grasses. There were two seasons of rain with intervening dry seasons. The population followed a twice yearly series of short feeding shifts in response to changes in grass quality.

There were four major social classes: territorial males, isolated and mobile adult males, male groups, and females with their offspring. Territoriality was the dominating influence in the study area. 226 adult males and 37 adult females were individually recognized using photographic record cards. 26 calves ear-tagged at birth gave information on development up to 32 months of age.

Territorial males defended their immediate surroundings more often than distant parts of the territory. The area in which frequency of defence was over 50% was called the Actual Defence Area (ADA)

At ten months of age males, unlike females, started to behave submissively towards a territorial male. The mother/male offspring bond ended when offspring were between 10 and 30 months old. Above 20 months males joined male groups. Agonistic interactions in these groups resulted in a linear dominance hierarchy. On achieving high dominance status at 3-4 years of age males attempted to take over territories. Interactions between territorial males and intruders varied, but always resulted in the withdrawal of the intruder from the ADA and sometimes from the territory. Interactions between territorial males were more stereotyped. Territory demarcation was principally by the construction of dung piles at boundaries

There were 73 territories on average in the study area, resident males forming 38% of the adult population. The territories were divided into six ecological types and mean territory size was 0. 31 $km^2$. There was evidence that territories crossing two or more ecotones were preferred. Ecotone territories were occupied for 86-88% of the time and other territories for 40-57%.

Most ownership change occurred when isolated high status non-territorial males occupied termporarily vacant territories. Fights followed the return of the previous occupant. The loser rejoined a male group but might later then return to the area of the previously held territory. Of 76 instances of a second period of territoriality, 62% were reoccupation of a previously held territory. The mean number of territory changeovers in the 3 years was 2. 8, values for ecotone territories being higher. Males first occupied territories between 3 and 4 years and finally lost them at 7 to 8 years. Territorial males attempted to stop females leaving their territories but in general only temporarily halted such movements. Conception occurred throughout the year but there was a consistent peak in June/July and a less consistent peak in about November, with consequential calving peaks in February/March and about July. The timing probably ultimately related to calf survival since new grass was present 4 months after birth when suckling was almost terminated.

The most important predators were lion and cheetah. 80% of cheetah kills were animals under 1 year old. Lions selected old animals and of 33 kills of adult Hartebeest

26 were males. Females were probably not vulnerable to predation until they became senile (rare in the young population of the study period). Of the adult skulls collected 37% were of females although females represented 58% of the live population.

The numerical success of Hartebeest in Nairobi National Park is attributable to the strategy of feeding, which was adapted to the dynamic ecotone conditions of the Park, and the timing of breeding which took advantage of all grassland productivity through the year.

## INTRODUCTION

Coke's Hartebeest is a large antelope of the tribe Alcelaphini (Simpson, 1945). Adult males average 142 kg in weight and adult females 126 kg (Sachs, 1967). The subspecies was once extremely common over central and southern Kenya and northern Tanzania (Stewart and Stewart, 1963; Sydney, 1965) but its numbers are now reduced and it retains its former density in only a few protected areas. The present study was carried out in Nairobi National Park, Kenya, where the animals have been protected since 1946, when the area was gazetted as a National Park. During the study period from November 1965 to December 1968, hartebeest were the most numerous ungulate and had the highest density in the subspecies range. Before 1960, however, wildebeest (*Connochaetes taurinus albojubatus* Thomas) outnumbered them by about two to one. During 1960/61 there was a catastrophic drought in which large numbers of both species died (Stewart and Zaphiro, 1963; Foster and Kearney, 1967). From 1962 the numbers of Hartebeest increased at an average rate of about 150 per yr. and in late 1967 numbered about 1, 400. Numbers remained similar during 1968 and 1969 but have recently increased again (Stanley-Price, 1971). The recent increase may be a long term result of the removal, in 1967, of over 900 cattle and 450 sheep which had previously been kept in the Park. As hartebeest numbers rose after the drought wildebeest numbers declined and reached about 250 in 1966. Since 1966 the population has remained at about this level. Wildebeest feed most efficiently from short to medium grasses (Bell, 1969) while hartebeest feed selectively in medium to long grass communities (present study). The reciprocal changes in the numbers of hartebeest and wildebeest pose a problem which is related to the more specific aim of attempting to explain the numerical success of hartebeest in the Park.

It became clear during preliminary observations that a proportion of the adult male class occupied territories and also that territoriality was a dominating influence in the social organization of the population. Because of this most effort was devoted to a study of male behaviour. It immediately became obvious that behaviour at the organizational level was inextricably related to the ecology and population dynamics of the population. An integrated approach encompassing these aspects was thus adopted with the aim of obtaining an understanding of the adaptive significance of the observed social organization and, in particular, as it related to male behaviour and social development. The integrated approach adopted has since been called Social Ethology by Crook (1970) following the precedent of Waxweiler (1906).

## METHODS

The study was carried out entirely in the field. Observations were made from a Land Rover which allowed closer approach to animals than was possible on foot. Zeiss 8 × 50 binoculars were used and notes were either written in the field or transcribed later from a Phillips Cassette Recorder. Large numbers of monochrome and colour photographs, and a few moving films, were taken of behaviour sequences. Inter-individual distances were measured by Wild rangefinder.

A total count of the study area was done at fortnightly intervals. The numbers of the sexes and of various age classes were recorded on a data sheet and the locations of all animals were placed on a large scale field map. The presence of known individuals improved the accuracy of the counts by acting as group 'indicators' and preventing recounting; the average percentage of known individuals in the totals recorded was 13.4%.

Individual recognition of adults relied on natural variation. Horn shape and the complex pattern of ridges on the horns were unique for each individual and provided a final check on identity. 226 adult males and 37 adult females were recognised; photographic record cards were made for each individual and were carried in the field. 26 calves were ear-tagged shortly after birth; subsequent data on these animals provided information on growth and social development up to 32 months of age. On every visit to the study area the locations of all known individuals seen and their associates and behaviour were recorded; locations were marked on a field map.

The skulls of 171 animals which had died naturally were collected. Those under 2 years old were aged from horn development. Those over 2 years old were placed in classes based on the eruption and wear of the maxilliary tooth row. Provisional ages were assigned to the series by reference to physiological longevity, by comparisons with the congeneric wildebeest (Watson, 1967) and by assuming a linear decrease in the length of the thrid maxilliary molar after a maximum at 2-3 years of age.

Rainfall data were obtained from two meteorological stations near the study area, and averaged. Changes in grassland were monitored by regular colour photography and by field notes. Grass state was assessed from the photographs on a '% green' frequency scale. The distribution of major grass and scrub communities was mapped from aerial photographs and from field observations. The latter included a series of transects in which such variables as the leaf table height and the amount of graze were recorded in addition to the common grass species present. Grasses were identified at the East African Herbarium in Nairobi.

## ACKNOWLEDGEMENTS

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I would also like to thank the Trustees of the Kenya National Parks for allowing this study to be carried out, and Professor D. S. Kettle for facilities provided in the Department of Zoology at the University of Nairobi.

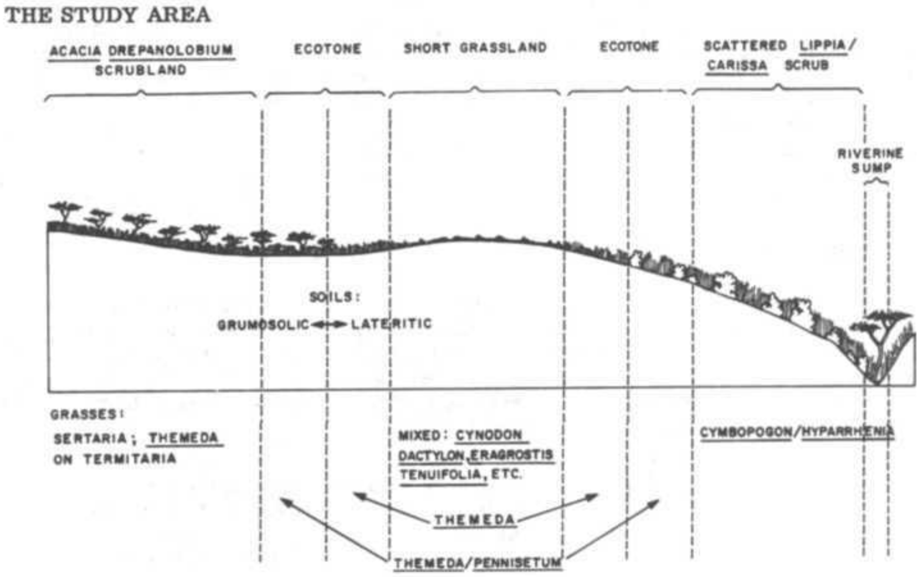


Fig. 1. Study area profile

A 30 km$^2$ study area was selected. It contained representative areas of most of the major vegetation zones in the Park (Fig. 1). The northern zone (13. 1 km$^2$) was characterized by a sparse to dense stand of the dwarf tree *Acacia drepanolobium* on black grumosols; the dominant grasses were *Sertaria* spp. In the middle reaches of the streams which dissected the area were areas of lateritic soil which bore a heterogeneous short to medium length open grassland. There were four such plains which totalled 4. 0 km$^2$. The total length of the ecotone between open grassland and *A. drepanolobium* 'scrubland' was 21.1 km and taking a mean width of 30 m its area was 6.3 km$^2$. This ecotone contained dense monodominant stands of *Themeda triandra* and, further in towards the scrubland, mixed stands of T. *triandra* and *Pennisetum mezianum.* The remaining 6. 6 km$^2$ consisted of medium to steep rocky slopes which led down to river beds. The dominant grasses were tall coarse tufted species such as *Cymbopogon excavatus* and *Hyparrhenia lintoni* which were mixed with smaller species such as *Michrochloa kunthii.* Two bushes, *Lippia javanica* and *Carissa edulis,* had a scattered distribution in the same zone.

## CLIMATE AND SEASONAL CHANGES IN THE GRASSLAND

The most important climatic factor was rainfall and its distribution through the year. Rain fell in two periods, the Long Rains in March to May and the Short Rains in November (see Fig. 9.). There was thus a Long Dry Season from June to October and a Short Dry Season from December to February. Evapotranspiration was lower in the Long than in the Short Dry Season because of relatively cold overcast conditions; drying out of soils and grasses therefore proceeded more slowly.

During the rains free water was widely available in temporary pools and streams but as the dry seasons progressed it became restricted to a few permanent pools. During the long rains grumosols became waterlogged and impassable while the more sandy lateritic soils remained firm.

Grass started to sprout within a few days of the start of the rains. Bright green flushes first became visible on heavily grazed areas and in particular on the short grass plains. Productivity was more massive in the Long than in the Short Rains. In June and December, the start of the two dry seasons, grasses started to dry out and by the late dry season consisted of a dry standing hay with poor nutritional qualities.

## POPULATION DYNAMICS

The average number of hartebeest in the study area from 64 fortnighly counts was 671. The proportion of animals over two years old, which were referred to as 'adults', was 68% and of these 42. 4% were males and 57. 6% females.

The 26 calves ear-tagged on the day of birth were photographed when possible. From the photographs it was shown that horn growth was rapid up to two years of age. Up to this age animals could be aged to a month class.

A provisional survivorship curve was calculated from the distribution of age at death in the 171 skulls which were found during the study (Fig. 2). Because the population had not been stable in the decade before the study this curve can only be regarded as an approximation. The curve shows few survivors over the age of 6 years which corresponds with the time from the drought of 1960/61 to the study period. This indicated that the ageing method might be a good approximation, as did checks with the proportions of broad age classes in the live population. The proportions of 0-1 and 0-2 year classes in the live population were established from counts at 26% and 32% respectively; the same proportions from the survivorship curve were 22% and 37%. Another check was available from the survivorship of ear-tagged calves: 19 of the calves were observed for over a year and of these 13 (68%) survived to one year; the equivalent value calculated from the survivorship curve was 60%.

The survivorship curve clearly shows that most of the population were under 6 years old during the study period. This fact assumes considerable importance when the competition between males for territories is considered.

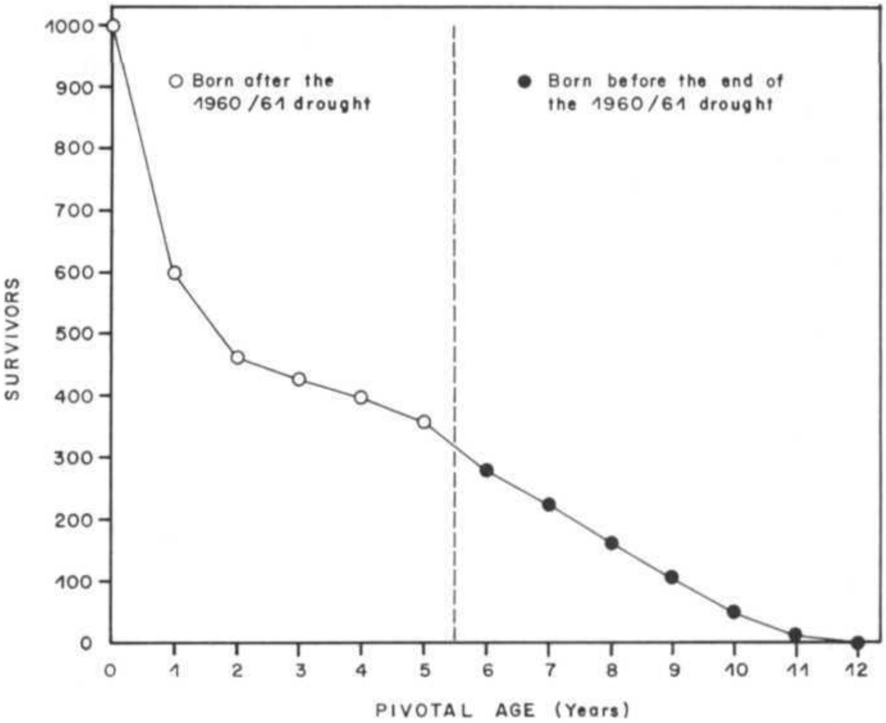


Fig. 2. A survivorship curve based on the age at death of 171 Hartebeest. The curve was calculated by assuming that the survivors in the unadjusted data were females and that females above 2 years old produce one calf per year. The first assumption was necessary because of the low proportion of female remains found (see text) which would have resulted in an underestimate of natality. The proportions surviving to pivotal ages of 1 and 2 years are as in the unadjusted data.

## GRASSLAND UTILIZATION

The distribution of all hartebeest in the study area was mapped at fortnightly intervals and the proportions occupying major grass zones were calculated. It became clear that there was a characteristic cycle of movements in response to seasonal changes in grassland. In the early rains hartebeest dispersed to areas where there had been intensive grazing in the preceding dry season and where sprouting grass first became visible. The grass was not heavily utilized until it was over 10 cm high. As the rains progressed they moved out of the waterlogged grumosol areas and fed from *Themeda* and *Themeda/Pennisetum* grassland in the higher levels of valley slopes. As the rains ended there was a movement of the distribution mode to the *Themeda* and *Themeda/Pennisetum* communities at the ecotone between short grassland and *A. drepanolobium* scrubland. This movement continued into the medium length grasses of *A. drepanolobium* scrub as the dry season progressed. The dominant *Sertaria* species were avoided in favour of more nutritious grasses found on termitaria and in small clearings. At the end of the dry season animals formed large resting aggregations around permanent water holes and during grazing periods dispersed in small groups and selectively utilized sump grasses and the tall *Cymbopogon/Hyparrhenia* communities on the lower parts of valley slopes. The long thin muzzle and narrow incisor row of hartebeest appear to be adapted for selective feeding in medium and long grassland. This contrasts with the wildebeest which has a broad muzzle and incisor row and which feeds non-selectively from short mat-forming grass types (Bell. 1969).

The movements undertaken by hartebeest were essentially a series of short perpendicular shifts across a series of parallel grass zones and their intervening ecotones. These were rapid because of the two periods of ephemeral grass productivity in each year. In these shifts hartebeest utilized all the major grass communities of the area in contrast to those herbivores which fed on short grasses such as wildebeest and Thomson's gazelle (*Gazella thomsoni* Guenther) which were mainly restricted to short grass plains. Wildebeest and Thomson's gazelle only utilized long grass areas when a mosaic of short grass had been created within these by hartebeest grazing. This facilitative succession is known as a 'grazing succession' (Vesey-Fitzgerald, 1960). Hartebeest were independent of herbivore precursors for their movements into any grass communities.

## PRELIMINARY OBSERVATIONS ON SOCIAL ORGANIZATION

Preliminary observations indicated four major social categories:

1. Single adult males which were resident in small areas; these males were sometimes alone and sometimes with female groups.
2. Isolated adult males which stayed briefly in any one area and then moved on.
3. Groups of males in which the mean inter-individual distance (I.D.) was under 15 m;male groups sometimes contained a few sub-adult males.
4. Groups of females with their offspring in which the mean I.D. was less than 10 m.

Interactions, identified as being agonistic through the occasional occurrence of overt aggression, were seen between all classes of males. The resident males were always dominant over all other males while in their areas. It was concluded that these males were territorial.

A continuous network of territories covered most of the study area. All the males resident in territories and a sample of non-territorial males were individually recognized. By the end of the study 226 males had been recognized although some of these were killed or disappeared during the three years.

## TERRITORIALITY AND ACTUAL DEFENCE AREAS

A fundamental property of territory defence in hartebeest was that territories were not defended uniformly at any one time. Intruders near to a territorial male elicited aggression more frequently than those in distant parts of the territory. Following the precedent of Marler (1956) in his treatment of I.D. phenomena, the area around a resident male in which the frequency of an aggressive response to intruders was over 50% was used for convenient reference and was called the Actual Defence Area (A.D.A.). This concept will be discussed later.

## MALE SOCIAL DEVELOPMENT UP TO JOINING MALE GROUPS

The first period of a male's life was spent with its mother in female groups. Females moved through the territory system and were accompanied by up to four consecutive offspring. Up to 10 months of age there were no stereotyped interactions between male offspring and territorial males. After this age, when the first curve of the horns appeared, the behaviour of young males underwent a striking change. This change did not occur in females. When territorial males approached, male offspring assumed the Head-in posture (Fig. 3) and emitted juvenile 'quack' vocalizations. Territorial males sometimes Head-tossed towards the young males, a rapid movement retracting the muzzle and bringing the horns forward, but did not usually chase them away. When young males were chased by territorial males they lowered their necks and extended the muzzle into the Low-head posture. When young males were chased out of territories, or out of the A.D.A. of the territory, their mothers almost invariably accompanied them.

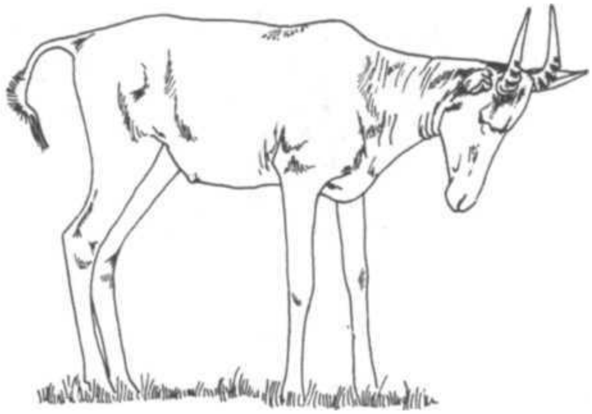


Fig. 3. The head-in posture, adopted here by a 12-months-old male

The age at which young males separated from their mothers was measured during a sample count in which 160 males were aged from horn development and in which it was recorded whether or not each male was with its mother. A few males were separated at 10 months, about half by 17 to 23 months and most by 30 months. Two calves ear-tagged at birth separated at 18 and 26 months, respectively.

Separation from the mother often coincided with the birth of a new calf, after which the mother did not allow such close approach by elder offspring as previously. In addition mothers did not accompany their male offspring so readily when they were chased by territorial males.

When separated from their mother the Head-in posture did not occur. Territorial males singled out isolated young males and chased them, often at a gallop, until they were out of the territory. During these chases territorial males often Hooked at the rump of the fleeing animal, first lowering the head and retracting the muzzle then rapidly raising the head while extending the muzzle so that the horns moved in a fast upward arc. Contact, when made, was by the horn tips and severe injuries were sometimes inflicted. Successive chases by a series of territorial males often resulted in young males fleeing to scrubland areas where the density of territorial males was lower than on plains.

When separated from their mother sub-adult males attempted to join male groups but were sometimes chased away. Sub-adult males were thus often isolated in scrub or else formed small groups with males of a similar age. This was not invariable: sometimes small sub-groups of young males were seen in or near groups of adult males.

## SOCIAL DEVELOPMENT IN MALE GROUPS

When over 20 months of age males usually became regular members of male groups. These groups contained from 2 to about 100 animals. They were flexible in composition being constantly splitting and reforming. The home ranges of individually known males were shown from accumulated point observations of each male. Five randomly selected males which were seen between 77 to 146 times had ranges of from 6. 7 to 10. 3 $km^2$. Home ranges usually included three of the four short grass plains and variable amounts of adjoining long grass areas.

Agonistic interactions within male groups were very common and constituted the great majority of all interactions. The interactions always occurred at the Small I.D. (0-10 m) but the form and duration of the encounters were unstereotyped and from two to five males participated. The most common behaviour elements were grooming.

Horn contact behaviours often occurred. They included Forehead-pushing, in which one male pressed its forehead against the face or neck of an opponent, Horn-tangling in which the horns of two opponents were loosely interlocked and twisted about, and more rarely Clashes. In the latter two males faced each other then leapt forward into a kneeling position with the horns directed forwards. At the end of the movement the horns met with great force. Nearly all interactions ended with the withdrawal of a subdominant. Withdrawal was usually for a short distance only and a subdominant was rarely chased out of the male group.

Because of the high frequency of agonistic encounters and the large proportion of known individuals it was possible to examine dominance relationships within male groups over short periods. No dominance reversals were seen in the short periods involved and a linear dominance hierarchy was demonstrated. Before animals reached maximum size at 2. 5 to 3 years, dominance was directly related to size. Animals under 3 years old always had 'low dominance' status in a group, being dominant in less than a third of their interactions. In between 3 and 4 years individual males achieved 'middle' then 'high' dominance status.

Some high status males at first semi-isolated then completely left the vicinity of male groups and moved alone through their home ranges. Sometimes they remained in one location, often in scrub, for a day or two but them moved on. Such males were dominant over all males except those in territories. In some cases these males acquired a territory while in others they returned to a male group for a while before isolating again.

## TERRITORY DEFENCE

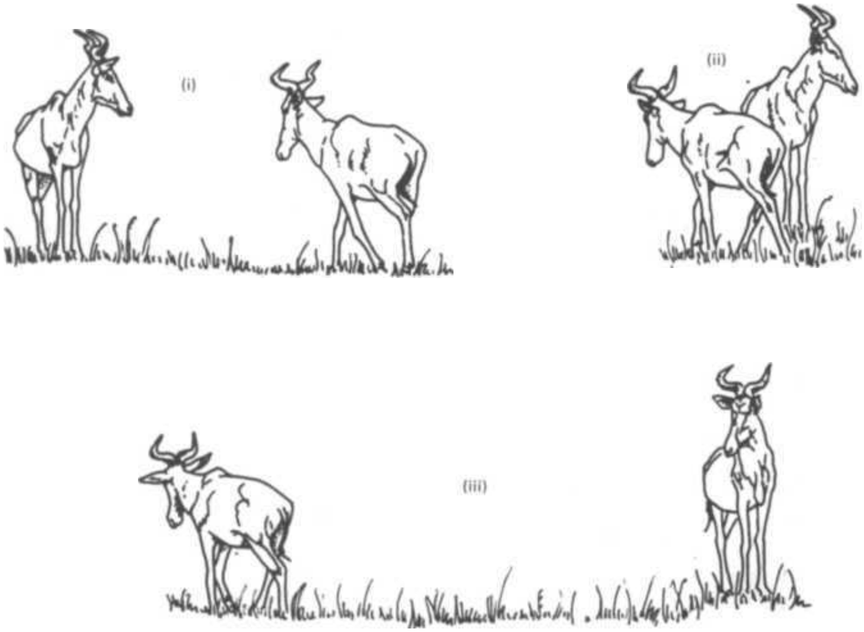


Fig. 4. An agonistic interaction between a male resident in a Pivotal territory and a non-territorial male:

(i) The territorial male (left) approaches then stands in the upright posture, facing-away, as the non-territorial male walks towards it.

(ii) The non-territorial male, with its head and neck held low, walks past the territorial male.

(iii) The territorial male turns its head and watches as the subdominant intruder withdraws.

The interactions between territorial males and non-territorial intruders were variable in form and duration. Sometimes as a territorial male approached from over a hundred metres away intruders turned and immediately withdrew. Sometimes the intruders waited until the territorial male had reached the Small I.D. and in some cases they approached. On reaching the Small I.D. territorial males usually stood in the Upright posture with the head and neck held high and the tail stiffly elevated. The head and tail positions of the intruders were generally lower (Fig. 4). Grooming was again the most common behaviour. Neck-sliding was also common and was usually initiated by the intruder; in this behaviour the muzzle was extended until it touched the upper neck of the opponent then pushed down along the neck with nibbling movements of the lips. Horn contact behaviours were brief and usually resulted in immediate

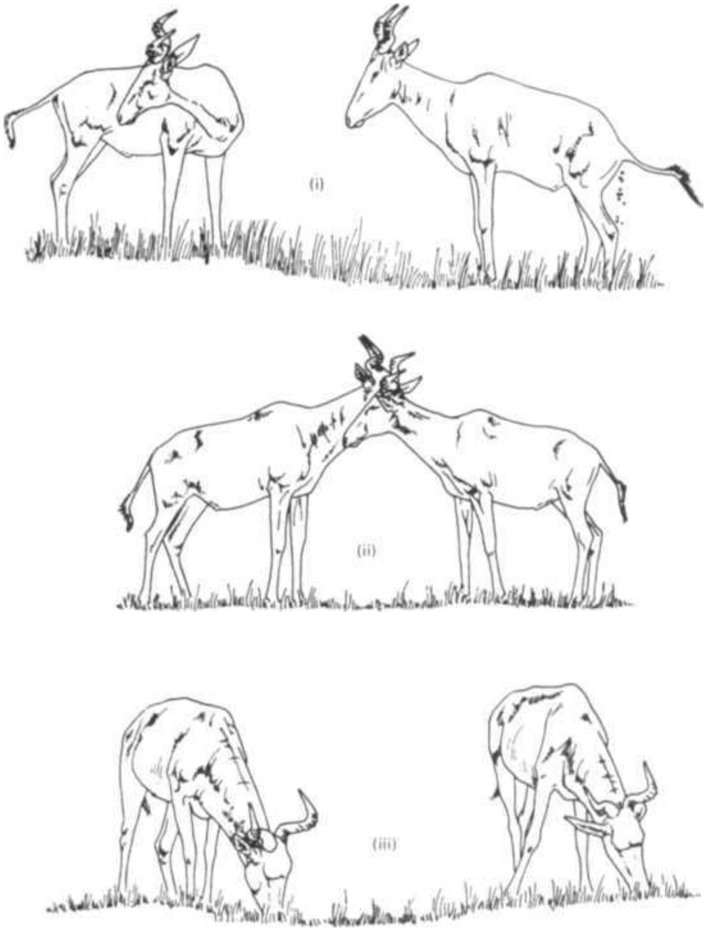


Fig. 5. Encounters at boundary zones between males in neighbouring pivotal territories

(i) A Defaecation encounter. The right-hand male defaecates: the left-hand male grooms and thus deflects its head from a Head-on inter-individual orientation

(ii) A Defaecation encounter: the right-hand male is Neck-sliding

(iii) A Forward-parallel grazing encounter withdrawal by the intruder. Interactions with high status intruders were more complex and prolonged than those with low status males.

The frequency with which territorial males reacted to intruders depended on a combination of factors. These included the proximity of the intruder to the territorial male, the prior activity of the territorial male, the behaviour of the intruder and finally climatic variations. The first of these has already been mentioned. When active territorial males responded more frequently to intruders than when inactive. When the intruder was more active a reaction from the territorial male was also more frequent. Running intruders, for example, elicited defence more frequently than did those which were walking. In other words the A.D.A.'s of territories became larger as territorial males and intruders were progressively more active. Climatic effects were predictable: in very hot periods territorial males responded less frequently to intruders than in cooler periods.

Interactions between neighbouring territorial males were more stereotyped than those between territorial and non-territorial males. They occurred in a number of forms. The most common were called Defaecation encounters because both males involved usually defaecated on dung piles in the common boundary zone where the encounters occurred (Fig. 5 (1)). Defaecation encounters lasted for, on average, 11 mins. Grooming was again the most common behaviour and Neck-sliding occurred in nearly all interactions (Fig. 5 (ii)). Horn contact was common but usually involved only Forehead-pushing and Horn-tangling and not Clashes. Before defaecating males nosed the ground, pawed, then knelt and rubbed the forehead on the ground. In the terminal phase of Defaecation encounters males grazed and slowly moved away from each other and back into their territories.

Grazing encounters at the Small I.D. were less common. In these encounters, which also occurred at common boundary zones, males grazed throughout. The most common inter-individual orientation (I.O.) was the Forward-parallel I.O. with the heads opposite and the body axes parallel (Fig. 5 (iii)). In this I.O. and in others males kept their body axes at a similar angle relative to the boundary zone as that of the opponent. Small changes in the orientation of one male were followed by readjustment of the other to the new position. The encounters were terminated by both males turning slowly away from each other and grazing back into their respective territories. Encounters of this type also occur between territorial male Thomson's gazelle (F. R. Walther, pers. comm.).

In addition to Small I.D. encounters there were also encounters in which the minimum I.D. attained was 30-100 m; these encounters were called Medium I.D. encounters. As with encounters at the Small I.D. the main varieties of Medium I.D. encounters were Defaecation and Grazing encounters. The encounters had periods of rapid I.D. reduction and enlargement at their start and finish, respectively, and action/response sequences in the behaviour of the interacting males were obvious.

## TERRITORY DEMARCATION AND BOUNDARY ZONES

The main observable method of territory demarcation was by faeces. Dung piles, often consisting of several thousands of pellets, were most common along boundary zones. In boundary zones the piles were of a scattered type because of the repeated pawing by males during Defaecation encounters. The relatively few piles within territories were not pawed and were usually very compact. The role of the interdigital and antorbital glands remains problematical. The former were the same size in males and females and produced a copious black secretion. The latter were larger in males but females and juveniles were seen marking at least as frequently as territorial males.

Boundary zones were quite well defined in the most frequently visited parts of territories but even here formed a zone a few metres across rather than a line. In less frequently visited areas boundaries were less well defined. Many boundaries corresponded with topographic features such as dirt roads and stream beds; possibly the males used these features as visual cues.

## PROPERTIES OF THE TERRITORY SYSTEM

Territories were mapped from accumulated point observations of individually known territorial males. Maps of the territory system were prepared for each of the three years of the study; the map for 1967 is shown in Fig. 6. There were on average 73 territories and their resident males represented 38% of the adult male population.

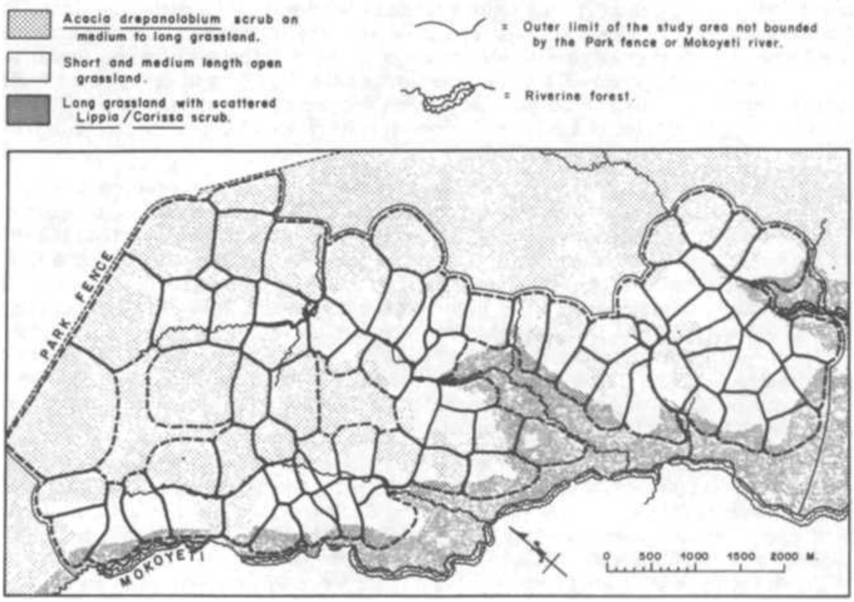


Fig. 6. The arrangement of territories in the study area during 1967. Broken lines indicate territory boundary zones which do not adjoin neighbouring territories or zones at the outer limits of the study area.

It was possible to divide territories into six major ecological types. These were:

1. Those which contained largely short grass and a little medium length grass.
2. Those across the grassland/*A. drepanolobium* scrub ecotone.
3. Those across the ecotone between medium and short grass and the long grass communities of valley slopes, sometimes mixed with *Lippia/Carissa* scrub.
4. Those in sparse *A. drepanolobium* scrub with small clearings.
5. Those in dense *A. drepanolobium* scrub.
6. Those in the long grass communities of valley slopes sometimes with *Lippia/Carissa* scrub.

In Fig. 6 it can be seen that territories across ecotones, as typified by Type 2 above were elongated in shape with their longitudinal axes perpendicular to the ecotone. Territories in homogeneous grassland, for example Type 5 above, were more rounded in shape.

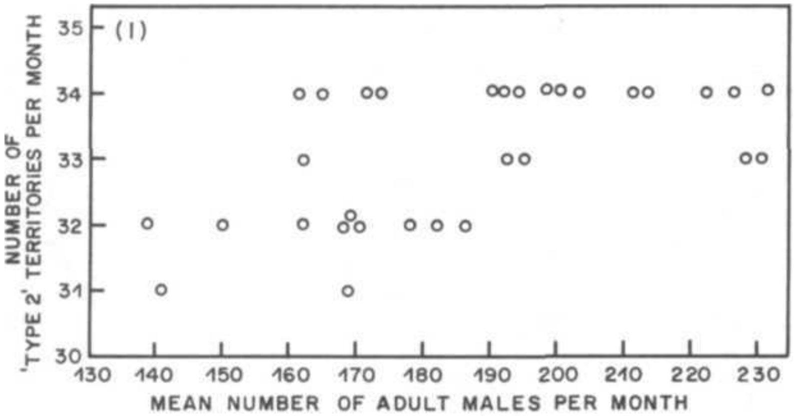
As far as the diversity of grass zones within territories allowed, the resident males followed a similar pattern of seasonal grass utilization to that described for the population as a whole.

The overall mean territory size was 0. 31 $km^2$ but as can be seen from Fig. 6 there was variation in size which was consistent with ecological type. Territories in *A. drepanolobium* scrubland for example, were usually much bigger than average.

Several separate lines of evidence gave information about the relative preference of males for the various types of territory. Sometimes a male occupied a territory of one type when a territory of a different type was available nearby. In one instance a male occupied a Type 3 territory and displaced the previously resident male to an adjacent Type 6 territory which had been vacant.

Vacant areas in some ecotypes suggested that these areas were the least preferred. On average 8% of the available *A. drepanolobium* scrub and 56% of the available long grass with *Lippia/Carissa* scrub were vacant. The unoccupied *A. drepanolobium* scrub was all dense. All other ecotypes were completely covered by territories. This indicated that the long grass communities, *Cymbopogon/Hyparrhenia,* with *Lippia/Carissa* scrub, were least preferred and dense *A. drepanolobium* scrub second least preferred.

The frequency of extra territorial movements also gave some information. Males in scrubland left their territories more frequently than did those in ecotone territories.



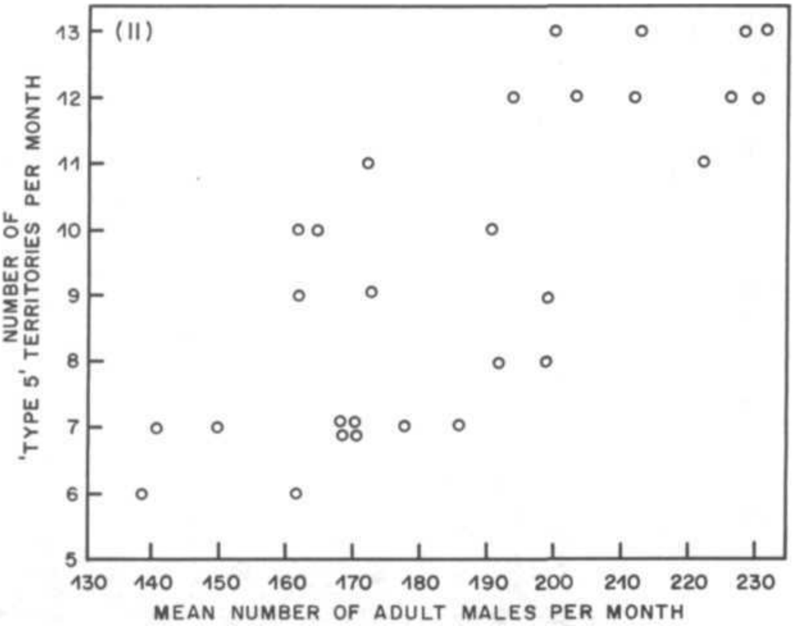


Fig. 7. The mean number of adult males per month in relation to territories of (I) 'type 2' and (II) 'type 5'

Males in Type 1 territories, the short grass type, sometimes left their territories to feed when medium grasses were the seasonally optimum food.

The numbers of adult males in the area increased throughout the study. This resulted in an increase in the number of territories. The different rates of increase in different ecotypes provided data which is relevant in assessing preference. A sample comparison, between Type 2 and Type 5 territories is shown in Fig. 7. It is clear that the number of Type 5 territories increased rapidly with increasing adult male density while Type 2 territories did not. These data conform with predictions which could be made from the 'elastic disk' theory of territoriality proposed by Huxley (1934). Type 2 territories, by this theory, had reached minimum compressibility by the start of the study period but Type 5 in a less preferred ecotype had not and continued to be compressed, by the establishment of new territories, at a later stage of the population expansion.

Reviewing all the evidence of the types mentioned it was concluded that Types 2 and 3 were the most preferred territories, that Types 1 and 4 were intermediate and that Types 5 and 6 were respectively the second least and the least preferred.

The proximity of water also influenced preference. Several examples were recorded of males moving from a territory away from water to one near it leaving the first territory vacant. There were however other consequences to occupying territories adjacent to permanent water holes. In the late dry season such territories were partly swamped by large aggregations of non-territorial males. The aggressive response of the resident territorial males declined in frequency and intensity and they often joined the male groups.

The duration of territoriality was analysed from 315 periods of territoriality involving 176 individually known males. These periods were grouped into three month classes. The frequency curve obtained is shown in Fig. 8. 44% of the periods were of less than 3 mths, and only two males were continuously territorial throughout the 3 yr. study period.

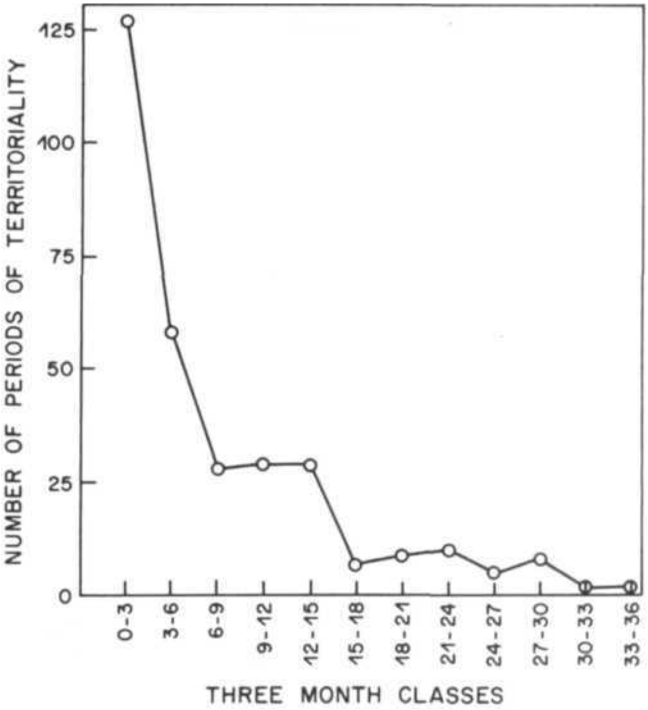


Fig. 8. The duration of territoriality. 315 periods were recorded and are grouped here in three-month classes

Males were not continuously resident in their territories. They sometimes left for periods of a few hours to a few days. The mean per cent occupancy from 64 total counts was 76%. Occupancy was highest in Type 2 and Type 3 territories at 86% and 88% and was 57% and 40% in Types 4 and 5 respectively. Data were too few to calculate comparable results for Type 1 and Type 6 territories but males were certainly most frequently absent from the few Type 6 territories. Occupancy in general was lowest during heavy rain when males left territories on grumosols because of waterlogging (Fig. 9 (I)). During extra-territorial movements males spent much of their time in male groups where they had high dominance status. In the late dry season many males left to drink and then joined the male aggregations around water holes.

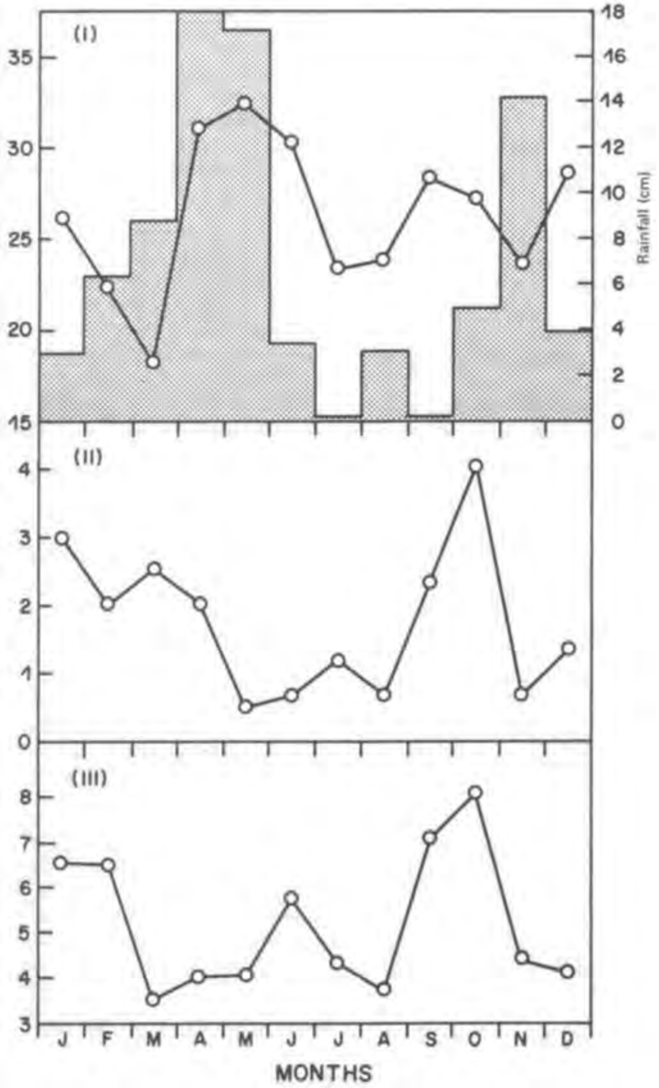


Fig. 9. Mean seasonal variation in (I) the percentage of males absent from pivotal territories (II) the number of central axial territories established and (III) the number of ownership changeovers in pivotal territories. The histogram in (I) shows mean rainfall in centimetres.

Some, and possibly most, territory ownership changeovers occurred as a result of these absences. While the territories were vacant they were sometimes occupied by one of the isolated high status males mentioned earlier. On the return of the previously resident male an agonistic encounter followed; the male which eventually proved dominant occupied the territory. Overt aggression was common in this context. It involved numerous Clashes and Wrestling with the two males, kneeling on their carpal joints with horns interlocked vigorously twisting their heads about and apparently attempting to force the head of the opponent to one side. When a male accomplished this it Thrust with the horns directed forwards or Hooked the horns in a sideways arc. Contact was with the horn tips and the resulting injuries were often severe. On two occasions males were found dead with typical fighting injuries and in another the femur of one male was broken. When one animal was defeated it was often pursued for several kilometres.

Territory changeover also occurred after the establishment of small territories near to the activity centres of the usual large territories. The latter were constant in size and shape within a range of adult male population density and were called Pivotal territories. The small territories were called Axial territories and to distinguish them from a second type of Axial territory, which will be mentioned below, were called Central Axial territories.

Central Axial territories were established across or next to a boundary zone. At first the resident males were subdominant to the males in adjacent Pivotal territories although all other intruders were expelled. Encounters with the neighbouring males were frequent and sometimes involved intrusion into one Pivotal territory and defaecation on the dung piles in it. Sometimes males became dominant in a Central Axial territory over the neighbouring males and sometimes they eventually displaced one of the resident males and occupied the whole or a large part of its Pivotal territory. More frequently the males abandoned Central Axial territories without accomplishing a takeover. These territories were always short lived and were not permanent features of the territory system. This contrasted with Pivotal territories which within a range of adult male population density retained similar boundaries through changeovers.

Peaks of Central Axial territory formation occurred in the late dry season (Fig. 9 (II)). Many were established near permanent water holes. The seasonal distribution was probably influenced by the decline of the territorial male aggressive response frequency in the hottest and most arid times of the year and the related reduction in the size of A.D.A's.

Three peaks of Pivotal territory changeover occurred in an average year (Fig. 9 (III)). Two were in late dry seasons, January/February and September/October. These corresponded with high frequencies of Central Axial territory establishment and also the time when many males left their territories to drink at permanent water holes. The third peak was in June which was a month of high conception frequency.

The mean seasonal frequency distribution of injuries from fighting showed highest values in June/July and in September. The high values of June/July were probably caused by the resistance of resident males to takeover attempts plus some fighting between resident males which sometimes occurred at peak conception times. The September value suggests that changeover was resisted when conditions were not as arid as in the following month. In the late dry season changeover was probably accomplished with comparatively little injury because of the decline in aggressive response mentioned above.

The second type of Axial territories were called Peripheral Axial territories. They were always in scrubland and away from the activity centres of territories. Activity centres, the most intensively defended part of territories, were usually on short grass areas. Peripheral Axial territories were occupied by old males which were unable to regain their previously occupied Pivotal territories. They were not consistently reoccupied after the death of the resident male and were thus not permanent features of the territory system at a stated male population density. Peripheral Axial territories were few in number reflecting the small proportion of old animals in the population. They were occupied throughout the year with little seasonal variation.

After males had lost territories they were isolated for a short time then joined male groups. After a variable period they reisolated and often returned to the area of their previously held Pivotal territory. Sometimes they were successful in reoccupying a territory in one of the ways described.

Seventy-six instances of a second period of Pivotal territory occupancy were recorded. Of these 62% were reoccupations of the same territory, 25% of one adjacent to it, 4% of one a single territory distant and 9% of one more than one territory away. There was thus a high degree of area loyalty to a previously occupied territory.

The mean number of changeovers per Pivotal territory in the three year study period was 2.4. The mean number of individually known males in successive occupancy was 2. 8. These values varied between territory types. Types 2 and 3 had the highest mean number of territory changeovers, 2. 8 and 2. 4, and the highest number of resident males, 3. 2 and 3. 0. Types 4 and 5 were lower with 1.4 and 2. 0 changeovers and 2.1 and 2. 2. males, respectively.

Patterns of territory occupancy were plotted for all territories in a diagrammatic form in which a horizontal line represents one territory throughout the study (Fig. 10). Breaks in each line represent changeovers and each period of territoriality is marked with the male in occupancy. In the Figure, examples of territories splitting and in one case coalescing can be seen; these changes are related to variation in population density which will be considered in another paper.

An age scale was fitted to the occupancy pattern, in the first instance, from animals which were either aged from horn development when young or which were collected after a natural death and aged from their teeth. In Fig. 11 the social development of

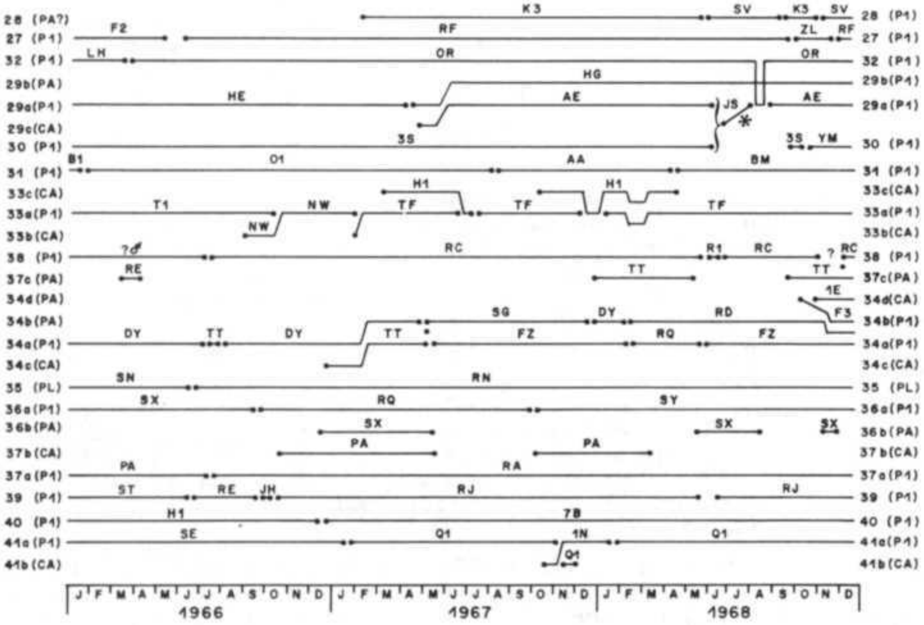


Fig. 10. Diagrammatic representation of territory occupancy. Horizontal lines represent continuous occupancy of territories which are numbered at the right and left of the diagram. Males in occupance are referred to by two-letter codes above each line. Dots show the time of arrival or departure of a male. Oblique lines show movements of males from one territory to another. P1 = Pivotal Territory; CA = Central Axial Territory; PA = Peripheral Axial Territory. Where a territory is labelled PA or CA at the left of the diagram and P1 at the right it had assumed pivotal status during the three years.

20 aged males is presented diagrammatically. Horizontal lines represent each male and are subdividied into sections representing different social states. Only those males which were seen frequently are included. The data suggest that males initially occupied Pivotal territories at between 3 and 4 years of age. One male lost its territory soon after, then quickly regained it. The stage from 4 to about 7. 5 years was characterized by long periods of continuous occupancy. After this males lost their territories and only reoccupied them for short periods. In the post-Pivotal territory occupancy period males sometimes unsuccessfully occupied Central Axial territories and sometimes Peripheral Axial territories. They were frequently isolated and at such times were often found in scrubland because of the higher density of territorial males on the plains.

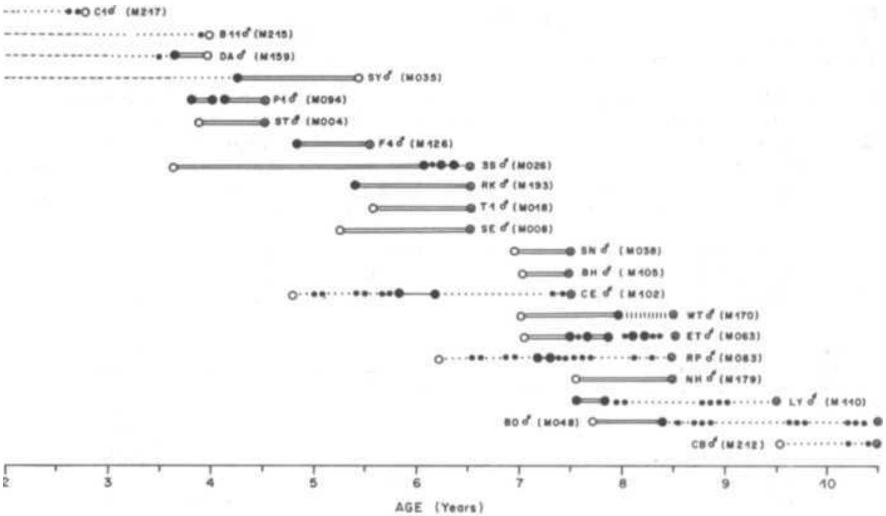


Fig. 11. Diagrammatic representation of the social development, at age, of 21 male Hartebeest over the age of two years. Horizontal lines show the time spent with the mother (- - - - -), with male groups (. . . . .), isolated (•), in pivotal territories (═══), in central axial territories (———) and in peripheral axial territories (||||||||). o: the beginning or end of the study period; ● the beginning or end of a period of territoriality; ⊗ the death of a male.

C1♂ was ear-tagged at birth. B11♂, DA♂ and SY♂ were aged from horn development while sub-adult. The remaining 17 males were found dead and were provisionally aged from tooth eruption and attrition; ageing was to a one year class; for the purposes of the diagram it is assumed that the males died half way through the year.

Provisional ageing of a large sample of live animals confirmed this overall pattern. It also gave more examples of the short initial periods of occupancy which were more common than is suggested in Fig. 10. Sometimes more than one short period occurred and often the territories occupied were more scattered than in later stages of the life history. This suggested that males established specific territory loyalty after an initial exploratory phase.

When a young mature male competed for a territory with an old male the latter was eventually displaced and seldom regained the territory. When two young mature males competed the outcome was not predictable. Often such a pair alternated in the occupancy of a Pivotal territory; in some cases one of the males was permanently excluded. Regarding such situations as inefficient it is possible to conceive an ideal and stable pattern of occupancy in which a male 3.5 years old replaces a 7.5 year-old male and is itself replaced by a 3.5 year-old male when it reaches 7. 5 years.

The number of males over 3 years old which would theoretically be required for this model pattern of occupancy was calculated as 117 for the average number of 73 territories in the study area. In fact there were about 141 present or 21% more than required. In addition the survivorship curve presented earlier indicated that most of these were young. Intense competition for territories might thus be expected and this might explain the high frequency of injuries from fighting which sometimes resulted in death.

## REPRODUCTION

As females walked towards a territory the resident male approached and stood at the boundary zone in the Ear-down posture (Fig. 12.). As the females passed the male wheeled around and nosed their vulvae.

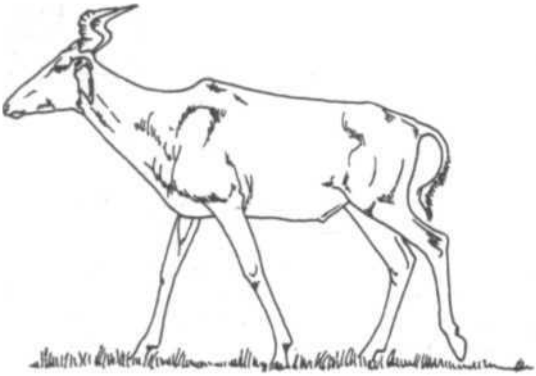


Fig. 12. The ear-down posture

When females attempted to leave a territory the resident male often positioned itself between them and the boundary zone. Sometimes male adopted the Upright posture at this point then turned and threatened the females with Head-tossing. When females ran past a herding male the male sometimes ran and attempted to cut them off. Once females had started running however they normally soon escaped. In general herding behaviour by territorial males only temporarily halted interterritorial movements by females. When oestrous females were concerned, however, males herded more vigorously, often at a gallop, and were frequently successful in keeping the females in their territories for long periods.

In precopulatory behaviour males walked in front of a female and stood in the Ear-down posture. After a period of immobility the male wheeled slowly around and attempted to nose the vulva. Females usually withdrew at this point. When they were in oestrus withdrawal was progressively reduced and eventually the male mounted.

Mating interactions involving repeated copulation were seen on 24 occasions. In all cases the male involved was resident in a Pivotal territory.

During mating interactions with oestrous females there was sometimes interference by males of three classes. These were male offspring in female groups, intruding high status non-territorial males, and intruding territorial males from adjacent Pivotal territories. In the 24 observations of mating the numbers with interference by these three classes were 14, 4 and 5 respectively. In all cases the mating male left the oestrous female at the approach of the other males and chased them away before returning to the female. The interfering males were always immediately subdominant. The disruption caused by this interference sometimes resulted in females leaving the territory. More usually the male quickly relocated the oestrous female and mating continued.

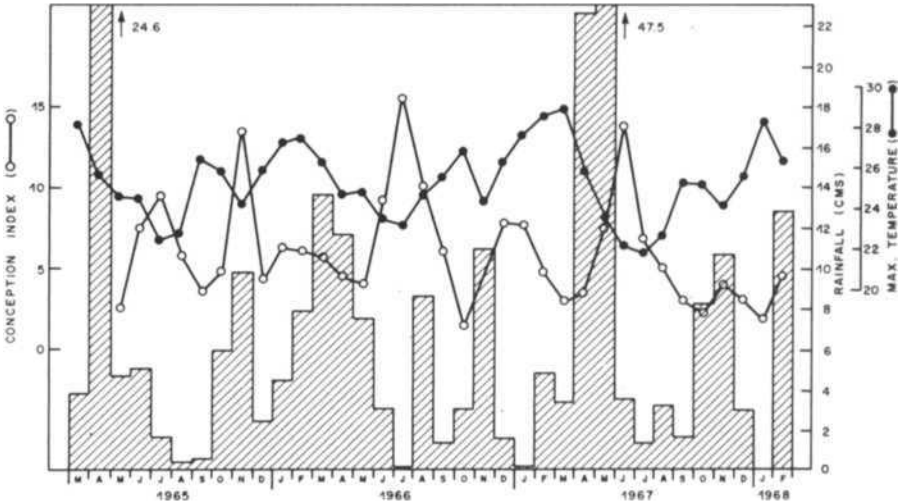


Fig. 13. The frequency distribution of conception in relation to the variation in rainfall and maximum temperature during the period March 1965 to February 1968. Data are expressed as monthly means.. The conception index is explained in the text.

From counts of calves under a month old an index of the seasonal frequency of parturition was calculated. The values obtained were set back 8 months to give the seasonal frequency of conception (Fig. 13.). Conception occurred throughout the year with a distinct peak in June/July and a less consistent and smaller peak in about November. The proximate initiating factor for conception may have been low temperature since there was a statistically significant inverse correlation between monthly conception values and monthly mean maximum temperature (r = —0.498, 31 df, p = 0.443 at 0. 01 significance level). There was no correlation between territorial male per cent occupancy and conception (r = 0. 024, 19 df, p = 0.433 at 0.05 significance level). Occupancy frequency showed different patterns in the three years but the major features of the conception pattern persisted.

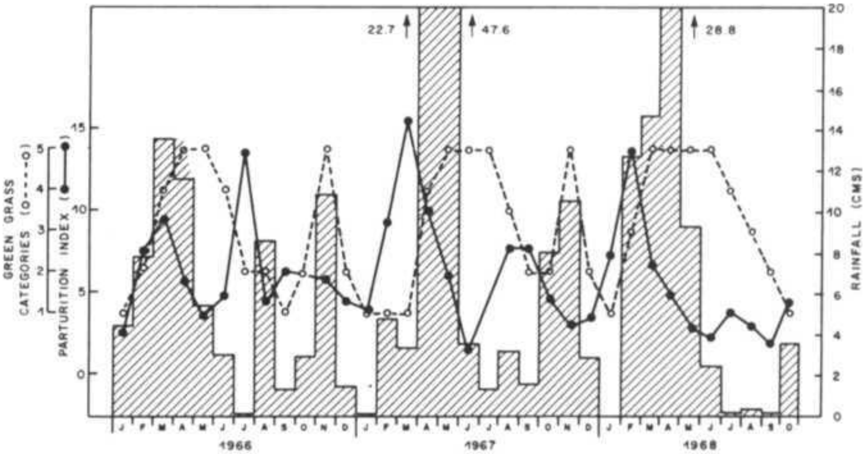


Fig. 14. The frequency distribution of parturition in relation to variation in rainfall and the percent cover of green grass. Data are expressed as monthly means. The parturition index is explained in the text. The grass categories are : '1': 0—5% green; '2': 5—25% green; '3': 25—50% green; '4': 50—75% green; '5' 75—100% green

Parturition peaks occurred in February/March and in a more variable position during the middle of the long dry season (Fig. 14). From the parturition indices obtained during fortnightly counts it was calculated that 55% of all calves were born in peak months.

When calves had reached the age of 4 months they were suckled only infrequently and were almost entirely dependent on grass for food. The calves born in the February/ March parturition peak had fresh grass when four months old from the growth of the long rains. Those born in the peak which was in about July were 4 months old when the growth of the short rains started. The females producing calves in the February/ March peak were lactating during the long rains but those calving in July were lactating in the late dry season, the most arid time of the year. The consistent feature of the pattern was that when the calves born in peaks were 4 months old there was usually high quality grass available.

The ultimate factor determining the seasonal distribution was thus thought to be calf survival; females which conceived in 'peak' months might theoretically make a greater contribution to the gene pool. The lower level of calving in 'non-peak' months was probably a reflection of an unpredictable element in the rainfall regime. Calves born in such months might have unseasonal new grass when weaning.

The home ranges of four randomly selected females which were seen from 18 to 115 times were from 3. 7 to 5. 5 $km^2$. Female home ranges, which were thus about half those of non-territorial males, included one, two or three of the short grass plains. 24 females which were observed over 20 times and up to 224 times were seen in from 7 to 26 pivotal territories; taking into account incomplete observation 20 to 30 territories is probably a correct range for most females.

Pivotal territories contained females for 29% of the time on average. There was however considerable variation between territory types: Type 2 and Type 3 territories contained females for 34% and 29% of the time respectively and Types 4 and 5 for 21% and 16% respectively. Type 6 territories rarely contained any females.

## PREDATION

The most important predators on hartebeest were lion (*Panthera leo massaica,* Neumann) and cheetah (*Acinonyx jubatus raineyi*, Heller). Black-backed jackal (*Canis mesomelas mcmillani,* Heller) probably killed a few very young calves. In Nairobi National Park cheetah often use cover for stalking prey before attempting to run them down (McLaughlin, 1970). Lion rely largely on concealment and a short dash in capturing their prey (Kruuk and Turner, 1967).

Hartebeest reacted to lion and cheetah by snorting and by the assumption of an erect posture in which the head was elevated to its maximum and the ears directed forwards toward the predator. For a variable period after detecting the predator they often kept a fixed distance from it by retreating or approaching as the predator moved towards or away from them. The animals which fled first from this fixed distance were usually females with young calves. Territorial males rarely left their territories in response to the presence of predators.

Twenty-six cheetah kills and 27 lion kills were collected and aged. About 80% of cheetah predation was on animals less than a year old; most of these were under three months. From data supplied by R. McLaughlin, who studied cheetah predation in the Park, it was calculated that at least 9% of the annual calf crop was removed by cheetah. Cheetah predation was thus a major source of mortality in the first year of life since as mentioned above only 28% of 19 calves ear-tagged at birth died in their first year. The aged cheetah and lion kills were placed in year classes and a correction factor was applied to take account of the variation in the numbers of each class available; the numbers available were taken from the calculated survivorship curve. The frequency distributions obtained (Fig. 15.) show definite selection by cheetah for young animals and selection by lion for old animals. The selection of young animals by cheetah was confirmed by field observations of predation (McLaughlin, 1970).

Out of 33 Lion kills of adult hartebeest which could be sexed, 26 (78%) were of males despite the fact that males were only 42% of the adult living population.

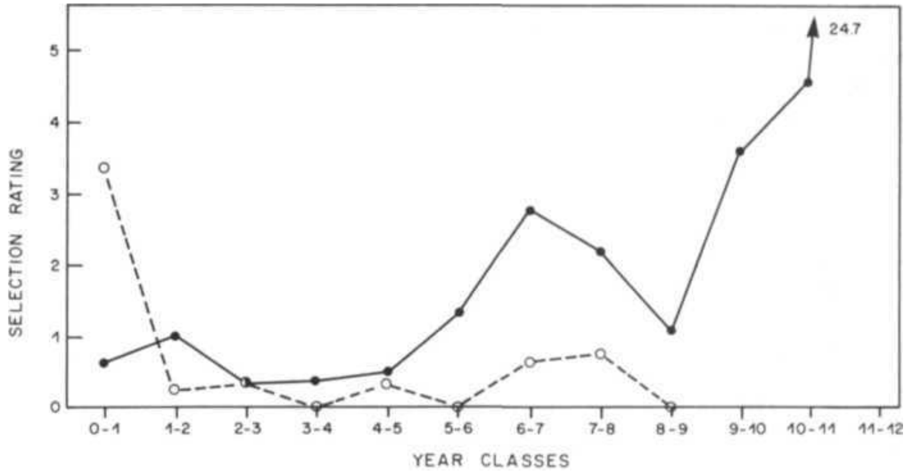


Fig. 15. The frequency distribution of Hartebeest kills by cheetah (o-----o) and lion (●——●) correlated to take account of the relative proportions of Hartebeest available in each year class. The proportions available are taken from the survivorship curve shown in Fig. 2. The correlation figures, A selection rating, are calculated from:

$$\frac{\text{no. kills per class}/\Sigma\ \text{all kills}}{\text{no. survivors at pivotal age}/\Sigma\ \text{all survivors}}$$

N = 26 and 27 respectively.

*A priori* several factors probably increase the chance of predation on hartebeest. These are:

(a) Isolation.
(b) An unfamiliar area.
(c) Cover for hunting cheetah and especially lion.
(d) Physical incapacity.

The occurrence of these factors at different stages of social development was considered in relation to data on the frequency of mortality. The best information was from 14 individually known males whose social development had been recorded up to the time of death. 9 were in the post-Pivotal territory occupancy stage and of these 5 were killed in long grass with *Carissa/Lippia* scrub. 5 were in Pivotal territories when killed and 2 of these were in scrub. This indicates the vulnerability of old post-Pivotal territory males which were often isolated in scrub and injured from fighting in attempts to take over territories. There were many more males in Pivotal territories available but fewer were killed. Males in Pivotal territories were isolated for about 71% of the time but they were in small familiar areas, were seldom injured and usually had short grass areas where they rested.

Young males after separation from their mothers were often isolated in unfamiliar scrub areas and were sometimes injured. In the 10-20 month age span 9 male corpses and 4 females were found. No data is available for the isolated phases before and after Pivotal territory occupancy but these times might also be expected to be of high vulnerability to predators.

In general the transition stages between major social states were considered to be the periods of greatest vulnerability to predation. The most vulnerable of all was possibly the post-Pivotal territory occupancy period which can be regarded as a prolonged transition period enforced by exclusion from territories. Females did not undergo such drastic transitions during their social development. Apart from a brief isolation during calving (Gosling, 1969) they were usually in a group, were in quite a small home range and were very seldom injured. Females are thus likely to be most vulnerable to predation when they became senile. Since most animals in the Park were probably born after the 1960/61 drought few females would have reached the age of senility during the study period. This may explain the fact that in the entire skull collection only 37% of the adult skulls were female despite females representing 58% of the live adult population.

## DISCUSSION.

The grasslands of the study area were essentially a series of distinct communities and their ecotones which were arranged concentrically around short grass plains; along any radial line they were a series of narrow parallel divisions. A twice yearly pattern of wet and dry seasons resulted in two periods of ephemeral grassland productivity. Hartebeest responded to changes in grass quality by a series of rapid shifts perpendicular to the grass zonation. They occupied and selectively utilized all the communities available, presumably when each provided seasonally optimum food. This pattern of movement is that of an animal well adapted to the dynamic ecotone conditions which characterize Nairobi National Park.

This situation contrasts with that of wildebeest which were partly limited by the relatively small amounts of short mat-forming grasses. Before 1960, wildebeest were twice as numerous as hartebeest (Foster and Kearney, 1967; Stewart and Zaphiro, 1963) and by the resulting high grazing pressure they probably maintained optimum short grass conditions. After the drought of 1960/61 numbers were halved and a year of torrential rain followed. These factors possibly combined to allow a fundamental change in the majority of the grassland in the Park; from being short swards they may have changed to the longer grass communities which now characterize most of the Park and which are optimum for hartebeest. This explanation largely conforms with a general theory of the relationships between grazing herbivores, their feeding methods and the nature of grasslands which has been suggested by Bell (1969).

An explanation for the observed seasonal pattern of breeding is that it is ultimately adapted to the probability that high quality grass will occur in the fourth month after birth; at this age calves are dependent on grass. Female hartebeest isolate to scrubland for parturition and calves 'lie-out' for the first fortnight of life (Gosling, 1969). This behaviour probably reduces predation pressure to similar low values throughout the year and allows a pattern of reproduction adapted to variation in grassland quality. Wildebeest, on the other hand, give birth on short grassland and the calves are very vulnerable to predators (Estes, 1966). Wildebeest calve synchronously and the high numbers of calves produced in a short time may 'swamp' the predation effort and thus reduce the proportion of the calf crop killed.

Several independent lines of evidence demonstrated that the most preferred hartebeest Pivotal territories were those whose longitudinal axes were perpendicular to a series of parallel grass communities. These territories contained several of the communities which were optimum at different times of the year. Within the limitations of their territories individual territorial males followed the same seasonal movements in response to changes in grass quality as the population as a whole. It seems likely that territorial males were defending a year round food supply. This would be adaptive because females come into oestrus throughout the year and males which could stay in their territories throughout the year could thus make a potentially larger genetic contribution than those which were forced to leave for food.

Territories were not defended uniformly at a point in time. Within each territory there was an 'aggressive response curve', of the type quantified by Patterson (1965), with the apex at the location of the resident male. Regarded in this light there is a direct link between territoriality and individual distance phenomena as envisaged by Marler (1956). The area around the territorial male in which the frequency of an aggressive response was over 50% was called the Actual Defence Area (A.D.A.); the radius of the A.D.A. is thus similar to the '50% distance' of Marler (1956) in his treatment of individual distance.

Since the locations of males while grazing in their Pivotal territories were determined by the seasonally optimum grass communities, the A.D.A. of ecotone territories covered much of the best quality food in the territories. Females and their offspring could thus utilize the optimum communities but male groups were to some extent excluded. The exclusion might explain why the home ranges of non-territorial males were twice as large as those of females; theoretically, high quality elements would be more widely distributed in sub-optimum pasture and non-territorial males would thus be forced to range more widely in order to obtain sufficient food. Males which occupied territories in which optimum food was regularly distributed, as in the case of territories in *A. drepanolobium* scrubland, could not defend a seasonally optimum food in the manner described.

These properties of territoriality in the preferred ecotone territories suggest the adaptive significance of the prolonged mother/male offspring bond. By staying with their mothers young males could utilize optimum food within the A.D.A.'s of Pivotal territories. In addition the young males probably experienced a reduced chance of predation through group living. The Head-in posture probably had the function of inhibiting the aggressive response of territorial males to male intruders. It would have been non-adoptive for territorial males to drive out male offspring because, when they did so the potentially reproductive mothers left with them.

Males resident in Pivotal territories experienced a low rate of predation as is the case with territorial male Thomson's gazelle (Walther, 1969). The transition stages after severance of the mother/offspring bond and before and after periods of territoriality were probably the most dangerous. Even males in scrubland Pivotal territories were not heavily preyed on, which can be explained by the advantage of living in a small familiar area.

Only males in residence in Pivotal territories were seen mating successfully. The interference by intruding males during mating and the way in which these males were expelled, demonstrated that an area of undisputed dominance was necessary to achieve successful copulation. In the high population density situation in the Park, interference by other males was probably more disruptive than in more normal lower densities.

There was no correlation between the frequency of conception and per cent territory occupancy. The values obtained showed that high levels of conception could occur when relatively low proportions of males were in their territories. The males absent were in general forced to leave their territories during waterlogging of grumosols or to drink in the late dry season. It would thus be an advantage for individual males to obtain territories which did not become prohibitively waterlogged and which were within easy reach of permanent water. The ecotone territories were again optimum from these points of view because they contained areas of lateritic soil which did not become impassable when wet and were in and around the short grass plains most of which contained permanent water.

The primary function of Pivotal territory occupancy was probably to secure an area of undisputed dominance for mating. Since oestrous females were available throughout the year it was necessary for males to defend their territories throughout the year. The ecological properties of the territories thus become critical: males needed a year-round food supply, easy access to permanent water and a substrate which did not become impassable when wet. These requirements were fulfilled most completely in the ecotone territories which because of their optimum character were preferred by males competing for territories, as indicated by their higher owner changeover rate, and were also more frequently visited by females. In this interpretation the anti-predator function of Pivotal territory occupancy is regarded as secondary; the reduced frequency of predation might even have been simply a consequence of living in a small familiar area with a reduced necessity for injurious fighting.

Pivotal territory occupancy can be regarded as the culmination of a continuum of male social development. In this light an important aspect of the pre-territorial behaviour of adult males is explainable. When males joined male groups they competed for dominance and after achieving high status isolated and attempted to take over Pivotal territories. Although one function of gregariousness in non-territorial males was probably anti-predator, possibly more important was the opportunity to encounter and establish dominance over all potential competitors for Pivotal territories.

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