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VOLUME 2

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

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VOLUME 1

VOLUME 2

Introduction to Volume 2

by VALERIUS GEIST AND FRITZ R.WALTHER

The contents of this second volume tend to be more concerned with the ecological aspects of ungulate behaviour and also stress some of the management problems of today. These topics and the behavioural aspects emphasized in Volume 1 cannot be logically separated; many papers could equally well have been allocated to either volume. However, for operational convenience and ease of reference, a rough and ready but fairly equal division of the papers has been made, although those interested in ungulate management will find much of interest in Volume I, just as the papers which follow here in Volume 2 often devote attention to ethological and physiological features in the life of the ungulate species discussed.

This is a good opportunity for expressing our particular gratitude to Dr. Ian McTaggart Cowan who wrote the concluding paper, following his attendance at the symposium and after he read some additional papers we sent to him later. This task consumed a good part of his demanding schedule and we are certain that his thoughts as one of the world's leading authorities on wildlife conservation and mammalogy, will be of profit to those concerned with academic matters or with management.

Paper No. 26

Behaviour, Dynamics and Management of Elephant Populations

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ABSTRACT

Studies related to the management of elephants (*Loxodonta africana* Blumenbach) in Africa are described in detail for one Uganda population and their implications discussed in a wider context. First, the population aspects of behaviour are considered. These include the concept of unit populations; individual and group densities, which show highly clumped distributions especially in high density areas; group size frequencies, which increase disproportionately as density increases; and an analysis of group structure. Then, population dynamics are introduced by the analysis of a number of samples obtained in the course of management cropping. To obtain unbiased samples, cropping is done by a method which depends on the elephants' group behaviour. Population models have been constructed for the Uganda population for the years 1946, 1966 and 1971 and show that a population decline has occurred. This decline has been associated with control shooting and reduced recruitment due to the operation of natural regulatory processes; but although there has been a decline in numbers, estimated at 64% , and in population biomass, estimated at 54%, the elephant biomass per unit area has remained virtually unchanged. This is due to a halving of the range available to elephants over this 25 year period, and a 30% increase in unit elephant weight due to a reduction in the abundance of the younger age groups. The implications of these findings for the management of this and other elephant populations are discussed.

INTRODUCTION

The past decade has seen a developing interest in elephant ecology in Africa because widespread habitat change from closed bush, woodland or forest vegetation towards open grassland has occurred in National Parks and other wildlife areas. The evidence has been presented elsewhere and need not be dealt with here; papers by Buechner and Dawkins (1961), Glover (1963), Lamprey *et al.* (1967), Laws (1969b, 1970), Laws *et al.* (1970 and 1971), Savidge (1968) and van Wyk and Fairall (1969) describe the process in a number of areas in Africa and cite other relevant publications. It is now generally accepted that a major factor in this process is elephant damage to woody vegetation and elephant cropping has now been carried out in a number of National Parks and Game Reserves in Kenya, Tanzania, Rhodesia, South Africa, Uganda and Zambia.

The most intensive cropping and research so far has probably been that carried out in the Murchison Falls National Park, Uganda and its vicinity, where in two years (1965-1967) some 2, 000 elephants were cropped in a carefully planned operation supported by the East African Wildlife Society (Uganda National Parks, Annual Report, 1965). A study of the biological material made available by this cropping has resulted in a better understanding of the structure and dynamics of elephant populations; such an understanding is very relevant to similar situations developing in other areas where management is being undertaken or is needed. I have confined myself in this paper to an appraisal of the population inhabiting the southern part of the Murchison Falls National Park (MFPS) and its vicinity. In this area the habitat change, induced by contraction of the elephant range, has perhaps progressed further than anywhere else. It has been accompanied by a population decline, mainly due to reduced recruitment resulting from deferred maturity, reduced fecundity, and increased calf mortality.

Some results of these studies have been described elsewhere (Laws and Parker, 1968, Laws, 1969a, Laws *et al.*, 1970 and 1971) and consequently further management cropping has been recommended. A discussion of the behavioural and population dynamics foundation of these proposals is presented here and their relevance to other situations discussed.

SOCIAL ORGANIZATION AND BEHAVIOUR

For various reasons, observations on elephant behaviour could not be undertaken as planned; but there is available another source of factual quantitative information on the organization of elephant populations, namely observations on distribution, densities and social structure, as shown by classified counts and sampling by cropping and post-mortem examination. As pointed out by Laws and Parker (1968) and Laws *et al.* (1970 and 1971) the cropping method of taking complete elephant groups is humane, causes no disturbance to the residual population and results in samples almost free from bias. The discrete groups can be analysed in terms of age, sex and reproductive status and history.

Unit populations. The first requirement in making stock assessments is to define the unit population. To date this has only been done for a few areas on the basis of geographical distribution as established by aerial reconnaissance flights. Observations on marked animals, immunological studies and investigation of population structure could provide confirmation. If spatial distribution is to be taken as the criterion, then the flights must provide seasonal coverage to plot the changing distribution patterns. An example is the series of monthly flights carried out by R. M.Watson and myself in the Tsavo ecological unit in Kenya and northern Tanzania (Laws, 1969b). These flights and a later count (Watson, Parker and Allan, 1969) indicated that there were some ten unit populations in the Tsavo National Park and its vicinity, totalling some 40, 000 elephants and occupying an area of about 30, 000 km^2 (Laws, 1969b, Fig. 2). Thus, in that region there was an average of about one unit population to 3, 000 km^2 with a population size averaging about 4, 000 at an overall density of about 1.33/km^2. This is an area of *Commiphora-Acacia* bush and low rainfall.

The results of aerial counts in the Murchison Falls Park and vicinity, an area of higher rainfall, indicated a population of about 9, 400 elephants occupying an area of about 3, 200 km^2. Initially this was not a single unit population, for there are some peripheral sub-groups, including a population of about 400 resident in the Budongo Forest. The contraction of the elephant range has led to crowding of the sub-units and the population has therefore been treated as a single unit although conspicuous substrata can be defined on the basis of elephant density, next to be discussed.

Individual and group densities. Over an area of 3, 200 km^2 in North Bunyoro, the average density was about 2.9/km^2 (Laws *et al.*, 1970) which is much higher than reported elsewhere except for small localized populations (Laws, 1970). However, sub-areas in the North Bunyoro elephant range have densities much higher than the average, and indeed on analysis an interesting pattern emerges. This analysis is based on data from three aerial counts, giving fairly adequate seasonal coverage, and related to a grid of 10 km^2 squares (Fig. 1). Squares with high elephant densities lie on the periphery of the population, as a crescent surrounding a central zone of medium densities. Two density strata have been defined with average densities of 3. 8/km^2 and 1. 9/km^2 for high and medium density strata respectively.[1] The high density zone corresponds to the distribution of large herds and concentrations, the significance of which in North Bunyoro and other elephant populations has been discussed elsewhere (Laws, 1970, Laws *et al.*, 1971). Such high densities are commonly found at the periphery of the elephant range and adjacent to areas of human settlement or other activity. They often result from displacement of elephant populations from areas formerly occupied by them.

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[1] Values of 3.7/km^2 and 2.1/km^2 were published by Laws *et al.* (1970), but were derived from a slightly different stratification.

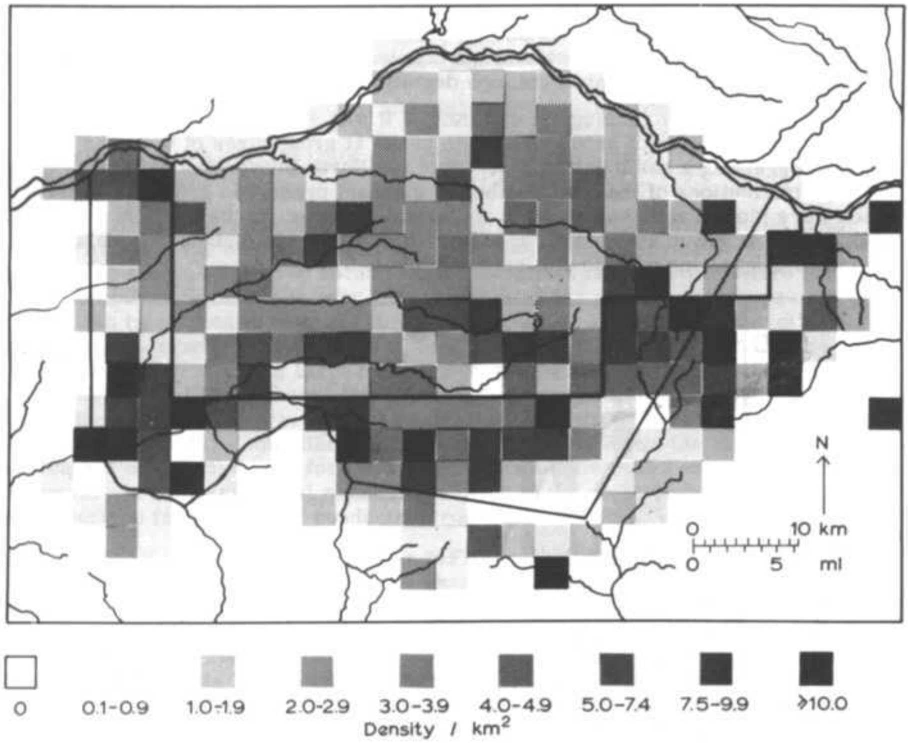

Fig. 1. North Bunyoro elephant range showing mean elephant densities per 10 km^2 quadrat for the three aerial counts. National Park boundary (thin line) and boundary between strata (thick line) are indicated.

The density distributions in terms of population units or groups per unit area have also been examined. The average group numbers per 10 km^2 were 1.71 and 2.91 for high and medium density strata respectively, but at any one time the spatial distribution of groups was strongly clumped. For the medium density stratum the negative binomial model is a reasonably fair fit ($k = 1.900$ and $p > 0.09$), and for the high density stratum the negative binomial is a very good fit ($k = 0.786$ and $p = 0.44$). When the data for the three counts are combined and the resulting average density distribution examined, the group densities for the medium density stratum show a very good fit with a Poisson distribution ($p = 0.42$) suggesting a random pattern of habitat use, but the Poisson distribution does not fit the data for the high density stratum ($p < 0.001$) even when the three counts are averaged. In the medium density stratum (and even in the high density stratum) with data from a larger number of counts, the average distribution would tend to be more regular, resulting in a more even pattern of habitat use. Laws (1970) has discussed the consequences of uneven habitat use over quite short periods of time.

Croup size frequencies. In the course of the three aerial counts over the grassland part of the North Bunyoro elephant range, 2029 discrete elephant groups were counted (including 439 single animals). They contained 24, 405 elephants, giving a calculated mean group size of 12.0. When the mean group sizes are calculated separately for the two density strata they average 6.6 and 22. 5 for medium and high density areas respectively; and comparing the data for the two strata, it is found as expected that the frequency distributions are significantly different ($p < 0.001$). Because large herds are characteristic of the peripheral area, the frequency distributions of group sizes up to 30 have also been compared and are also significantly different ($p < 0.01$); the difference is not due solely to the very large herds. When groups containing up to 20 animals are compared, the two strata are not significantly different ($p > 0.05$). This suggests that above a group size of about 20, corresponding to an 'extended family' or a herd containing 3-4 average family units, clumping occurs in both strata, but to a much greater extent in the high density stratum.

In a study in the Tsavo ecological unit, Kenya, it was shown that there was a polymodal frequency distribution of group sizes with peaks at group sizes of 6, 12 and 18 (Laws, 1969b), suggesting a basic unit of six. From the North Bunyoro aerial counts the frequency distributions of the total number of elephant present in groups of different sizes were plotted and show similar polymodal patterns. In the medium density zone peaks occur at group sizes of 6, 11, 17 and 23, and in the high density zone at 6, 10, 14 and 19, suggesting a basic unit size of about 5-6 (Fig. 2).

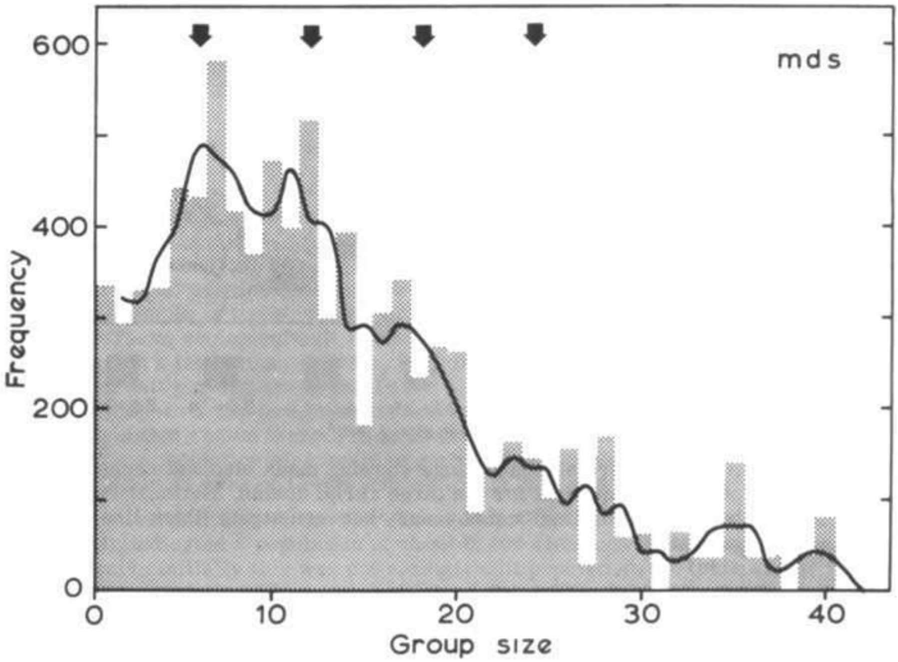

Fig. 2. Frequency distribution of elephants counted in the medium density stratum (1966-1967) by group sizes. The frequencies have been smoothed.

The examination of group densities and group sizes confirms the reality of the difference in the organization of the populations in the two strata, originally defined on the basis of population density alone. Associated with a 100% increase in population density (from 1.9/km^2 to 3.8/km^2) there is a 41% decrease in group density (from 0.29/km^2 to 0.17/km^2), and a 241% increase in average group size. The increase in group size is probably related in a fairly simple way to increasing frequency of contacts at higher densities. By virtue of their nutritional requirements elephants are very mobile animals and there is a high probability of inter-group contacts occurring by chance. Because they are also highly social animals, it is likely that contacts result in more than transitory aggregation, and also that increased group size is an extension of the contagious distribution of discrete groups that has already been demonstrated.

Let us suppose that the absolute density of a hypothetical population is doubled, as in MFPS. If the group density is to remain the same then, other factors being equal, groups at the higher density will average twice the former size. But if they are larger, they need to cover more ground for feeding and contacts would become more frequent, the average group size larger, mobility even greater and group density less. This interpretation is supported by the lower group density and much higher group size found in the high density stratum. However, if the quadrats containing two or more groups of elephants (i.e. excluding squares with single groups or none at all) are examined, it is found that for the medium and high density strata the respective mean group densities are $0.43/km^2$ and $0.4l/km^2$. This suggests that within the neighbourhood of concentrations a certain pattern of group spacing obtains, irrespective of absolute population density.

Group structures. Group structure and behaviour can be studied by means of field observation although the elephant poses more problems than many other species. For example in such a long-lived animal information on age and reproductive status is incomplete unless the study is very long term. Also the number of groups or populations that can be studied in detail is limited. If cropping is necessary for other reasons, then post-mortem examination of complete groups can provide accurate information on the structure of large numbers of groups. So far the structure of 261 mixed herds and 125 bull herds from five different populations in East Africa have been examined in this way, providing information on group structure, on reproduction, nutrition, condition and disease (Laws *et al.*, 1971). While the information obtained cannot obviate the need for field observation studies, the two approaches are complementary and observational studies owe much to the detailed quantitative information derived from properly conducted cropping operations.

Bull herds. Of 800 elephant cropped in MFPS in 1965-1967, 14.6% were in bull herds, a proportion comparable to that found in several elephant populations in Kenya and Tanzania (Laws, 1969b). In the MFPS the mean bull herd size was 3.08 (range 1-11), and in Murchison Falls Park North (MFPN) 2.39 (range 1-9). For 427 bull herds recorded in aerial counts in Tsavo National Park, Kenya, the mean group size was 2. 42 (range l-14);nearly 50% were singles (Laws, 1969b). All the animals examined in bull herds in MFPS were sexually mature and their mean age was 30.9 years. There may be a wide range of ages in a bull herd, but the age range is often quite small and may be bimodal, as if two groups of differing ages had joined up. The age distribution of solitary bulls was not significantly different from that of all bulls in bull herds.

Solitary females. In the course of the operations in MFPS six solitary cows were cropped and examined. They were all anoestrous and not lactating, with an average age of 55 years (range 52-59). Before being shot they were seen to be slow-moving, senile-looking and in poor condition. Because they were unable to maintain their position or to keep up with the younger animals, they probably had become detached from mixed herds of which they had formerly been matriarchs. Solitary females were not taken in cropping operations in MFPN, Tsavo or Mkomazi.

Family units. In the cropping programme in MFPS, 59 mixed herds were taken, of average size 11.6 (range 2-29). Animals in these family units comprised 85% of the sample and this is a basic social unit in elephant populations. A further 129 mixed herds were analyzed from MFPN, 25 from Tsavo, 23 from Mkomazi East and 25 from Mkomazi Central. These groups comprise adult females, immature females, immature males and some mature males; judged by the imcompatibility of their ages the latter are usually unrelated to other members of the group. Some relationships were evident before shooting or on superficial observation (e.g. cows with suckling calves), and others become apparent on analyzing the group's structure in terms of age, sex and reproductive status.

In both Murchison Falls Park samples, some 45% of groups had sexually mature males with them, but for Tsavo and Mkomazi nearly 75% of the family units contained sexually mature males, a discrepancy which may be related to the earlier age at puberty in the latter populations (Laws, 1969a, Laws *et al.*, 1971). For the MFPS sample there were on average 2.15 adult males in each family unit containing them, a figure not significantly different from the mean group size of bull herds sampled ($p > 0.05$); this suggested a temporary aggregation between mixed groups and bull herds. There was a highly significant difference ($p < 0.001$) between the mean age of bulls in a family unit (24.4 years) and in a bull herd

(30. 9 years). The mean age of bulls whose ages were compatible with close familial relationships within the mixed herds was 21.0 years, again highly significant. This suggests either that some bulls may remain with the family units for some years after reaching sexual maturity, or that younger mature bulls spend more time associated with the family units. There was no significant seasonal difference in the proportion of adult males within family units.

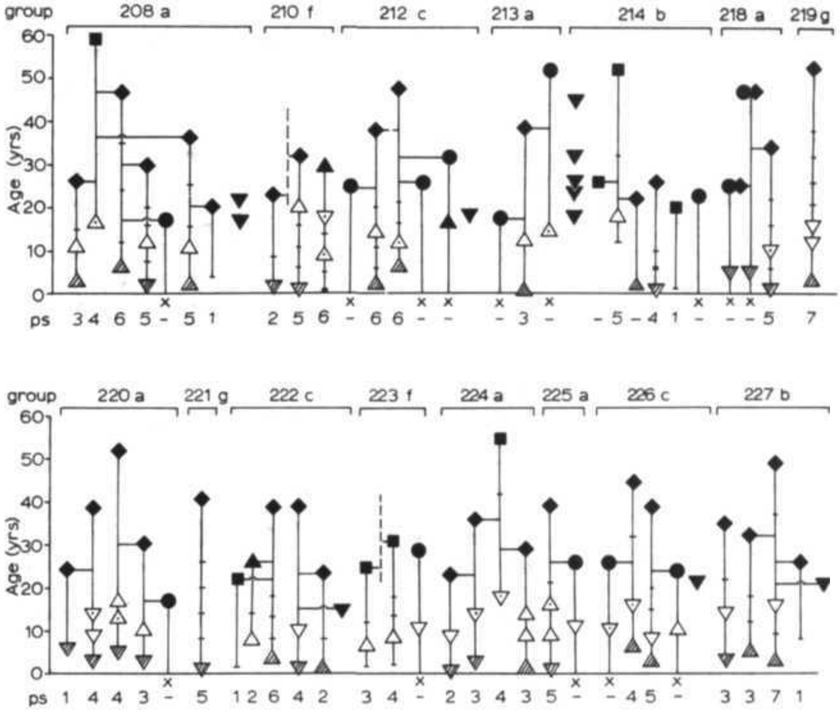

Fig.3. Structure, by age and reproductive status of 15 representative mixed herds. Presumed relationships are indicated by the lines, a broken line indicating a possible relationship via a matriarch, now dead. Placental scar counts are given for all non-pregnant mature females and a possible spacing of pregnancies indicated.

Key: × foetus or embryo; ▲ suckling male calf; ▼ suckling female calf; △ sexually immature male; ▽ sexually immature female; ▲ pubertal male; ▽ pubertal female; ▲ sexually mature male; ▼ cycling, ● pregnant, ◆ lactating, ■ anoestrous mature females.

Figure 3 illustrates the composition by age, sex and reproductive status of some representative family units cropped within the MFPS. Records of the occurrence of placental scars (Laws, 1967) have helped in the interpretation; for example a recent scar implies a suckling calf and a young female with one placental scar would not have more than one offspring. A full description of the presumptive group structures is given by Laws *et al.* (1971). The simplest group is a single adult female accompanied by immature animals that are clearly her offspring. These mother-offspring groups average 2.75 animals in size, that is one adult female to 1.75 offspring. Considering the total family units sampled the average ratio (adult females: immatures) is found to be 1 : 1.24 in MFPS and 1.73 in Tsavo. The ratio does not change with increasing group size and, as might be expected, it would appear that the mother-offspring unit is the fundamental population unit. However, the polymodal group size frequency in elephant populations indicated a unit of 5-6 animals, suggesting that usually two or three mother-offspring groups are combined to form a small family unit. The diagrams in Fig. 3 suggest that in larger family units these mother-offspring groups are often related as a matriarch and her immature offspring, together with one or more mature daughters and their offspring as 'extended families'. The younger females may not be related to the matriarch because most larger groups are thought to be random aggregations of smaller groups (Laws *et al.*, 1971) but the group structure is often very suggestive. An animal like the elephant which is a member of a family unit for 10-20 years while immature, can be expected to develop strong social bonds with its mother and siblings.

Other groups are best interpreted as associations of siblings or related females, the original matriarch having left the group or died. As the groups studied become larger, so the possible relationships increase, but they all fit a basic pattern dictated by the aggregation of sub-groups similar to those described. A presumptive classification of family units is given in Table 1, and matriarchal type groups comprise 74% of all groups examined.

TABLE 1. PRESUMPTIVE CLASSIFICATION OF FAMILY UNITS ANALYSED

Class	frequency[2]	%	mean age of oldest female (yrs)	Average size
matriarchal	16	24.6	46	6.0
			55[1]	13.01
matriarchal/mother-offspring	15	23.1	49	13.2
matriarchal/matriarchal	11	16.9	49	12.8
matriarchal/sibling	6	9.2	52	16.2
sibling	5	7.7	40	8.4
mother-offspring/sibling	4	6.2	34	9.5
mother-offspring	4	6.2	47	2.8
sibling/sibling	2	3.1	40	14.0
mother-offspring/mother-offspring	1	1.5	(38)	15.0
matriarchal/sibling/mother-offspring	1	1.5	(48)	18.0

[1] Four large groups

[2] Although there were only 59 groups in the sample six have been included twice because their structure was ambiguous.

The mean age of solitary senile females was 55 years, that of matriarchs in the first four categories of Table 1 averaged 49 years, while the mean age of the oldest females in the last six categories was 40 years. It has been shown by Laws *et al.* (1971) that age-specific fecundity reaches a peak between 30 and 40 years and then declines in older females, producing the nearest parallel to the human menopause that has yet been established for a wild population. The implication is that, as in man, the grandmother is an integral part of the group and has an important leadership and infant care function. This must be considered when planning management schemes, for selective cropping could have disastrous behavioural consequences.

The relationship between members of a family unit and their leader has practical value for management cropping. In undisturbed situations involving a large family unit, short-term observation of group behaviour does not necessarily reveal the matriarch, although she is usually the largest female in the group. However, when alarmed or alert, there is an immediate tendency to bunch on the matriarch. If she has insufficient stimulus to flee the group remains with her until the alarm has passed. If she is sufficiently frightened she runs, the herd bunched about her, and if she is aggressive they often back her up. Even when fleeing, if the matriarch is shot it is usual for the whole unit to stop and cluster about her, often with much nudging and efforts to lift her (Laws *et al.*, 1971). As a result of this behaviour it is possible to make herds bunch, shoot the matriarch first and then the others. It is this that makes the taking of complete herds possible as a management cropping technique. The shooting of bull herds is more difficult but still feasible.

The huge herds containing hundreds of elephants are found at the periphery of elephant populations and in conflict with man (Laws, 1970, Laws *et al.*, 1970). It is from these peripheral areas that control shooting takes its toll and it has been suggested that the large herds are a gross manifestation of bunching, developed to an exceptional extent because many leaders have been removed.

The management implications of the overwhelmingly matriarchal structure of elephant populations is that selective cropping of old or barren cows, as in the early years of the Luangwa Valley, Zambia, cropping scheme (Bainbridge, 1967), or as a likely consequence of implementing Sikes's (1966) proposals for selective culling would be disadvantageous. It removes from the population the adult females with the lowest reproductive rate, which is unhelpful in the context of most elephant problems, though not under a sustained yield regime. Perhaps a more serious factor in selective culling is that it removes the leaders. While the full consequences of this are unknown, the elimination of their accumulated experience must add appreciably to the disturbance factor and may well lead to the formation of larger groups, with more unfavourable effects on the habitats due to more intensive use (Laws, 1970). A great advantage of non-selective cropping by taking entire groups at random is that it is possible to reduce the population size without altering its structure and social organization.

POPULATION DYNAMICS

Effects of control shooting. Excluding the war years, 1940-1945, for which there are no records, a total of over 16, 000 elephants were shot in Bunyoro from 1925 to 1968. The numbers shot increased sharply after 1957 when a plan to control elephant in the economically important Budongo Forest was implemented and averaged about 600 annually from 1961. The majority, perhaps three quarters of those recorded, were shot in the vicinity of MFPS and the Budongo Forest.

Until 1966, shooting in the forest aimed at chasing elephants out of the young regeneration areas where no attempt had been made to prevent them entering and where they had halted the successional changes. This method was initially considered successful but probably only resulted in enhanced movement of the elephants since emergent tree species continued to be suppressed (Laws *et al.*, 1971).

Since 1966, the shooting programme has concentrated more on keeping elephants out of the forest but, after initial success, the operation failed, probably because the elephants modified their behaviour, confining their movements to the late hours of darkness, and entering the forest before dawn. As well as causing considerable disturbance, the control shooting over the years has been wasteful, uneconomic and grossly unhumane. Evidence has been presented which suggests that in recent years some 20-30% of elephants shot on control in or near Budongo were mortally wounded, but died lingering deaths, while an unknown proportion were shot but survived (Laws *et al.*, 1971).

Under natural conditions populations usually stabilize, or fluctuate around a level in approximate equilibrium with environmental resources. Hunting or control shooting disturbs this equilibrium by reducing numbers, and compensating mechanisms may come into play. These include reduced natural mortality, faster body growth, increased fecundity and earlier puberty, because the limiting factors are relaxed and more food is usually available. In the case of the North Bunyoro elephants, despite intensive hunting and a decrease in total numbers, the compensating mechanisms have operated in the other direction. There has been slower growth, later puberty, a decrease in the birth rate and increased calf mortality (Laws and Parker, 1968; Laws, 1969a and 1970; Laws *et al.*, 1970 and 1971). The constraints on numbers have not been relaxed, but rather increased because there has been a progressive reduction of the elephant range. This indicates that control shooting has not been the primary factor in the population decline.

An estimate has been made of the real reduction in population size represented by the offtake of 9, 200 elephants between 1946 and 1968. It was assumed that there was a stable population in Bunyoro in 1946, with a natural mortality rate of 6. 4% annually, and a value of about 6, 000 for the net population reduction from this cause seems reasonable (Laws *et al.*, 1971). It is considered that the effect of control shooting and licensed hunting is fairly random with respect to age, but it has only taken place at the periphery of the elephant range and elephant in the central area (where the 1965-67 sampling occurred) were probably not directly affected by it. It has been suggested that some unit populations or clans at the periphery of the elephant range were eliminated by control shooting, but this is reasonably well documented only in the case of the Butiaba Flats population, formerly numbering about 1, 500 elephants (Buechner *et al.*, 1963; Buss and Savidge, 1966; Laws *et al.*, 1971).

AGE AND SEX STRUCTURE OF ELEPHANT POPULATIONS SAMPLED

The age structures of samples from a number of populations in East Africa have been analysed for males and females separately and reasons have been given for believing that the samples are representative of the populations from which they were taken (Laws, 1969b; Laws *et al.*, 1971). The method of age determination, based on tooth eruption and wear, has been described by Laws (1966). The age structures show a sex differential survivorship in favour of the female and there are large variations in age class size from year to year. These do not necessarily reflect inaccuracies in the ages assigned. There are similar large variations in the numbers of foetuses conceived in successive years and in yearling numbers, in which case the ages assigned are not in doubt. Larger fluctuations with a wave length of about 6-8 years are thought to represent cycles in recruitment correlated with rainfall (Laws, 1969a), but this still needs further checking by resampling a population to see whether the peaks and troughs are displaced appropriately (Laws *et al.*, 1971). Whatever their explanation the fluctuations in apparent year class abundance complicate analysis of age structures, and the construction of population models involves heavy smoothing.

Population models for elephants. Laws (1966 and 1969b) has shown that in the elephant the mortality rate for much of the lifespan is nearly constant. For a number of elephant populations that have been sampled, the relationship between year class abundance and age has been examined in an attempt to obtain estimates of z, the instantaneous total mortality rate, from the linear segment of the plots. By plotting the natural logarithms of year class abundance (N_t) against age (t) and fitting a regression, z is estimated from the slope ($-z$) (Beverton and Holt, 1957; Ricker, 1958). In this method, the catch curve of fishery biologists, mortality is estimated from the relative abundance of successive age groups and a steady state of recruitment has to be assumed. Trends in recruitment can of course influence the apparent mortality rate and the possibility of a curvilinear relation between year class abundance and age cannot be ruled out. But for the present purpose the assumption is unlikely to introduce large errors and there is sufficient justification for accepting a linear relation over much of the lifespan. The similarity between data from a number of populations suggests that adult natural mortality rates are relatively invariable, and the component of total mortality due to control shooting operations is likely to be fairly random over most of the age range.

The analyses were initially confined to the data on female age frequencies. Average N_t values for 5-year classes were used and the slopes estimated (with 95% confidence limits) by fitting regression lines, using the method of least squares, to the segments 0-50 years, 10-50 years and 20-50 years. Some examples are shown in Figs. 4-6 and the results summarized in Table 2. Animals aged 50 years have been omitted from the analyses since there is good evidence of an increased mortality rate in the oldest animals.

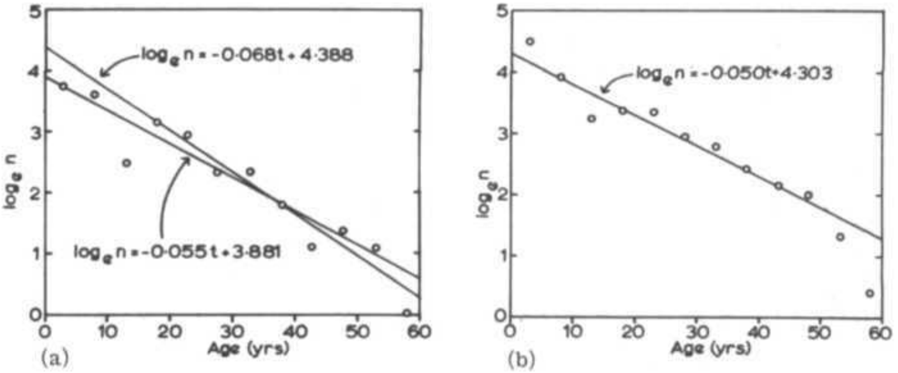

Fig. 4. Plots of the natural logarithms of year class abundance against age (5-year class interval) for (a) Mkomazi Central females. Regressions calculated from the age range 0-50 years (below) and 20-50 years (above). (b) Tsavo, Voi-Aruba females. regression based on age range 0- 50 years.

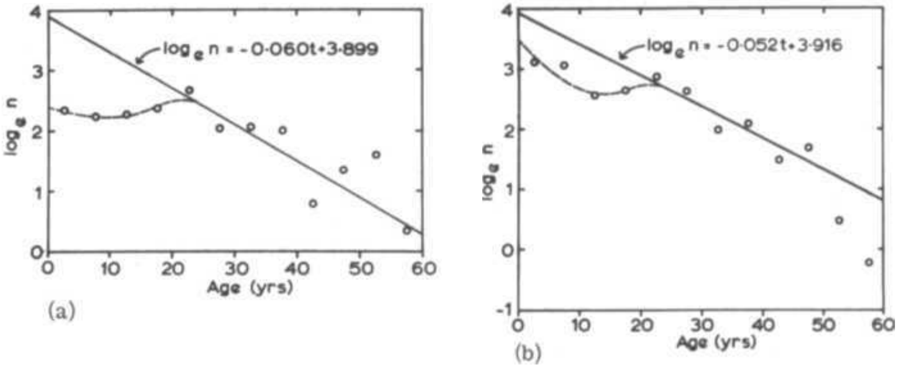

Fig. 5. Plots of the natural logarithms of year class abundance against age (5-year class interval) for (a) MFPS females, (b) MFPN females. Regressions calculated for the age range 20-50 years.

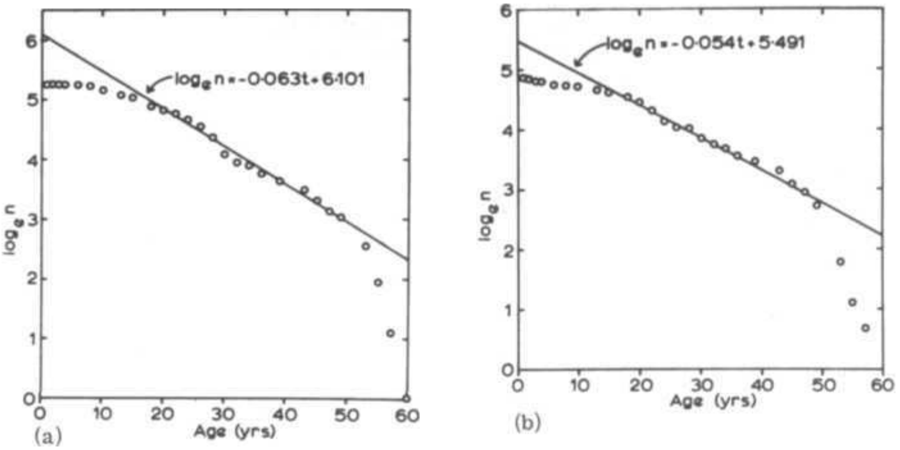

Fig. 6. Survival curves for (a) Murchison Falls Park and (b) Queen Elizabeth Park elephants. Constructed from data on natural deaths, sexes combined, presented by Laws (1966). Regressions based on the age range 20-50 years.

TABLE 2. ESTIMATES OF THE INSTANTANEOUS MORTALITY RATE (z) FOR A SERIES OF ELEPHANT POPULATIONS SAMPLED. ITALICS INDICATE 'BEST ESTIMATE' ON INSPECTION OF GRAPHS.

	z for different ranges of *t*			*r* for
Population	0-50	10-50	20-50	'best' estimate
Mkomasi Central	.055	.051	*.068*	.938
Mkomasi East	.050	*.060*	*.080*	.912
Tsavo Koito	.050	.046	*.063*	.912
Tsavo Koito[1]	—	—	*.063*	.740
Tsavo McKinnon Road	.038	.041	*.059*	.993
Tsavo Aruba—Voi[2]	.050	.042	*.054*	.992
MFPN	.034	.035	*.052*	.922
MFPN[1]	—	—	*.052*	.604
MFPS	.026	.039	*.060*	.851
MFPS[1]	—	—	*.052*	.567
BCFR	.034	.049	*.062*	.927
MFPS/BCFR	.028	.040	*.058*	.932
MFPS a[2]	.027	.040	*.057*	1.000
MFPS b[2]	.026	.045	*.062*	1.000
Murchison Falls P.[3]	.048	.058	*.063*	.992
Queen Elizabeth P.[3]	.042	.051	*.054*	.992

Except where otherwise indicated *z* is estimated from grouped data.

[1] *z* estimated from ungrouped data.
[2] age composition derived from aerial photographs using age/length key (Laws, 1969b).
[3] *z* estimated from data on found jaws, representing natural deaths, presented by Laws (1966).

In some samples the plots suggested a near linear relationship over the whole life-span (e.g. Mkomazi Central, Fig. 4a). In others the linear segment is restricted to older animals, owing to reduced recruitment (e.g. MFPS, Fig. 6a). The correlation coefficients were helpful in deciding which was the best estimate of *z*. The confidence limits are not given, but they ranged from ± .027 to ±.035, and the best estimate values of *z* shown in Table 2 are not significantly different ($p > 0.05$). Because of the large fluctuations in recruitment very much larger samples would be needed to establish whether there are real differences in 2, but such samples are unlikely to be obtained. Exceptions are the data from found jaws, representing natural deaths, for Murchison Falls Park and Queen Elizabeth Park (Laws 1966) and data obtained by applying age/length keys where a considerable smoothing effect is introduced by the method of analysis (Laws, 1969b).

The range of estimates of *z* is from .052 to .068, corresponding to annual survival rates ($1 - e^{-z}$) of .949 to .934, or annual mortality rates of .051 to .066. The estimates for the Murchison Falls Park and Queen Elizabeth Park, derived from ages at death, are very similar to those derived from the age structures in life, supporting the belief that the sampling by cropping was unbiased.

Models for the MFPS population were constructed, assuming a value for z of . 052 (ungrouped data, Table 2). First, in constructing a model representing the hypothetical population of MFPS before recruitment began to decline, year class abundance was calculated from the equation $N_t = N_0e^{-zt}$, with an assumed value for N_0 of 1, 000. The resulting curve is shown in Fig. 7 (dotted line, right hand scale). It was adjusted by calculating female natality, assuming puberty at 12 years, a 50% pregnancy rate of mature females (mean calving interval 4 years) and a sex ratio of 1 : 1 at birth (Laws, 1969a). This gave a natality of 1, 197 and involved only slight adjustment of the origin and of early mortality rates. The tail was adjusted slightly to allow for increased mortality in old age. This model is not arbitrary because it is similar to the current pattern of year class abundance in some other populations sampled. The adjustments make little difference to the results. Male survivorship was assumed to be identical with that of the female up to 30 years, when an increased mortality rate results in no survival beyond 52 years (Laws, 1969b). The model is taken to represent the structure of the North Bunyoro elephant population in 1946 or earlier since this is the last year group to show no reduction in natality (Fig. 4a); this will be referred to as the 1946 population. Habitat change was, however, noted in North Bunyoro before 1946 and serious damage by 1949 (Laws *et al.,* 1970 and 1971).

Next this model was adjusted to represent the situation in 1966 by taking account of the initial 5-year means of year class abundance in the sample, showing reduced recruitment (Fig. 4a). Female natality was calculated on the basis of puberty at 18 years, 29% pregnant (mean calving interval 7 years) and a sex ratio at birth of 1 : 1 (Laws, 1969a). This gave a natality of 457, and year class abundance was adjusted by interpolation up to 4 years. These two models suggest an increase in total calf mortality (birth to 4 years) from 29% (1197 to 856) in 1946, to 43% (457 to 261) in 1966.

Since 1966, the parameters have probably changed little and a similar model can be constructed for the 1971 population. The major difference is that the abundance of all year classes that have been affected by reduced recruitment since 1946, i.e. those less than 20 years in 1966, will have declined in the intervening five years. This decline can be estimated by $1 — e^{-5z}$, that is $1 — e^{-..26}$ or 22. 9%. Natality calculated as for the 1966 model is 407.

These models suggest that relative natality fell from 1197 in 1946 to 457 in 1966 and to 407 in 1971, decreases of 62% and 66% respectively; and that relative recruitment at 4 years fell from 856 in 1946 to 261 and 212 in 1966 and 1971 respectively, that is by 70% and 75%. Although the models are rather crude, it cannot be doubted that there has been a great change in population structure over two or three decades and a significant reduction in natality and recruitment.

So far the relative year class abundances have been related to the initial arbitrary values for a cohort of 1197 at birth. The next step was to sum the N_t values, for both sexes, for each of the three models in order to obtain relative population sizes. For 1966 the arbitrary total was 21, 195 and since the population size at that time has been estimated at approximately 9, 400 (Laws *et al.,* 1970 and 1971), a correction factor has been applied to derive estimates of absolute population sizes in 1946 and 1971. The left hand scale of Figure 7 relates to these estimates which indicate a population size of about 16, 000 in 1946 and 7, 900 in 1971. When adjusted for the net reduction due to control shooting discussed earlier, this indicates a population of about 22, 000 elephants in North Bunyoro before 1946.

On the basis of these models the population decreased by 57% between 1946 and 1966, of which about half was due to control shooting and sport hunting and half to natural regulation. The estimated 1971 population is 36% of the 1946 population, a decrease of 64%. Natural regulation alone was apparently responsible for a population decrease of about 41% to 1966 and 51% to 1971 (in numbers from 16,000 to 9,400 and 7,900). This very substantial decline has still been inadequate to achieve population stability; to find an explanation it is necessary to examine the related changes in biomass.

Changes in standing crop biomass. The numerical models can be converted to biomass models by applying weight at age data (Laws *et al.,* 1970 and 1971) to the age frequencies for each sex and age class, to obtain biomass at age (N_tw_t) and popula-

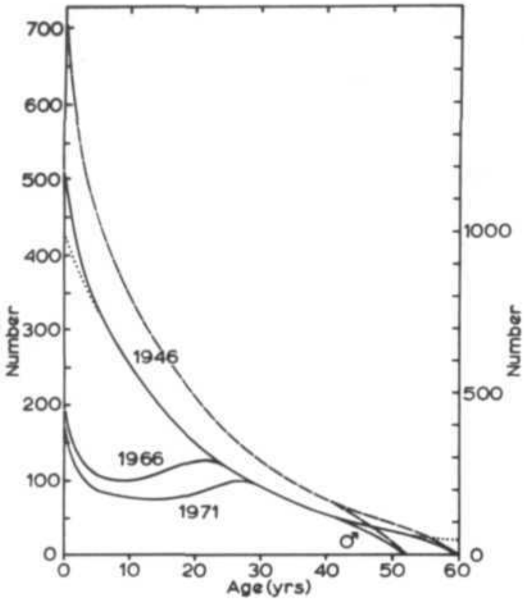

Fig. 7. Population models (numbers) for the North Bunyoro elephant population in 1946, 1966 and 1971. Solid lines: population structure estimated from year class abundance data derived from sample cropping in 1965-67 and by extrapolation. Pecked line: makes allowance for numbers taken in control shooting operations since 1946. Dotted line: estimate based on instantaneous total mortality rate.

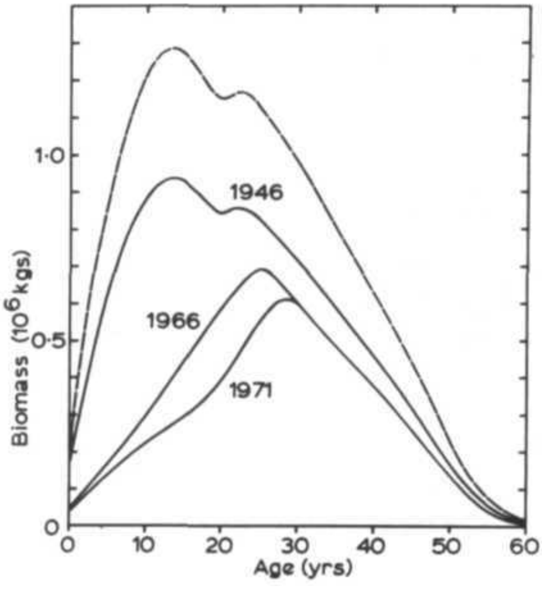

Fig. 8. Estimate of standing crop biomass at age for three population models of the North Bunyoro elephants, sexes combined. Pecked line: allowance made for numbers taken on control shooting operations.

TABLE 3. SUMMARY OF CONCLUSIONS DERIVED FROM POPULATION MODELS. THE 1975 FIGURES RELATE TO THE FUTURE POPULATION SHOULD THE PROPOSALS MADE BY LAWS *ET AL,* (IN PRESS) BE PUT INTO EFFECT.

	1946	1966	1971	1975
Area of range (km^2)	6,300	3,200	2,800	2,600
%	1.000	0. 508	0.445	0.413
Population size (${}^{S}N_t$)	22,000	9,400	7,900	4,200
%	1.000	0.427	0. 359	0. 191
Population biomass (${}^{S}N_t w_t$ 10^6 kgs.)	41.789	20. 996	19.442	10. 336
%	1.000	0. 502	0.465	0. 247
Mean weight (w kgs.)	1,894	2,234	2,461	2,461
%	1.000	1. 180	1. 299	1. 299
Weight/unit area(w/km^2)	6,633	6,561	6,965	3,980
%	1. 000	0. 989	1. 050	0. 600
Density (N/km^2)	3. 50	2.94	2.83	1.61
%	1.000	0.840	0.809	0.460

tion biomass (${}^{S}N_t w_t$). The data are presented in Fig. 8 and Table 3. In 1946 the biomass peak was at 13 years, and the secondary peak at 23 years is due to a supposed male post-pubertal growth spurt (Laws *et al.,* 1970 and 1971). The effect of reduced recruitment has been to postpone the biomass peak to 25 years in 1966 and to about 28 years in 1971.

Population standing crop biomass, rounded to the nearest 1, 000 kgs, is estimated at 41. 789 × 10^6 kgs in 1946, 20. 996 × 10^6 kgs in 1966 and 19. 442 × 10^6 kgs in 1971. These estimates represent a decrease in total standing crop biomass since 1946 of 49% to 1966 and 54% to 1971. The mean elephant weights are easily calculated and, according to the models, it is found that there has been an increase in unit weight from 1, 894 kgs in 1946 to 2, 234 kgs in 1966 and to 2,461 kgs in 1971. This is due to the reduced recruitment which has resulted in a preponderance of heavier older animals in the population.

In addition the elephant range has decreased from an estimated 6, 300 km^2 in 1946, to about 3, 200 km^2 in 1966, and to an estimated 2, 800 km^2 in 1971. Applying these area estimates to population size gives mean elephant densities of 3. 50/km^2 in 1946, 2.94/km^2 in 1966 and 2. 83/km^2 in 1971, a decrease to about 80% of the 1946 level. However, the increase in elephant unit weight has had the effect of limiting the change in biomass per unit area. The mean biomasses per km^2 are estimated at 6, 633 kgs. in 1946, 6, 561 kgs. in 1966 and 6, 965 kgs. in 1971. Thus, over twenty years there was a very slight reduction, but with further contraction of the range there was a slight increase by 1971. This is a crucial factor in the continued habitat deterioration caused by the elephant population.

Clearly the reason for the failure of control shooting and reduced recruitment to lower the standing crop per unit area, is that the area available to elephants has been contracting too rapidly. With little change in biomass per unit area since habitat deterioration began, the habitat change has been progressive. The rate of reduction of the size of the elephant range has not been uniform and at times when the contraction was more rapid the habitat change presumably accelerated.

MANAGEMENT

A number of detailed management recommendations have been made by Laws *et al.* (1971) but the most important involves rapid reduction cropping. Laws (1970) has suggested that under natural conditions when population density tends to increase and groups to enlarge in size, the greater mobility of the larger groups, which is necessary for feeding, leads naturally to dispersion. Combined with the broad regulatory mechanisms that have been discussed elsewhere (Laws and Parker, 1968; Laws, 1969a, 1969b; Laws *et al.*, 1970 and 1971), this allows for very sensitive adjustment of the grazing pressure on habitats. That the dispersion behaviour has probably been an important part of the process of population regulation in the past is demonstrated by the failure of the control by reproductive and mortality changes to halt habitat overuse in a number of elephant populations that have now been studied. Laws (1970) has discussed some case histories.

Viewed in this way, it is evident that management by reduction cropping can substitute for that part of the population regulatory process that was formerly achieved by dispersal or emigration from an area as densities built up or food resources declined. The contraction of elephant ranges has reversed the process and in a number of areas has led to concentration rather than dispersal.

The proposals for management of the MFPS elephants involve reduction cropping in two stages: first to reduce the population density in the high density stratum to the level of the medium density stratum and, secondly, to reduce the overall density to about 1. 6/km^2. This would involve cropping some 3, 700 elephants, leaving a residual population of about 4, 200 (Laws *et al.*, 1971). In the face of further contraction of range, long term sustained cropping may be necessary as a continuing substitute for dispersal. These recommendations were based not only on a consideration of densities and habitat damage, but on an examination of growth, nutrition, reproduction and population dynamics (Laws *et al.*, 1970).

Predicted in Table 3 are some effects of reducing the population to 4, 200 by 1975, by cropping, as recommended by Laws *et al.* (1970 and 1971). By then it is estimated that the elephant range will have decreased to at most 2, 600 km^2, or 41% of the 1946 area. At a level of 4, 200 the population would comprise about 19% of the 1946 total, and the standing crop biomass of the population would be about 25% of the estimated 1946 level. The mean elephant unit weight should be rather less than the estimated 1971 unit weight and the density about 1. 6 elephants/km^2, or 46% of the 1946 level. The weight per unit area after reduction is estimated at about 3980 kgs./km^2, or 60% of the 1946 level.

The habitat has changed from a forest—woodland—medium height grassland mosaic, favourable to elephant, to tall grassland; and the quality of the available food has deteriorated. Browse and herbs are a preferred component of the elephant's diet comprising, under optimum conditions, some 40-50% of the diet but now only 10-20% of the diet in North Bunyoro. Browse and herbs have thus been progressively and selectively over-used, at least since 1946, and this is the major cause of habitat changes in this area. There is no evidence of any significant change in the quantitative food intake per unit area by elephants. However a small sample collected by Buss (1961) in wooded country had significantly higher stomach fill weights (when allowance is made for body size) than the later samples. From the results of weighings in 1965-67 the average daily food intake has been estimated at 3. 94% of body weight for males and 4. 68% for females (Laws *et al.*, 1970 and 1971). It was shown that the daily intake, proportional to body weight, did not vary with age or sex but was significantly higher in lactating females. At the estimated weights per unit area (if food intake proportional to body weight has not changed) annual food consumption was 10. 33, 10. 19 and 10. 53 metric tons/km^2 in 1946, 1966 and 1971 respectively, on the basis of our models, and would be reduced to about 6 metric tons/km^2 at a population size of 4, 200 in 1975. This should result in a reduction in the grazing pressure on woody plants and, hopefully, permit habitat recovery. Other management action such as fire control has been proposed; but in view of the results described in this paper it is difficult to see how any management policy that does not include population reduction can succeed.

These findings have implications for other elephant populations with limited ranges where similar habitat changes are occurring. The aim of management should be first to define unit populations; then to ascertain the status of each unit population, including its age and biomass structure and reproductive performance. This is best achieved by sample cropping and investigation of the historical changes in its distribution, as recommended by Laws (1969b) for the Tsavo ecological unit. Depending on the results of this preliminary study it may then be necessary to undertake reduction cropping. The objective would be reduction of the population to a level at which the natural regulatory mechanisms can operate to stabilize population density and, more importantly, biomass per unit area (and therefore food intake) at a level in equilibrium with the habitat. It is probable that in situations where the available range is restricted or decreasing, now almost universal, limited sustained cropping may be necessary as a continuing substitute for natural dispersal or emigration. In implementing these recommendations the nature of the social organization of elephants is important because it allows the rapid removal of the indicated proportion of a population without altering its structure or causing disturbance.

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Paper No. 27

Management of Ungulate Herds in Relation to Domestication

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(Paper dedicated to the memory of A. N. Severzov of the USSR Academy of Sciences)

ABSTRACT

On the basis of studies of native herding systems of livestock found in Central and Eastern Asia, as well as the behaviour of domestic livestock and their wild counterparts, it is possible to identify the principles of herd control. Native herdsmen use a number of acoustic and visual signals that are surprisingly similar in different cultures and which can be transferred successfully from one species of livestock to the next. Thus the herding signals of the reindeer herder can be effectively used with yaks or sheep. Herders exercise control primarily by keeping the animals in a compact mass when moving them, by conditioning the animals to assume specific activities at the convenience of the herder, such as grazing, resting or rotating the herd, thereby keeping it compact, as well as by taking advantage of the animals' inherent tendencies. These practices as well as behavioural observations relevant to understanding them are discussed in detail. A theory of ungulate domestication is proposed. Herding originates in the hunting practices of early man. It is shown that control of herds of wild, undomesticated ungulates is not difficult if one follows the herding principles discussed. Some suggestions are made for changing conventional herding practices in order to save labour and costs and to take advantage of the favourable attributes of free, uncontrolled grazing under which animals grow and fatten at superior rates. The concepts discussed in the paper should lead to better methods of ungulate management in the future.

INTRODUCTION

The term 'management' is used here to describe the methods whereby herders impose a given behaviour on a herd of ungulates. The relationship between man and the herd is only part of a more complicated system, encompassing the total environment of the herd. Man is the dominant component of the environment, and influences the other parts of the system.

When investigating the behaviour of a herd, we identify those elements that differentiate a herd from an unorganized grouping of animals. From recurrence of successions of behavioural phenomena we argue that a causal connection exists between them, and evaluate the development of the system from a knowledge of the behaviour of the species. In addition we receive information about an individual animal's behavioural development from herders. Finally, we aim at predicting the development of an ungulate-environment system giving essential information about its elements at any given time.

Cowboys and hunters, of course, do not act on the basis of scientific concepts about the herd's behaviour; they use empirical rules. They have worked out practices of herd management which are handed down from generation to generation. The problem is to replace these empirical practices with scientifically correct rules of management. Such rules would have more than theoretical value, although it is granted that herdsmen manage rather well without them. A model of herd behaviour and management is important for further investigations and would be important for the development of new principles of animal domestication.

I have had the opportunity to study the native herding practices or 'management schools' of the Tchukchies, Korjakies, Evensks, Dolgans and Samiees, as well as those of the Turkmenis, Kirgies, Tadjikis and Uzbekis. This as well as observations of reindeer, sheep, goats, camels and yaks has allowed me to recognize some principles in the management of herd-forming ungulates. I have also studied wild reindeer, wild sheep (*Ovis ammon, O. canadensis*), Manchurian red deer (*Cervus elaphus xanthopygus*), wild goats (*Capra aegagrus*) and Siberian ibex (*C. siberica*).

There is usually a considerable resemblance between the responses of all these wild and domestic ungulates to man. Where they differ, it can be traced to differences in the conditions forming the behaviour of wild and domestic forms. Thus domestic animals live for long periods under the unusual conditions of big and compact herds, combined with the presence of men who both threaten and defend them.

THE RESPONSES OF UNGULATES TO SIGNALS.

Herd management is achieved by means of signals. The reactions of wild and domestic forms to such signals have a certain similarity. Many of the reactions of domestic animals appear to be a product of learning.

Auditory signals are used more often than others in herd management. It is surprising to note the great resemblance between the various shouts and whistles used by the herders of different nations. Furthermore, I have found that auditory signals learned from reindeer herders are surprisingly efficient in managing sheep and yak herds. The signals were similar in the pattern as well as in the intensity or loudness of the sounds used. Long whistles and long but not loud shouts calmed the animals. A repertoire of short words was used when getting the animals to move. Sharp and loud shouts or whistles act to stop animals or inhibit animals in or from a given activity, and when lengthened to halt their movements or make them look up and pay attention to events in their immediate surroundings.

Visual signals are used in support of auditory ones, particularly when frightening animals. The herdsmen wave arms or clothing, or throw rocks. Some hoist their caps on top of sticks. In this instance the animals may regard the man as being unusually tall. It is possible to frighten even the aggressive wisent (*Bison bonasus*) of the Caucasian reserve by this method. Reactions of herd animals to visual clues is very interesting. The direction of the movement is closely related to the direction of the herder's hand movements (Fig. 1). Using this principle, a herdsman standing in the centre of a herd can manage the movement of the animals.

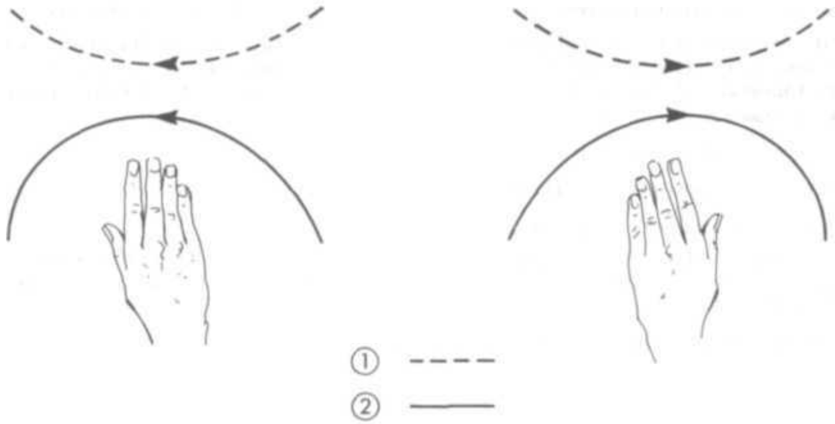

Fig. 1. The direction of a herd's movement (1) influenced by the parallel movement of the herder's hand (2)

Since the animals respond to only a few key features of shape and motion of the objects they encounter, it is possible for herders to assume a 'reindeer' configuration to attract reindeer. The essential features of the 'reindeer' configuration are a dark, horizontal object of reindeer size and 'antlers' at the forward-moving end. This can be imitated by a man stooping forward and raising his hands over his head. Pruitt (1960) described how caribou used 'bobbing' to attract one another; he attracted caribou by imitating this behaviour.

It is well known that reindeer move more readily into a corral made from well-spaced poles than into corrals with solid walls that obscure vision. They also enter a corral more readily if they cannot see its back wall. This can be achieved by building corrals of S-shaped form.

Olfactory signs have some importance in herd management. We know that many ungulates have interdigital glands and that these glands are presumably capable of producing scent-impregnated tracks. However, our experiments failed to furnish supporting evidence of this: we put masks over the heads of sheep and allowed them to roam freely; but they never tried to orient by following tracks; on the contrary, they soon began moving in the direction of the sun, either because the masks did not exclude light completely, or because they did not prevent sheep from orienting towards the warmth of the sun. According to Kirgiz herders, however, blind sheep may live a long time in herds and would appear to be guided by scent, as they stay on the lee of the herd.

Again, in Turkmenia, herders alerted me to the significance of freshly made tracks. At night their sheep strive to remain within the area trampled over by the herd. This behaviour is put to good use by the herders, who every evening move the herd round and round the same spot several times before leaving the herd for the night. The animals remain within the trampled area and thus any splintering of the herd or individual dispersal is successfully avoided.

Herd management is based primarily on the defensive responses of the animals, but herders also occasionally take advantage of normal feeding rhythms, maternal behaviour, etc. The activities of the animals dictate the appropriate management techniques: a calmly grazing herd cannot be expected to follow a lead animal which has been trained to lead the herd, but a group of frightened animals, which has gathered into a compact herd, can be successfully controlled by this method. Herd management is thus based on changing the activities of the animal to those corresponding with the intentions of the herder. Sometimes the herder waits patiently for the appropriate activity to appear spontaneously. For instance, when a calf has been placed with a foster mother, he must wait till he notices the appropriate maternal behaviour in the female, indicating the awakening of her maternal instincts before leaving. However, it is more common for the herder to change the activity of the animals by giving appropriate signals. The herd is being conditioned to associate specific signals with specific activities. There is the 'soothing whistle'; there are signals stimulating nutritional reflexes; an imitation of raven calls stimulates females to look for their calves.

Animal behaviour is composed of elements that have significance to the animal's surroundings. L.V. Kruschinski (1960) suggested terming such elements 'biological forms of behaviour'. We may, for instance, note that calmly grazing sheep show the following features:-

(1) grazing posture in which the head is lowered;

(2) moving to a new place on the pasture; and

(3) looking around with raised head.

These behaviour elements or behaviour patterns may follow each other in arbitrary succession. It may be that competition arises between grazing sheep, and we may then note the following activities:-

(4) nuzzling of each other's preorbital glands;

(5) walking back prior to clashing or butting; and

(6) actual butting or clashing with the forehead.

Other sheep, meanwhile, are resting after having foraged and we note:-

(7) some sleeping while lying down;

(8) others resting and ruminating; and others again

(9) standing and ruminating.

If the sheep receive a signal indicating danger, we note:

(10) jumping up from resting;

(11) shying back from the dangerous stimulus;

(12) running to the main part of the herd; and

(13) following a leader.

Figure 2 illustrates possible relationships between these behavioural elements.

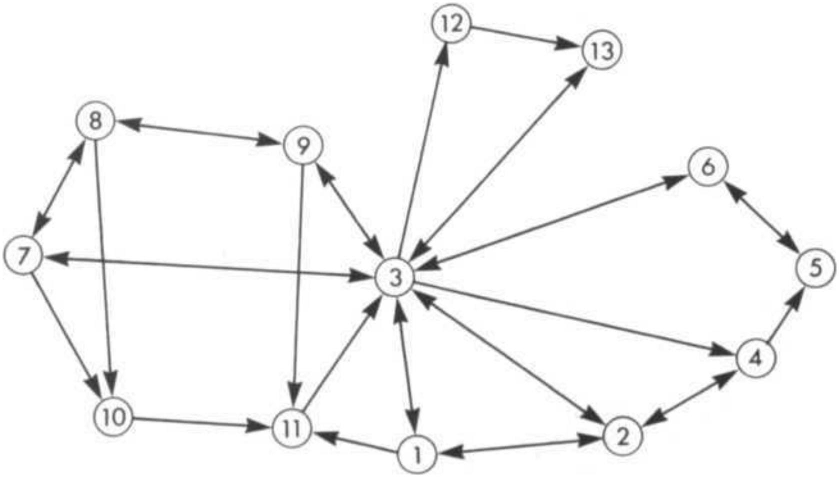

Fig. 2. Simplified scheme of possible relationships between the thirteen activities noted in a calmly grazing herd of sheep

In some cases one kind of activity predominates (A. A. Uchtomski, 1950). Defensive, nutritive or sexual motivations may determine the responses of the animals to specific signals, in accordance with the innate release mechanisms postulated by ethologists, including appetitive behaviour and consumatory acts. The spectrum of possible behaviours depends on the motivational state of the animal. Note the behaviour patterns of a frightened and a grazing sheep (Figs. 3a & b respectively).

This is an important consideration in herd management. Fright motivation permits close herding even if it counters the 'natural wishes' of the animals to graze, rest, etc. It is used in driving the herds long distances or when catching animals. Nutritional motivations can interfere considerably in herding. It is evident that the signals used by herders must strongly evoke the desired motivation. The most powerful signals are those the animals are exposed to under natural conditions. Thus the appearance of a barking, attacking dog, or the sight of another frightened herd are the most powerful signals for evoking fright motivation in reindeer or sheep. Yaks on the other hand,

Fig. 3. Reactions, extracted from Fig. 2, when the dominant behaviour is (a) defensive or (b) nutritive

are most sensitive to the noise of falling stones. V. J. Kriagev (1955) calls such signals 'biological signals'.

The same signal may provoke different responses under different conditions. This was noted in reindeer (Baskin, 1968). It has also been shown in other species: thus a herder's figure may trigger a fright response among cattle in the open field, but evoke feeding activity when the cattle are at a shed. The significance of this change of meaning of a stimulus depending on external circumstances was of course investigated by J.P.Pavlov and his pupils.

One must notice that motivations are hierarchically organized. When the animal is confronted simultaneously by diverse signals, i.e. signals evoking feeding and signals evoking flight, the animal responds with flight. One may rank motivations in decreasing order of dominance as follows: fright, sex, maternal, feeding, attention and orientation, comfort. However, it is also known that such a hierarchy of motivations may break down, and biologically expedient activities prevail. Examples are sexual activities when a female is in heat, feeding activities when the first green forage becomes available in spring after a long period of snow, or drinking by camels or sheep suffering from thirst in summer.

In the laboratory, the investigator simplifies the situations found in the natural environment. Thus a dog is faced by a dish of food and, if it approaches, an electric current delivers a painful stimulus. In the field, many stimuli impinge simultaneously on the animal; the food, herd, herders, etc. The stimuli vary in different parts of the pasture. There are gradations of stimuli varying with the number of animals, the distance between herder and herd, or the quality of the pasture. From this flood of stimuli, animals selectively respond to some more than others.

Herd management is not built on a simple concept of a signal by the herder being followed by a prompt reaction by the animal. The herder may by his very presence attract or frighten the animals. The herder's figure provokes a fright response the faster he approaches the animals, and the more he shouts or throws stones etc. On the other hand, the presence of the herder may signal a pleasant stimulus. The young animals are equally conditioned to associate the presence of man with pleasant circumstances. His special shouts and whistles calm the herd in the presence of a predator or other dangers. During snowstorms or in fog the herder's whistle and call calms the herd and prevents panic. Hence man appears in two contradictory situations, and the animals prefer to stay some distance from man.

One can contrast this with the behaviour of the wild relatives of domestic stock. In open country, such as tundra, steppe or bare mountains the animals see man a long way off. In the mountains of Kopet-Dag (Turkmenia) urials (*Ovis ammon cycloceros* Hutton) prefer to keep at least one kilometre away from a man. If a person walks any closer the sheep quit grazing and move off. They get frightened the moment a person disappears from their sight and they differentiate quite well between a person on foot or on horseback, and between a herder who calmly manages his herd, persons simply travelling along the same route as themselves, and the hunter attempting to make a stalk and hide himself. Hunters say that urial deliberately come down to stay close to villages where there are few predators.

In the tundra of Kamchatka and the Taimyr peninsula grazing wild reindeer also tend to keep a kilometre or more away from persons and regard this as a safe distance. But there may also be localities where the animals appear to feel secure after having been put to flight and where the presence of man leads to no further flight.

The fright response is the one most used for herding animals. Extreme gregariousness is apparently a derivative of protective behaviour on the part of the animals (see A. D. Slonin, 1949, whose views on this subject I share).

When motivated by fright animals draw closely together. Shortly thereafter one animal stands out as the leader and the others follow. Fright motivation narrows the range of behavioural activities, but at the same time reveals new rules of behaviour. Thus in compact herds the individuals lose their independence of action and imitate their neighbours. B. J. Chotin (1947) was able to show experimentally that 76 percent of the reindeer and 100 percent of the sheep in experimental groups preferred to imitate their neighbours even though the neighbour's behaviour contradicted their own experienc

The locality determines the speed with which the animals congregate after they sense danger. Forest prevents the spread of excitation in the herd. The quality of forage on a pasture is also important. If forage is scattered the animals scatter and the herd as such may disappear. If the animals on one side of the herd are frightened, the other side of the herd may remain oblivious of the danger. The level of the fright response depends on the excitability of the animals and their reactivity. Excitability characterizes populations as a whole; it depends on genetic as well as on ontogenetic components, in particular the experiences of the population. Excitability also depends on the physiological state of the animal i.e. tiredness or illness. Sick or tired animals permit the progressive approach of hunters. The reactivity of an animal appears to be an individual characteristic, which depends primarily on the animals acquaintance with similar fright-inducing situations.

The fright response is least in animals within a herd. The expression of fright depends on the size of the herd (Baskin, 1970a). If the fright response is strong enough to overcome the psychological protection derived from being in the herd, then the animals seek rescue outside the confines of the herd (Naumow and Baskin, 1969). The first animal to move off is followed by others and becomes the leader. In herds of reindeer 20-29 percent of the animals may be potential leaders, but in a herd of 600 fat-tailed sheep from the Pamir I could only find four individuals (0.7%) that displayed leadership potential. In Turkmenia I found only 10-15 potential leaders among 800-900 adult Astrakhan sheep.

Sometimes juveniles can become leaders. When repeated attempts are made to catch a certain reindeer, it may bolt and take the whole herd with it. As a rule adult leaders are more important in herd management due to their greater experience. Such animals often have the ability to avoid danger. Young animals may act in accordance with naturally conditioned reflexes to various natural stimuli, but experienced animals respond primarily to the herder and thus permit him to manage the herd.

Big herds of juvenile animals are hard to control. They are easily frightened by the herder and may scatter in all directions: they can become unmanageable in their fright and may not stop for a man even if he appears directly in front of them. However, the herd can be brought under control by the addition of even a single older animal, which then becomes the leader.

It is common practice to mix goats and sheep together in a herd. Sheep may not leave a corral if the first snow significantly changes the known features of the land, but the

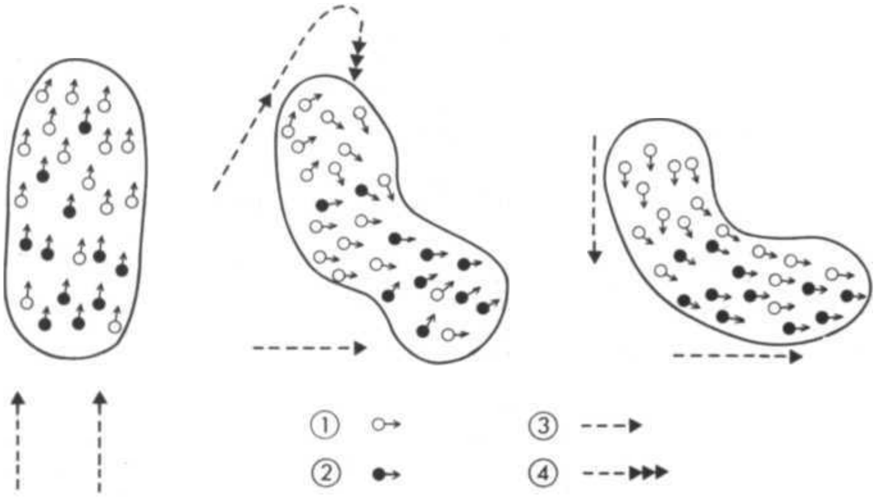

Fig. 4. Turning a reindeer herd by exerting the main influence on the animals at the rear: (1) reindeer; (2) potential leader; (3) direction of herdsmen's influence; (4) direction of shouts, stone-throwing, etc.

shepherd then simply chases the old lead goat forward and this experienced animal leads the way to pasture. It has to be a particular animal since not all goats act so independently; in the majority the 'herd-instinct' prevails. Goats usually keep together within a mixed herd. They are the first to follow a leader. They move somewhat slower than sheep when grazing and usually fall behind the herd; they also prefer crags and rocky places whereas sheep prefer flat terrain. In the absence of a shepherd sheep and goats would soon separate. I have never seen any sign of goats becoming natural leaders of sheep; they become leaders only when the shepherd gathers the animals into a compact herd and the movement of the lead goat then stimulates the sheep to follow.

When the herd is moving calmly, young animals are found in the vanguard. Careless shouting or movements by herders may make the juveniles turn and dash into the herd where they attempt to hide. The herdsman has to be very careful how he attempts to turn the vanguard of the herd. He may well turn the herd more successfully by first turning the older, independent individuals, which one finds at the rear of the herd and which respond quite readily, and only then alerting the young animals at the front of the herd. It has been found that it is better to shout signals that halt the vanguard, rather than signals that force the animals to turn quickly and to follow the leaders (Fig. 4).

Herdsmen concentrate their attention on the animals that act most independently. Sometimes it takes special means to find such animals. Goats of course are easily recognized in a sea of sheep, and the shepherd will concentrate on them to get the herd to do what he wants. But if the herd is large and consists only of sheep he may have to search for a long time to find an outstanding animal: he then moves it to the head of the herd and directs its movements by means of the hand motions described earlier, although he himself may be in the centre of the herd.

MANAGING THE CALMLY GRAZING HERD.

When undisturbed the grazing herd is dispersed and the animals maintain some distance between themselves and the herdsman. They move simultaneously in the same direction by responding to each other. The various behaviour patterns are in some flux: feeding may be terminated by satiation; or the herder's actions may frighten or calm the animals; or the distribution of individuals within the herd may arouse competitive reactions.

The herdsman has several methods at his disposal to synchronize the activities of the individuals, or to control each activity by intensifying or halting it according to his wishes. For instance, in reindeer, all feeding activity is halted when the herdsman quickly gathers the animals into a compact mass; once this is done, the animals quickly calm down and often lie down. On the other hand if the herdsman wishes to change the direction of a calmly grazing herd, he can do so by exercising minor disturbing influences: he may carefully shift animals from one side of the herd to the other, or he may slow down the vanguard of the herd or accelerate the speed of animals in the rear of the herd; in trying to get the herd to change direction, he always insures that the herd continues feeding. He steps in only if the herd begins to move in a wrong direction: his aim is to stimulate the fright response while keeping the animals grazing, as this maintains the allelomimetic behaviour of the animals. If herding is well done, then animals approaching a 'danger spot', such as the herder himself, simply look up, turn towards a grazing neighbour and continue grazing. In a badly managed herd, the animals get frightened, clump together and interrupt their grazing or, conversely, wander widely and are in constant danger of getting lost.

Ungulates tend to graze and rest in that part of a pasture in which they are least disturbed. If the herdsman wants the animals to avoid a certain place he simply makes his presence known by shouting: of course, if the place is particularly attractive to the animals, such as a salt lick, he may have to shout more than normally.

When studying the methods used by the best herdsmen, I marked on a map the direction of the moving herd, wind direction, the location of the best pastures, and the points where the herdsman was obliged to step in to correct the herd's movements. If the animals know the pasture well they move towards localities offering the most abundant food; and they also show a tendency to move into the wind. If this is contrary to the herdsman's wishes he blocks the herd's way.

The herdsman's task is relatively easy if the herd is moving in one direction as a unit. However, it often begins to move in two or more directions at once. When this happens, the herdsman uses auditory signals: he stops the part of the herd moving in the undesired direction and frightens it if it persists; the animals soon associate that part of the pasture with fright and thus turn to an area in which conditions are more peaceful (Fig. 5). If, however, the auditory signals are insufficient to turn the animals, the herdsman is forced to move to each part of the herd in turn. In broken, mountainous or forested country, he will need several other herdsmen to help him; this is usually the case on the summer pastures of reindeer in north-eastern Siberia, or on the sheep pastures in the hilly deserts of Turkmenia.

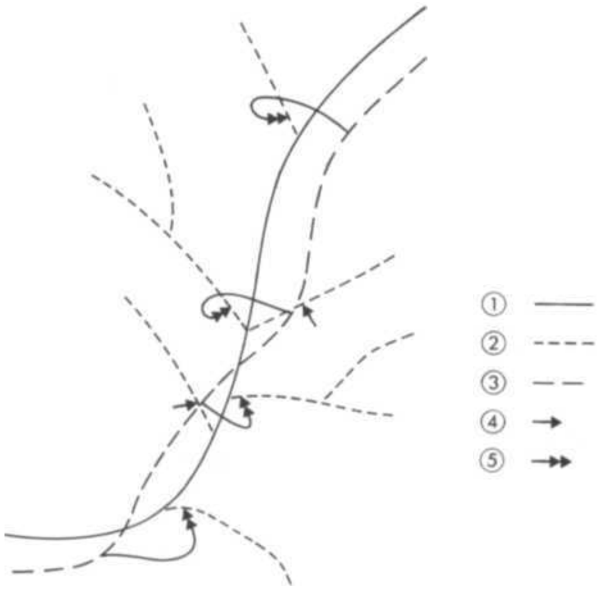

Fig. 5. Diagram showing the control of a herd of sheep: (1) general direction taken by herd; (2) attempted deviations; (3) track followed by herdsman; (4) direction of herdsman's influence; (5) herdsman deviates to shout, etc.

SOME HYPOTHESES OF UNGULATE DOMESTICATION.

The methods used to herd domestic ungulates may work with undomesticated ones as well. In Kamchatka we successfully directed the movements of wild reindeer with the aid of several herdsmen using draft domestic reindeer. In two instances herders succeeded in driving a group of 10-15 wild reindeer into a domestic herd. N. P. Naumov (1933) reports cases of large herds of wild reindeer being herded past their tents. On Wrangel Island there are five thousand feral reindeer. We were only able to approach them to within 1-1. 5 km on our first attmpt, but to within 50 meters on our third and fourth attempt and, finally, we were able to corral the animals. In the Caucasus Reserve we were able to control the movements of a group of wisent over several days and to draw the animals into a corral (Kalugin, 1968). In the Petchora region we have similarly had an opportunity of directing the movements of migrating moose and catch them in corrals (Josan, 1961).

The resemblance between the herding methods of different tribes suggests these methods are derived from a common origin, namely from ancient methods of following game herds by hunters that preyed on the herds.

Domestic animals are closely associated with man and are at his mercy. It is probable that when man changed from being a hunter to becoming a herder he retained stock in order to insure production and the availability of meat at a desired time. About 9-11 thousand years ago man discovered the possibility of managing ungulates that were kept in compact herds. This represented a neolithic economic revolution (Baskin, 1970b).

Ancient hunters undoubtedly followed the herds. They observed the behaviour of the animals and put these observations to good use when directing the movements of animals. They studied the herds' behaviour and realized its role in keeping the animals in their vicinity. It can be assumed that these hunters and primitive herders wanted to keep the animals somewhere near them during unfavourable seasons of the year, such as during winter in the North. Deep snow aids man in keeping the animals in areas of thin snow. In the sourthern areas the season of scarcity is summer when the water holes go dry: the Turkmenis, today, still catch feral camels near draw-wells.

Man could also use wolves to serve his purposes, since wolves by their very appearance keep ungulates in tight herds. It is conceivable that primitive man domesticated wolves to help him keep ungulate herds in compact units. Compact herds, however, quickly damage grazing grounds, so that herding and nomadism became linked. This hypothesis suggests that herding of social ungulates is a gradual development from hunting. Clearly, we will not be able to find direct evidence for the validity of this hypothesis. However, there is no doubt that the main principle in herding ungulates is to keep the animals in a compact herd and this principle has been handed down to us in the lore of our ancestors.

It is typical of herds to split into small groups if unattended by man. The size of these groups varies with the characteristics of the species. In the tundra in winter reindeer readily stay together in large herds as long as the localities with a soft and thin covering of snow are widespread. Once the snow becomes deep, the herds break up. Places suitable for foraging become fewer and more scattered, and small groups of reindeer form. Similarly, in the taiga in winter the reindeer separate into groups of varying sizes and remain more or less in the same localities throughout winter.

Wild sheep and yak live in small groups of females, juveniles, and young males during the greater part of the year. Adult males live alone or in small groups (Prater, 1947). Herds of domestic sheep often divide into groups of 20-30 animals, while domestic yak in Kirgizia prefer to keep in groups of 5-15 animals if they are females or juveniles, and 2-3 animals if they are adult bulls.

In Turkmenia free-living camels form female and juvenile groups of 10-15 animals which are accompanied by a male. When grazing, such groups break up into subgroups of 2-3 animals, which keep within 300-500 metres of each other. The camel's great height and its habit of gazing along ridges and sandy hills allows it to keep its companions in sight. As a result the unity of movement in a given direction is maintained. Such a herd structure is obviously useful in deserts with sparse vegetation. If the herd is under the direction of a herdsman, he gathers the animals together in a compact mass. Since man must keep the camels together if he is to control them he must travel and live with the herd. This obviously makes it difficult to alter and improve the herdsmens' way of life.

It is evident that one cannot change herding practices radically unless one abandons the principles of keeping domestic ungulates in compact herds. One desirable change would be to increase the distances over which herds could be managed. This would allow the reduction of labour costs and would permit the animals to live in almost natural conditions. It would lessen the harmful consequences of disrupting the natural structures of populations and biocenotic relationships. One example may illustrate this. Herdsmen usually cannot risk leaving the herd, because their animals are likely to stray over boundaries of the farm and are then difficult to retrieve. It would be useful to unite several neighbouring farms for the purpose of herding. One could not permit the animals complete freedom, however, since stocks of different races should not meet and hybridize. One cannot fence off the whole area of the farms. However, if the movements of the herds are known it would be possible to transfer the responsibility of herding and managing the migratory herds from farm to farm as the herds move through their respective territories.

One could possibly control herd movement and management over long distances by the use of mechanical barriers as well as scent markers, acoustic signals and the use of biotelemetry. The potential of well-trained 'cowboy' dogs is not yet fully appreciated either.

It is of interest to note how native 'herding schools' have solved the problem of herding ungulates over long distances by applying both natural laws of animal behaviour and also new methods of training animals. The first is exemplified by the herding of camels. Every morning experienced herders separate females from their unweaned yearlings and lead them to different parts of the range to forage. In many ungulate species if the dam and calf separate, both return to where the calf suckled last. Therefore the female camel and the yearling return 'home' themselves when the next suckling period approaches.

An interesting example of training is found among the practices of Turkmenian herdsmen. In accordance with tradition the shepherd stays constantly to the right of the animals. Consequently the animals are conditioned from their earliest youth to turn only to the left, away from the shepherd. The more experienced, older animals (including several goats) graze on the left side of the herd where they are furthest removed from him. During grazing goats move less rapidly than sheep. The left flank of the herd therefore tends to drop back to the rear of the herd. Here the animals are closer to the shepherd so accelerate their grazing to the left and ultimately form the left flank of the herd again. This results in a circling movement within the herd. Due to this rotation to the left, the herd movement is slowed down and no animals fall behind and are lost. Also, the shepherd has more control over the herd (Fig. 6). Incidentally, the herd continues circling to the left even in the absence of a shepherd, but after 2-3 days the circling weakens and gradually disappears (Fig. 7).

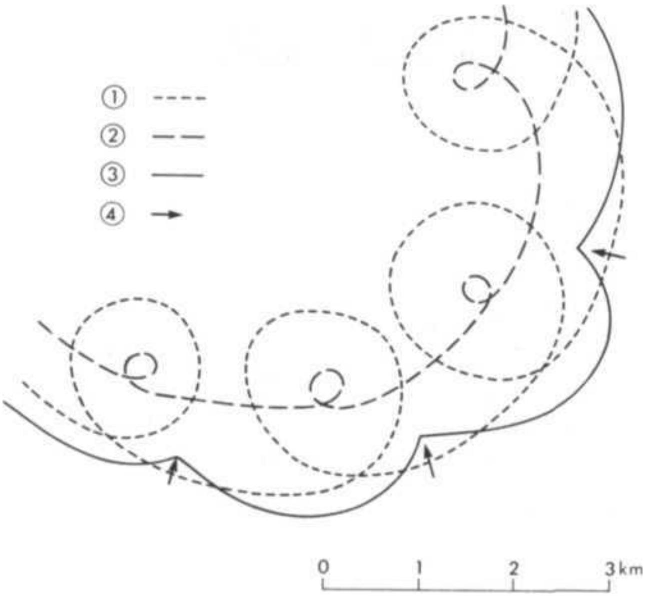

Fig. 6. Diagram of movements of sheep and shepherd in hilly desert: (1) track of the right flank of the herd; (2) track of the more experienced and slower animals on left flank; (3) track of herdsman; (4) points at which herdsman exercises influence.

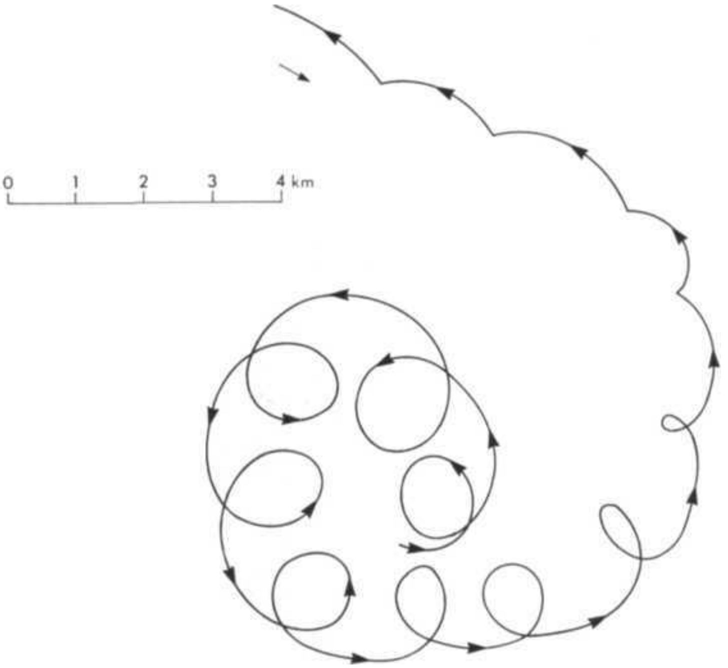

Fig. 7. Diagram of movement of herd of sheep in hilly terrain with no shepherd in control. The arrow at top indicates wind direction

The free pasturing of domestic ungulates without human control has a number of practical implications for the keeping of reindeer, yaks, camels and horses. One must be able to anticipate the direction of the animals' movements in order to find them. Amongst free pasturing livestock we find that groups assume a size and structure resembling those in natural populations. Domestic animals also choose the same sites for grazing as the wild animals. Free pasturing produces superior rates of body growth and fattening, and it allows a more even distribution of grazing which in turn aids in the conservation of the grazing grounds. However, free pasturing also has drawbacks: many animals are lost and fall victim to predators. The problems of locating and rounding up free grazing stock are not unlike those of hunting.

Some species of ungulates such as reindeer, saiga, gnu and zebras permit a rather large harvest. However, it is difficult to gather these animals for the purpose of slaughter at a convenient time, and to get the meat and other products to places of consumption. The reason for this lies in the low densities of the wild populations. We do have nevertheless some methods of gathering herds and driving them to a place of slaughter. This task is probably similar to that of ancient hunters when they tried to move herds closer to their living places.

We have followed a dialectic succession of steps in this study of managing herds of gregarious ungulates. We began with a study of native herding schools and hunters and their role in the domestication process, and have carefully considered certain aspects in the behaviour of wild ungulates and their domestic counterparts. Using the principles described, we should now be able to develop new methods for managing ungulate herds in the future.

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Paper No. 28

The Behaviour and Ecology of Camels in the Sahara, with Special Reference to Nomadism and Water Management

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ABSTRACT

Investigations of the ecology, ethology and physiology of camels indicate that they are the best domestic animals for hot desert conditions. Under free-grazing conditions they do not destroy the scattered vegetation since they take small parts of plants only and range widely. Their exceptional tolerance to dehydration permits them to use grazing grounds up to 80 km from the nearest well, a feat unequalled by other domestic stock. Camels compete neither with livestock nor with wildlife. Cattle can live in the southern semi-arid regions which are unfavourable to camels due to humid climates, insect pests and the absence of salt-loving plants.

Nomadism is essential to the maintenance of large camel herds that can exploit desert pastures. This way of life has survived to the present despite encroaching civilization. The pure nomad loves his traditional way of life, has subjugated himself to his herd's needs and lives in perfect harmony with his environment. It is not possible to turn nomadism towards what we call progress without precipitating its decay. In permanent settlements the nomad loses the physical and moral strength that allows him to overcome the extreme conditions of the desert. Yet these attributes of the herders are the only guarantee against starvation of the big camel herds during the drought period.

The desert pasture of the Sahara which cannot be exploited save by nomadism is home to over a million people. In Mauretania where $^4/_5$ths of the population are nomads or semi-nomads, nomadism retains the best chance of surviving. The generally deleterious effect of civilization on the native way of life can be balanced by improving the defective watering places, in particular by improving the utility of existing wells. Here an insignificant financial outlay that would strain the budget of no nation would significantly improve the welfare of men and animals. This welfare depends first and foremost on the availability of fresh water.

INTRODUCTION

The one-humped camel or dromedary was domesticated at least 3000 years ago. Even today whole tribes and populations in Northern Africa and the Near East depend on it. The life of these people may not differ greatly from that of the first camel breeders. Until a few years ago very little was known about the camel and most of the information was hearsay.

It is hard to visualize an association between man and animals more close than that between the nomad and his camels. The desert nomad can live only as a 'parasite' attached to his herd, and is forced to settle permanently should he lose it through illness or starvation. Camels, on the other hand, depend on man for water since nearly all watering places in the desert consist of wells of various depths. Most grazing grounds in the desert cannot be intensively grazed; this in turn dictates nomadism on the part of the camel herders. Consequently settling of nomads also endangers camel herding.

Even for those people who have settled, the camel retains its importance. In Mauretania, the prestige of a person still depends on the quantity and quality of his camel herds, may he be a minister or humble worker. The camel is of local economic importance as the main provider of milk and meat. It is indispensable as a beast of burden, despite increasing motor traffic. The camel offers free transportation, is adapted to almost all terrains, and is extremely hardy. On the other hand, car travel in the Sahara remains even today exhausting, expensive and even dangerous, and is not always faster than camel riding, if vehicle breakdowns are taken into account.

The following paper is not an ecological or ethological account of the camel; rather it focuses on the close relationship between man and camel in the desert and on the importance of maintaining this harmony. In a field study lasting two and one-half years, during which I was temporarily assisted by Miss R. Hartung, we investigated the behaviour and ecology of free-grazing camels in the north-western and western Sahara. During the study we lived with the nomads. We concentrated our attention on the extreme environmental conditions found in summer, when air temperatures exceed 40°C. In total we spent ten summer months in the field.

FOOD CONSUMPTION OF CAMELS

We investigated food consumption of 150 camels during 500 hours of observation at all seasons and on the different types of pasture available. Camels move continuously when feeding and only take small bites from each plant. Since the size of a bite of plant matter is rather constant for each plant species, it was possible to calculate accurately the amount of plant matter ingested by counting the number of bites, and weighing quantities of plant matter corresponding to the size of a bite. This appears to be the only method possible, since vegetation is distributed in a most irregular manner and the camels are widely scattered during grazing. Camel herds cover more than 20 km while grazing during a day.

Camels have seasonal food preferences which are independent of the moisture content of the plants. They often prefer dried plants to green ones, even in summer. Plants which provide the bulk of the forage during one season may be neglected in the same locality during another season. We identified about 200 plant species, mainly perennials, but rarely found more than 15-20 on one pasture.

Camels can thrive on the hardest, driest and thorniest plants. Thorns as long as seven centimeters are eaten, and the thorny acacias are among the favorite forage plants. It is amazing to find in how good a condition camels are on the poorest feeding grounds, even during the middle of summer.

The animals spend 8-10 hours a day grazing, irrespective of whether the pasture is good or poor. During summer, camels feed mainly at night, particularly during moonlit nights, and then rest from morning until afternoon wherever they happen to bed down. The highest food consumption of 30-40 kg fresh forage (8-12 kg dry weight) was observed on salty pastures and pastures containing annuals. These plants contain up to 80 per cent water. The lowest food intakes (5 kg/day) were noted from dried grass pastures and when the animals grazed Acacias. The latter are eaten slowly due to the woody and thorny branches.

PRODUCTIVITY AND CARRYING CAPACITY OF SOME PASTURES

In the regions that we visited in the north-western and western Sahara the annual food consumption of a camel varies between 2-4 tons of forage dry weight. This amount is small relative to the existing forage reserves, which are under-utilized in many regions.

Plant production can be illustrated by two typical grass-pastures of the western Sahara. The first is characterized by *Aristida pungens,* common to all deserts from the Atlantic to Central Asia, and the second pasture by *Panicum turgidum.* Both these plant species are very important food plants for camels, and are taken year round, be they green or dry. *Aristida* pastures are found typically on deep, sandy soils (dunes). Their productivity is very high. An average vegetation cover of 10 per cent is quite common over large areas, particularly when bordering big dune regions. Shrubs on these pastures may reach a height of 1.7 meters, and may be almost completely consumed. Because both flowers and stalks are eaten very slowly, food intake is very low: 5 kg/day. The average plant production on this kind of pasture is about 220 tons of dry matter per 100 hectares. This represents a food supply sufficient for 300 camels for five months. Hence 100 km^2 of *Aristida* pasture may feed 30, 000 camels for five months. Camels do move a lot while grazing even on the best of pastures and vegetation density varies greatly in large areas. Nevertheless the calculations suggest that a large herd of camels could be kept on such a pasture for a long period of time.

The second type of pasture, dominated by *Panicum. turgidum,is* generally less extensive in area than the *Aristida* pastures. They are localized in depressions and river beds on sandy soils of lesser depth than those found under *Aristida.* cover. *Panicum* pastures are very common in the central and western Sahara, and are often found along wadi-systems. *Panicum* sprouts at the slightest rainfall. Productivity is only one-third that found on *Aristida* pastures, about 80 tons dry matter per 100 hectares, while the average plant cover is only 8 percent. Theoretically, 80 camels could subsist on that amount of forage for five months. This would be a very high density of camels compared to actual grazing densities and is hardly ever realized. The productivity of this type of pasture compares favourably with pastures in South-West Africa where average rainfall reaches 100 mm (Walter, 1970).

Camels must often live on less productive pastures. In regions where the average annual rainfall is below 100 mm, the vegetation can be utilized only by highly mobile animals like the camel. Their low food requirement correlates with the sparseness and irregular distribution of the vegetation. In Mauretania we made measurements within grazing exclosures as well as outside and found that the grasses grew best outside the exclosures under regular grazing by camels. This did not apply where goats were allowed to graze the pasture. However, trees grew better in the exclosures.

Free-grazing desert camels, which take little food compared to their adult body weights of 300-500 kg, are much more hardy than camels from rich pastures in semi-arid regions. During months of travel our riding camels rarely obtained more than 10 kg of fresh forage per day, and still retained their capacity for work. The search for new feeding grounds over large areas is a constant exercise for free-grazing camels, which keeps them fit.

WATER SUPPLIED BY FORAGE

Camels can subsist for months without drinking on dry, almost monophytic pastures. The desert vegetation supplies the grazing animal with more water than is generally believed. In the regions we worked in, the amount of water in the ingested vegetation varied from 3-30 litres/day/camel, depending on season and the locality of pastures. These could be found on dunes., rocky plains, in wadi-systems or in salty areas.

The same terrain may have different plant communities, each providing different quantities of water. Thus the sand dunes in Mauretania have a different vegetation from the sand dunes in Algeria. In the big dune region of Algeria, the vegetation is made up mainly of shrubs which remain green even in summer. This is due to their long roots and the moisture trapped in the dunes. Even in summer camels may ingest up to 15 litres of water with the food per day per animal. The water content of the shrubs varies little over the course of the year. In the dune regions of the western Sahara one finds only grass pastures which dry up in summer. At that season a camel ingests on such pastures no more than one third of a litre of water per day with its food.

The variation in vegetation types on similar substrates can be illustrated by a second example. On the rocky plains of Algeria, in depressions and dry river beds, trees are scarce and the water content of the vegetation falls considerably during summer. On these areas in summer camels ingest at best one sixth of the water they obtain through grazing in spring. In Mauretania, on the other hand, we noticed more grasses and shrubs, as this region is subject to some summer rains: trees and shrubs, remaining green in summer, are frequent in dry river beds.

DRINKING RHYTHMS

How long a camel can go without drinking depends on meteorological factors, on the quality, quantity and water-content of the forage, on the age of the animal and its work load. The general figures quoted by most authors are of little value here.

During the cool seasons, when the vegetation is fairly green (water content 40-60%), camels can go up to six months without drinking. At this time the herds spread over a large area, and can exploit pastures which are out of reach in summer due to the absence of wells. Even working animals can go for as far as 1,000 km at this season without drinking (Monod, 1955).

When temperatures during the day reach the 30-35°C range, camels begin to visit drinking places. However, only when the daily temperature exceeds 40°C does their drinking rhythm accelerate and become regular. They visit wells at intervals of not less than 3-4 days, except when feeding on salty pastures. A drinking rhythm with such short intervals has been observed only during a six week period when temperatures at night remained in the 30-35°C range. Not only food, but also meteorological factors determine the drinking rhythms: in spite of high daily temperatures, slight meteorological changes such as a succession of relatively cool nights or an occasional rainfall extend the dehydration period by several days. In the Spanish Sahara, which is influenced by the maritime climate and in northern Mauretania, where cool winds and dew often occur in the middle of summer, dehydration periods may last up to ten days in summer. In central Mauretania, where the summers are longer and hotter, herds feeding in the dunes on dry grass pasture go only 3-4 days without drinking. On the rocky plains, where green grasses and shrubs are more frequent, the drinking rhythm is a few days longer. In southern Algeria, under similar meteorological conditions as in central Mauretania, we find that camels on rocky plains have a shorter drinking rhythm. These plains have rather dry vegetation forcing the camels to move about considerably between widely separated feeding grounds. In the big dune regions with their green shrubs, on the other hand, the drinking rhythm is extended to 4-7 days. When daily temperatures are below 40 °C, and the vegetation is not too dry, camels need not drink for 10-15 days. Herds unguarded by man, which are able to graze during the night, generally drink less frequently than guarded herds.

If water is freely available, as in rain pools after rains, the nomads water their herds daily in order to make camels feed more and increase their rate of fattening. In regions with few watering places, camels withstand dehydration better than in regions where camels have more frequent access to water. It is not known to what limits a camel may dehyrate since no camel owner will allow such an experiment. The appetite of camels decreases with severe dehydration, but not till the animals have dropped one third in body weight.

DRINKING WATER CONSUMPTION

The first investigations of the water metabolism of camels were made by K. and B. Schmidt-Nielsen of Duke University and their collaborators in 1954/55 in southern Algeria. They stated that camels do not store water in the rumen as had been asserted previously, nor does the hump play any part in the water metabolism. Camels drink just as much as the water lost in urine, feces and sweat during the previous deprivation period. Within two days the water drunk is evenly distributed throughout the body. Camels have a slow rate of water loss due to an adaptation which allows their body temperature to rise from 34°C to more than 40°C during dehydration. Excess heat is stored in the body and dissipated during the cooler temperatures at night without the animal losing water. The elevated body temperature reduces the heat flow from the hot environment to the body, and the camel begins to sweat only at the maximum body temperature. The fur of the animal acts as a barrier against environmental heat gain (Schmidt-Nielsen *et al.,* 1956, Schmidt-Nielsen, 1964).

According to the Schmidt-Nielsens and their co-workers, who were in the position to weigh their study animals, camels can tolerate a dehydration equivalent to 30 per cent of their body weight. For most mammals, including man, dehydration of 20 per cent is fatal. In the camel the blood plasma volume remains almost constant, thus maintaining circulation, while water is withdrawn from the extravascular space. Indeed, according to our investigations camels seem to tolerate a water loss exceeding 40 per cent of their body weight. Owing to this exceptional tolerance to dehydration and their slow rate of water loss camels can go without drinking longer than any other domestic animal.

We have measured the water intake on more than 800 occasions and in more than 500 camels, mostly in summer. Their capacity for drinking is very great. When the water loss incurred by the animal does not exceed 90-100 litres, which may correspond to 20 per cent the normal weight, the camel regains its original weight within a few minutes after drinking. If the animal is severely dehydrated it must drink two or three times over the span of a few hours to reconstitute its weight. However, it was found that camels in a good condition may drink the equivalent of almost one third of their body weight in about 10 minutes. The largest quantity of water ingested by any camel was 135 litres in 13 minutes. On the average camels drink 15 litres per minute. The highest total intake noted among several individuals in 2-3 drinking sessions was 200 litres. This far exceeds one third of the body weight. Even if this quantity is exceptional, since most camels drink only 120-140 litres at a watering in summer, it does indicate how resistant these animals are to desiccation.

Only well fed camels are capable of replacing even a high water loss in one single watering, thus sparing more time for grazing and not wasting a day at the well where there is nothing to eat. This gain in feeding time increases their capacity to drink. It is therefore most important in summer to maximize feeding time, particularly if pastures are far from the well. Conversely, normal grazing requires sufficient water.

Different authors have suggested that the more camels become dehydrated, the less they lose water (Schmidt-Nielsen, 1964, Charnot, 1960, Clair, 1962). It appears that under natural conditions water loss seems to diminish only after 4-5 days of dehydration, but exact observations are still missing.

SOCIAL BEHAVIOUR

(a) Free-living herds. Due to geographical and climatic conditions, camels are often managed in a semi-wild state. In different regions of the Sahara, such as southern Algeria, Tripolitania or Tibesti, herds are left on their own for 4-5 months in summer. The animals are used to returning to the same wells where their owners remain for the whole watering period. The old habit of nomads of returning to the same wells is generally noted among those tribes whose movements are of limited distance between favourable grazing grounds. In these districts camels mate at the beginning of the year, and there is no further danger of rutting males meeting accidentally and fighting. Nevertheless, a fight occasionally does break out. I watched a particularly violent encounter between two males in July, in which both would have suffocated each other, had it not been for the intervention of man. Camels attempt to suffocate the rival by bearing down on his neck.

Unguarded groups join together freely and the resulting herds may be stable in composition during the watering period. One encounters mixed groups of females, juveniles and several males led by an elderly female; small groups of females with offspring; and bachelor herds of males. Some of the old males as well as a few females with their young may go off by themselves. Camels are difficult to separate from their groups. I saw camels separated from their companions by their owner for work purposes, wait for days at a well for the return of their own group despite the fact that virtually no food was available at the well. Foals may leave their mothers to join a passing herd. French officers of the Camel Corps have related their experiences of how difficult it was to make a camel arbitrarily leader of a group.

(b) Guarded herds. During the mating season, herds are always kept under guard. Their composition is then determined by man. Male camels do not tolerate each other in the presence of females. They are somewhat intolerant even of castrated males and may be dangerous to man. Nomads have been killed by camels in the same way that camels kill rivals.

During the mating season one finds three types of herds: herds with one male and up to 30 females plus their one-year and two-year-old offspring; bachelor herds consisting of males; and herds of females with small foals. The breeding male keeps to the rear of the herd where he watches his females and keeps them together in one group. The herders take care to keep the different kinds of herds apart. Female camels breed every second year. The lactation period may last up to 16 months. Foals several months of age are however prevented from suckling during the day by covers placed over the teats of their dams. Thus the nomads who live largely off camel milk conserve milk for their own use.

In the western Sahara, the main nomad country, herds are guarded year round. Wells are few and far between, pastures are widely dispersed, settlements almost lacking. Movements are determined by rainfall and the necessity to move between the different types of pastures found on rocky, dune or salty soils. Many nomads travel in excess of 1000 km a year with their herds. Rich nomads who own more than 1000 camels, usually keep only lactating female camels close to their tents, while their remaining camels graze in herds which may be several hundred kilometres away. These herds are guarded by herders and their families. The search for new grazing grounds requires extreme mobility of man and animal, not to be found in big tented communities due to their dependence on wells in summer.

Rich nomads have parts of their herds guarded by poor relatives who, in turn, are allowed to use the camels as beasts of burden, as well as the milk and wool of the animals.

The management of camels in big herds as practised in the western Sahara makes for the best use of grazing grounds. The long distances between grazing areas and water have led to the breeding of hardy stocks of camels, which are most resistant to dehydration and capable of covering great distances on little food and water. In the Algerian Sahara semi-nomadism prevails, the herds move rarely more than 30 km from the wells in summer, whereas in the western Sahara they may move in excess of 80 km.

BEHAVIOUR OF CAMELS WHILE MARCHING AND RESTING

On the way to and from the watering places, camels move single file after an elderly female, while small foals keep together in a group. The animals follow winding trails that circumvent obstacles, as is typical of animal trails (Hediger, 1962). These trails may be very old. A concentration of trails always indicates the proximity of a well.

Camels show certain orientations and behaviours while resting which reduces dehydration. During the hottest hours of the day, they huddle in small groups on the ground. By pressing their bodies together they reduce the body surfaces exposed to the sun. There is less heat-flow between camels than between the camels and the surrounding environment. The surface of the fur exposed to the sun may heat up to 80°C (Schmidt-Nielsen, 1964). The compact resting groups are found most frequently on dunes, where the soil surface heats up most. Resting camels always face the sun and remain all day on the same spot, but adjust their position to the moving sun. In this manner they expose as little of the body surface to the sun as possible. If they had to change places during the day, they would experience a considerable influx of heat from the ground through their underside.

HOME-RANGE FIDELITY

Camels do not return readily to the camp of their owners, but they do return to places which they associate with something faviourable, i.e. wells. Certain nomads in southern Mauretania give their camels salt at specific localities such as a certain tree since in this region salt plants are absent. The camels return to these salting areas regularly, a fact which facilitates herding. Camels also return to good wells and pastures, which allows some tribes to be less mobile and let their herds roam freely in summer.

Camels are closely attached to their home ranges, which are exceedingly large in migratory herds. This makes the guarding of displaced camels difficult. In the western Sahara, where herds are usually guarded year round, one still finds individuals or herds that have escaped. Years after separation from their original home range, displaced camels still have the tendency to return to their original home range, and their owner sometimes finds them 1000 km away from the place they were lost. Females are particularly prone to return to the area where they first foaled. For this reason the nomads are anxious to buy a female camel before she gives birth to her first foal, if they intend to move her to a different region.

Officers of the French Camel Corps have collected many experiences in this matter. They stated that camels not only escape to their old home ranges, but may also move to feeding and watering places, outside their home ranges, with which they happen at some previous time to have become familiar. Such localities may lie several hundred kilometres from their normal home range. The camels move at 5 km per hour, not trotting, and may thus cover up to 100 km in one day. They possess a faculty for finding remote localities by the most direct route. Under favourable wind conditions, it is said that camels can perceive water pools and fresh pasture from a distance of 40-60 km. After heavy rainfall, some pools may of course be several kilometres in length (Denis, 1970).

The risk of losing newly displaced camels is particularly great after rain has fallen. On many occasions during riding I noticed how our camels turned their heads in the direction of heavy rain clouds on the horizon from where the wind blew, and tried to head in that direction. It often happens that one escaping animal takes along the whole herd. Such things as cars, planes, or strange persons cause frightened camels to gather in a tight bunch and flee. Camels are easily frightened, especially by uncommon optical stimuli. They are said to be insensitive to gunfire, but they do run off if a small piece of baggage becomes loose or the rider makes an unusual movement. If packs slide off the whole herd may panic and run off a long way (Denis, 1970).

Camels often imitate each other's activities, such as rolling in mud or in soft, sandy soil, rubbing on trees etc. A good leader is followed by the whole herd. An Arab proverb states that even a rat can lead a camel herd. Individuals which have been wandering for a long time are difficult to approach. Foals which lose contact with their herd remain in the locality where they lost contact for a few days. Such foals can be approached only when one is mounted on a camel, since the foals flee from men on foot (Denis, 1970).

Some nomads spend a good part of the year searching for lost animals. Instead of running after the escapees, they go from well to well before the end of the watering season because camels return to the wells they know. In summer time, escaped camels are easily distinguished from herded ones by their good physical condition. Such animals graze freely while guarded camels usually have their forelegs tied together at night.

Every nomad waters his own camels. Lost animals are not watered at the well, in order to hold them there and thus help the owner to find them. Camels cannot drink without help at wells since most wells are deep. One often finds dead camels close to wells, as well as the graves of persons that died there of thirst or in the battles which usually took place around water holes.

As soon as the daily temperature drops below 35°C camels drink less frequently, and start to stray away from wells altogether; they may not be found for months by their owners. Lost camels are mostly located with the aid of the 'Arab-telephone', communication from mouth to mouth which works well over hundreds of kilometres. The nomads are well acquainted with the footprints of their own animals as well as with the brands used by different tribes and families on the necks, faces and legs of their camels.

IMPORTANCE OF NOMADISM

Camel herding can be done by a few herders, thanks to the docile and gregarious nature of the animal. Nevertheless, camel management requires the periodic collaboration of the whole tent community which cannot be replaced by paid herders. Joint effort is required not only in the search for lost animals or new pastures, but also during the cleaning and repair of wells, and especially in watering the herds. At crowded wells some herds may have to wait their turn for one or two days.

Camel herding and nomadism are closely linked. The grazing grounds of the desert can only be exploited because of the great mobility of the herders and their herds. The greater the mobility the greater chances of avoiding drought. Nomadism makes large land areas useful which could not otherwise be exploited. The nomad always accommodates himself to the needs of the camel, his only means and reason for existing. His permanent struggle for survival depends on special qualities, such as great physical endurance and level-headedness, an ability to make decisions quickly, great confidence in himself and his abilities to master unforeseen events, as well as his infallible sense of orientation. He betrays little fear, doubts or worries. He is always on guard—a product of his lonely life. For the sake of the herds he must have the inner strength to resist the temptations of any easy life which is offered by encroaching civilization. In spite of roads, settlements and construction sites, with their easy access to food and water, he must maintain the normal movement patterns and feeding rhythms of the herd. Such nomads are free from the attachment to material things, they are satisfied with their traditional way of life and aspire to no change.

Nomads, who still live in harmony with the desert, are to be found in the western Sahara. There are few settlements and little economic development. Here endless rocky plains contrast with green wadis, bare mountains and enormous sandy areas. Pastures on rocky, sandy, and salty ground force the nomad to make long migrations. One tribe, which still displays its native vitality, the Reguibat, lives in an area encompassing about 600, 000 km^2. They are considered to be the greatest camel nomads of the desert: most members of the tribe are pure nomad who travel up to 1000 km annually with their herds. None of them are semi-nomads, and only a few have settled permanently due to the scarcity of villages. It is remarkable that the Reguibat were originally sedentary cultivators, then semi-nomads herding sheep, before becoming camel nomads. After they defeated their rivals at the beginning of this century they became the region's greatest tribe. Only after peace was definitely established in 1934, did they become nomads perfectly adapted to the desert. We spent half the time of our investigation in close contact with this tribe.

THE NEGATIVE EFFECTS OF SETTLING NOMADS

Any reduction in the mobility of nomads and their herds leads to over-grazing of pastures, most readily seen in the vicinity of wells and villages, while on the other hand some large pasture areas remain unvisited and unutilized. Roads, construction sites and railways tempt nomads to an easy life as they permit them to obtain food and water with less effort. We came across nomad camps that had remained for months or even years on the same spot. This resulted in deterioration of pastures and the condition of the herds. Nomads with small herds, which make small seasonal movements only, are most susceptible to the factors mentioned.

Restrictions imposed on the movements of the nomads are often the first step towards settling them. It is only in exceptional cases, such as the loss of their herds, that these people are settled quickly. Usually it is done gradually, but the effects on the vegetation and herds as well as well as the wildlife and the people themselves soon becomes noticeable. Political reasons are often decisive in settling nomads; the movement of these people is dictated by pastures and wells and cross political borders. Sometimes humanitarian grounds are cited as reasons for settling nomads; however these are not justified, with the exception of the case of very poor nomads. A successful nomadic life does depend on a certain capital in camels.

For the nomad whose health and standard of life is superior to that of the sedentary population, settlement means physical, moral and, unless some lucrative activity replaces the traditional way of life, also social decadence. The change from nomadism to settlement is generally irreversible. Settled nomads indeed maintain a nostalgia for the open desert and their herds, but they soon lose their stamina and ability to tackle the hard life of nomadism, once they are settled. Today the villages have grown to exceed their capacity to generate employment, so that one of the accompaniments of the settling of nomads has tended to be total unemployment. Economic development has not yet provided permanent employment and, moreover, nomads are by their nature less well adapted to regular work than villagers.

In comparison with Mauretania, nomadism in Algeria is being rapidly reduced. The number of camels is declining, nomadic movements are more limited, stays at oases during the summer more extended, while motor vehicles are becoming increasingly more important as a means of transportation. In Algeria nomads have been in longer and closer contact with Europeans than in Mauretania. The numerous villages and increased economic development act as attractions. In Algeria there are but few pure nomads left, but there are many semi-nomads and settled tribes.

The effect of settlement may be illustrated by the example of Beni-Abbe's oasis in southern Algeria, which I have visited several times within the last 17 years. A considerable population increase has occured over that period. The dune pasture, which a few years ago was excellent summer pasture, is now severely degraded. An increasing demand for firewood, construction material and food for the goats has led to the commercializing of the most important forage plants and trees. Previously, the long summer stay of nomads at this oasis with their free-ranging camels did little harm to the vegetation. Today, nomads extend their stay for commercial reasons well beyond the summer months, increasing still further the demand for firewood. As a result, plants of little forage value have increased on the overgrazed ranges and the herds are in poor physical condition. Conservation of pastures on the dunes would be most desirable, since they are adjacent to pastures on rocky and salty soils. It would also contribute to the maintenance of the semi-nomadism, which is best suited to the region. Here the nomads may own palm trees in the oasis and obtain an income and extra food from military sources: they are used to an easier way of life than the nomads of the western Sahara who are sustained by different types of pastures. The villagers could also well be encouraged to cultivate fodder grasses for their domestic animals and to use fuels other than wood.

The deleterious effects of settlement on wildlife deserve mention. The number of cars has increased. Dorcas gazelles (*Gazella dorcas*) are being persecuted with the aid of vehicles, since hunting is often the only distraction in remote places. Thus during a four-week ride in the summer of 1971, through the rather well vegetated grazing lands of northern Mauretania, we only saw two gazelle tracks, although our guide was one of the best hunters in that region. In southern Algeria in 1969, we saw only a few lonely gazelles, where in 1955/56 we had seen large herds of these animals.

ADVERSE CONSEQUENCES OF INEFFICIENT WELLS

A factor which affects the welfare of man, herds and pastures in the desert is the proper construction and maintenance of wells. All considerations on how to maintain nomadism in spite of increasing development of arid regions, are in vain unless due regard is given to the supply of water on which man and beast depend. Many of the watering installations in the main nomad country are very defective. It is just as important to equip already existing wells properly as to bore new ones. This has been done on a large scale only in the southern, semi-arid regions which are important agriculturally. Yet it is in the arid regions, where all life depends on water, that improvements of wells are essential.

Out of 50 wells visited in the western Sahara, in regions with high camel densities, just three were well adapted to the needs of camels, the available water yield and the existing grazing opportunities. Two of these were in villages. At most wells, watering is done from one or two barrels. This at best allows four camels to drink simultaneously. Yet in summer large numbers of animals, camels, sheep and goats, are lined up at the wells daily, with some herds waiting days for their turn. In some places where some form of trough or basin is provided, it is generally unsuited to the drinking habits of camels and the water is easily wasted.

Most wells in favoured regions are not ringed by a stone wall, which is indispensable to prevent water pollution. This makes frequent cleaning operations necessary which brings watering to a halt for hours. Excessively deep watering tanks at ground level often provoke accidents. Simply pulleys, for lifting water and easily constructed with local material, are missing at many productive wells. Temporary waterholes could be made to yield more water by deepening and encasing them. Finally, stone pillars placed close to wells and visible at long distances would sometimes save not only the lite of strangers but of natives as well. Every year about 50 persons die of thirst in the desert, many of them in the vicinity of a well.

Improvements of existing wells would accelerate watering of the herds which in turn would reduce overgrazing on pastures close to wells and allow the animals to return to grazing more quickly. This would lead to a better utilization of the forage and improved conditions for the animals. Many herds have to trek in high temperatures for two or three days to reach wells which are crowded: they arrive severely dehydrated, poorly fed and thus unable to compensate the entire water loss, with consequential loss of productivity.

Construction of new wells is needed on grazing areas which are presently under exploited and much more extensive than is generally believed. However, prior to such construction a complete study of the forage reserves should be made, and the water yield adapted accordingly. Artesian wells, which require a minimum flow of 500 litres per minute to be profitable, are costly and are ill suited to desert conditions. They produce water out of all proportion to the carrying capacities of the desert ranges. Vegetation density must limit the number of animals to be watered; the water yield of a well, on the other hand determines how often pastures must be changed. Several big wells in the southern Sahara yield 300 litres per minute, enough water for 600 cattle and 50,000 sheep. This is the very limit which even the best of pastures in semi-arid lands can carry. It is essential to space wells sufficiently far apart to ensure that grazing areas will not overlap.

Paper No. 29

The Role of the Environment in the Aggregation, Movement and Disturbance Behaviour of Caribou

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ABSTRACT

The aggregation, movement and disturbance behaviour of caribou (*Rangifer tarandus*) is discussed in relationship to the interaction of the extrinsic environmental factors:

1. other animals (wolves, insects, and caribou);
2. a-place-in-which-to-live (open habitats);
3. food (slow growing plants); and
4. weather (snow and wind).

It is hypothesized that wolves interacting with caribou in open habitats have been a consistent contingency resulting in the formation of nursery bands during calving. The gregarious herd structure during the rutting season is also believed to be a consistent contingency resultant from the intraspecific interaction of caribou in open habitats. It is also theorized that disturbance behaviour results from the above interactions. Movement and aggregating behaviour vary with various phases of the annual cycle and appear liable to adaptive modification. These facultative responses seem to be due to the interactions of the variable environmental contingencies of food × weather and a-place-in-which-to-live × insects.

INTRODUCTION

It is my thesis that caribou evolved in the relatively simple and open taiga-tundra biome and that early in their history they were preyed upon by wolves. Faced with an effective predator in a habitat lacking concealment, natural selection promoted a synchrony in activities and hence gregarious herd structure. However, the gregarious social structure was not compatible with a sedentary life in an environment dominated by slow growing plants whose availability in space and time varied with snow conditions. Thus, mobility had selective values and caribou developed their characteristically restless mode of life.

In order to illustrate this hypothesis, I have constructed a model of the interaction of the extrinsic environment on the aggregation, movement and disturbance behaviour of caribou (Fig. 1). The environmental components considered in the model are: (1) other animals, (2) a-place-in-which-to-live, (3) food, and (4) weather. These four environmental factors were considered by Andrewartha and Birch (1954) to be the functional components of the environment that could be used to explain the distribution and abundance of animals. They further indicated that 'other animals' should include animals of the same species and argued that the environment of every individual is different from the environment of all other members of the species, in that its environment includes the other animals of the species but excludes itself.

I will argue that the interaction of a-place-in-which-to-live (relatively open habitats) with other animals (wolves and caribou) is a consistent contingency in the life of caribou which requires obligate adaptations. Such adaptations would arise through natural selection and be primarily of a phylogenic origin. In contrast, the interaction of the environmental components of food and weather and other animals (insects) and a-place-in-which-to-live (open habitats) are variable contingencies which require facultative responses.

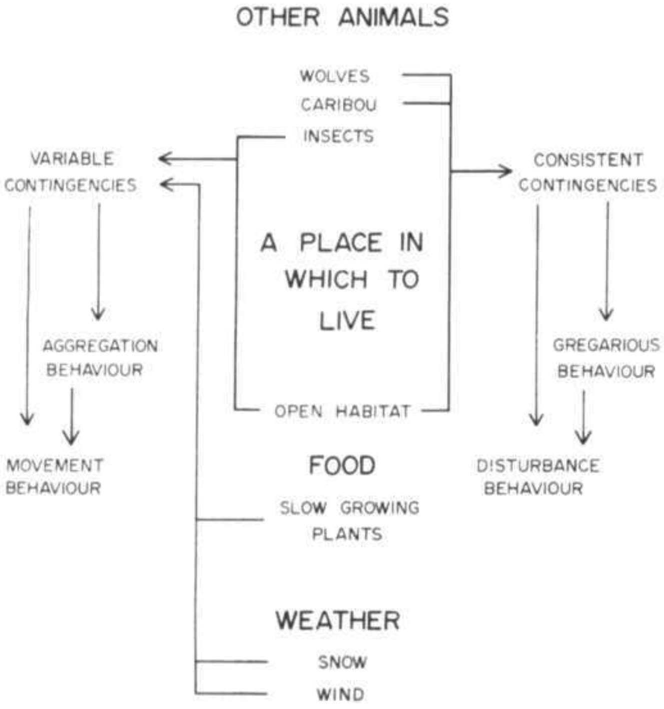


Fig. 1. Diagram of the proposed manner in which the four components of the environment interact as variable and consistent contingencies in the development of movement, aggregation, gregarious and disturbance behaviour of caribou.

Even if adaptive modification is shown, its basis would still be in the genome (Lorenz, 1965); the ability to show a variable response must itself have been selected for. Such phenotypic plasticity would suggest that environmental variability must have been a past contingency with which caribou had to cope.

Certain management implications merit attention, if such a distinction between facultative and obligate behaviour patterns is valid for caribou. Behaviour patterns that are fixed in the genome will require considerable time for alteration as the environment changes. Facultative modifications can be more rapid.

The data in this paper are based primarily on my observations of caribou in Newfoundland from 1957 to 1966 (Bergerud, 1971a). When possible I have tried to amalgamate these findings with those described for barren-ground caribou in Alaska and Northern Canada. Recently two extensive monographs have been published on these two populations by Skoog (1968) and Kelsall (1968). These monographs summarize and re-interpret numerous earlier studies and are quoted extensively in an attempt at a synthesis for North American caribou.

This paper discusses aggregation and movement behaviour by dividing the annual cycle into eleven periods: (1) pre-calving, (2) calving, (3) post-calving, (4) fly season, (5) fall shuffle, (6) pre-rut, (7) rut, (8) post-rut, (9) fall migration, (10) winter and (11) spring migration. Following the treatment of the annual cycle sections is a brief account of disturbance behaviour and the management applications of the model.

AGGREGATION AND MOVEMENT BEHAVIOUR

Pre-Calving and Calving

In Newfoundland caribou females were widely scattered in small aggregations in the pre-calving period (Fig. 2 and Table 1). Females did not appear to seek seclusion at calving but simply failed to keep up with other animals when in labour and thus were frequently alone at parturition (Table 2). This was also Lent's (1966a) and Kelsall's (1968) conclusion for barren-ground caribou.

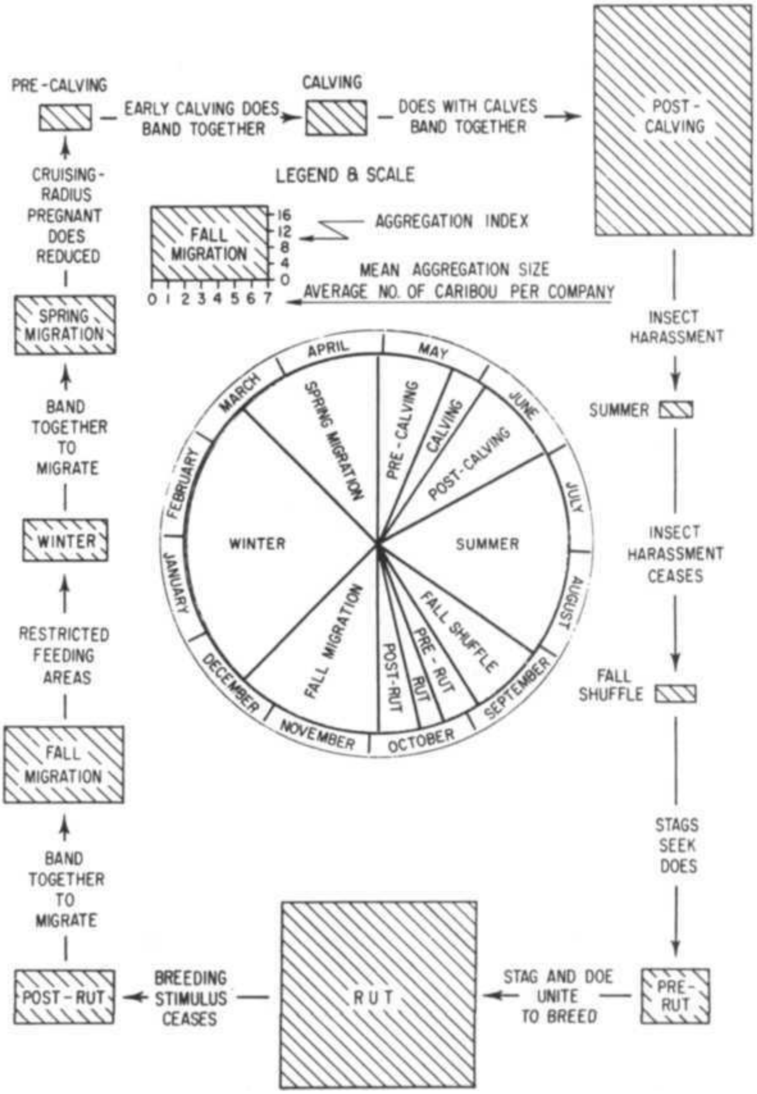


Fig. 2. The annual cycle of aggregating behaviour in caribou in Newfoundland (see Table 1 [bottom] for explanation of aggregation index).

TABLE 1. MEAN AGGREGATION SIZE AND AGGREGATION INDEX IN NEWFOUNDLAND

Aggregation Period	Dates of Period	Caribou in Sample	Aggregation Size Mean	Aggregation Size Maximum	Aggregation Index[1]
Pre-Calving	May 1-23	1,256	2.8	48	7.0
Calving	May 24-June 2	5,395	3.4	57	7.9
Post-Calving	June 3-30	10,835	9.8	250	55.6
Fly Season	July 1-Sept. 6	396	1.9	10	3.4
Fall Shuffle	Sept. 7-30	437	2.5	17	5.3
Pre-Rut	Oct. 1-8	1,180	4.2	52	12.3
Rut	Oct. 9-18	1,660	11.5	176	44.7
Post-Rut	Oct. 19-31	1,936	5.8	67	13.3
Fall Migration	Nov.1-Dec.14	3,304	7.3	102	19.1
Winter	Dec.15-Mar.13	3,548	5.0	38	10.1
Spring Migration	Mar.14-April 30	3,620	6.0	50	14.9
Total and Means		33, 567	5.5		17.6

[1] Calculated ($A_1 \times 1 + A_2 \times 2 + A_3 \times \ldots A_n \times n$)/Total Animals, where A_2 = total animals in aggregations of 2 animals. The aggregation index is weighted by the number of animals which are motivated to remain together, i.e., the behaviour of 3 animals is involved for an aggregation of 3 to exist. This index is not as biased as mean aggregation size by many small groups in which each group, regardless of the number of animals, contributes one unit to the divisor.

We watched three newly born calves during their first two days of life. During the first day the doe remained alone with her calf near the birth site and licked the calf for long periods. This early period of close association is probably necessary for the doe to learn to recognize her calf.

When the calves were two or three days old the does left the birth site and joined other females with young calves. In Newfoundland these doe-calf herds begin to coalesce within a week of the peak of calving (Table 3).

Does with young calves also joined together into nursery bands in Alaska and Northern Canada immediately following calving (Table 4; Pruitt, 1960; Lent, 1966a; Skoog, 1968; and Kelsall, 1968).

I suggest that this tendency for only does with calves to band together immediately following calving has resulted from the interactions of caribou and wolves (Fig. 1). Calves that for some reason did not join herds would be conspicuous to wolves and be selected against. Flocking and schooling behaviour in birds and fish has also been attributed to the selective advantage for individuals to be in groups when predators were encountered (Lack, 1954; Breder, 1959; and Williams, 1966).

These are several characteristics of caribou that argue that predation has been a potent force in calving behaviour. For example, the calving season for caribou giving birth in open habitats is very brief —90 percent of the calves are born in a two week interval (Bergerud, 1961; and Lent, 1964). This synchronization of births would greatly facilitate gregarious tendencies since calves would be of similar age and development.

TABLE 2, COMPARISON OF HERD STRUCTURE BETWEEN AGGREGATION PERIODS

Composition of Aggregation	Percentage of observations										
	Pre-Calving*	Calving*	Post-Calving*	Fly Season	Fall-Shuffle	Pre-Rut	Rut	Post Rut	Fall Migration	Winter	Spring Migration*
Solitary											
Stag	4	2	5	32	31	26	29	14	11	20	–
Doe	27	22	11	19	20	8	6	6	6	7	15
Yearling	1	3	1	2	2	–	–	1	2	–	–
Calf	–	–	2	1	–	1	6	–	–	–	–
Animal											
Stags	3	1	2	5	3	1	1	1	4	9	–
Does	39	18	4	4	6	4	4	6	9	11	24
Yearlings	2	1	2	1	–	–	–	–	–	–	–
Mixed											
Does and yearlings	19	16	3	1	–	2	–	3	4	1	59
Does and calves	–	25	47	32	12	10	6	14	15	14	–
Stags and yearlings	–	1	1	–	–		–	–	–	–	–
Does, calves, and yearlings	–	8	17	–	–	–	–	–	–	–	–
Stags, does, and others	5	2	3	5	26	47	49	56	50	37	–
No. of Aggregations	188	1219	742	186	121	243	84	262	220	70	41

*Stags under-represented, percentages not shown <00.5 percent

TABLE 3. GREGARIOUSNESS OF CARIBOU DOES COMPARED WITH THE CHRONOLOGY OF CALVING. NINETY PER CENT OF THE CALVES WERE BORN BETWEEN DATES ENCLOSED BY BRACKETS

Dates May and June	Mean Number of Adults per Aggregation[1]					
	1958	1959	1960	1961	1962	1963
20-21	3.5	3.2	–	–	–	–
22-23	5.5	2.5	2.1	–	–	–
24-25	5.0	2.0	2.8	3.8	4.7	2.2
26-27	3.8	2.0	2.6	2.6	3.7	1.6
28-29	5.1	2.5	2.5	3.0	4.1	2.3
30-31	5.0	2.4	2.6	2.7	4.2	2.3
1-2	5.3	3.1	5.7	2.9	4.3	3.0
3-4	6.4	2.2	4.0	3.3	4.3	2.2
5-6	–	2.6	–	2.5	4.6	3.0
7-8	5.1	5.2	–	4.2	4.3	2.4
9-10	6.0	6.3	–	3.7	4.5	4.2
11-12	12.7	–	–	3.3	6.8	4.8
13-14	–	7.6	–	3.2	5.7	5.3
15-16	8.4	3.8	6.8	5.1	10.0	–
Total Does in Sample	3179	1885	2746	1784	1065	1017

[1] Counts based mainly on groups segregated from ground—some bias involved in not attempting to classify larger groups.

Calves of similar age would appear more alike to potential predators than would calves of different ages.

It is interesting to note that in the wildebeest (*Connochaetes taurinus*), another highly aggregated species, Estes (1966) feels that predation by the hyaena (*Crocuta crocuta*) results in females with small young joining herds and in synchronous calving. He concludes: 'survival chances for new calves are best when there are numerous slightly older ones that make it hard for a hyaena to single out and keep a particular quarry in sight. By selecting against calves born outside the season. . .hyaena predation thus acts to maintain a 'sharp peak'.'

The short calving season for caribou cannot be explained by a mortality due to weather of calves born too early in the spring. Calf mortality due to windchill has been reported for the Canadian Arctic (Kelsall, 1968) but not for Alaska or Newfoundland (Lent, 1964;Skoog, 1968;and Bergerud, 1971a). Again in Alaska domestic reindeer calve a month earlier than caribou (Lent, 1964) and apparently have adequate survival.

Calves born late in the season, during the fly season, would be at a disadvantage because of fly harassement; however, in all the herds the young are born approximately 2 to 3 weeks prior to the insect season.

TABLE 4. COMPARISON OF AGGREGATION SIZES BETWEEN FEMALES WITH CALVES AND WITHOUT CALVES AND BETWEEN A LATER SPRING PHENOLOGY IN 1962, A MORE NORMAL SPRING PHENOLOGY IN 1961.

(Data from Northwestern Alaska from Lent 1966a:709)

	Mean No. of Females Per Group	
Year and Calving Phase	Groups with Calves	Groups without Calves
1961 (more normal phenology)		
Early Calving	4.7	24.4
Peak Calving	38.6	5.8
Late Calving	306.0	15.0
1962 (late phenology)		
Early Calving	14.3	15.0
Peak Calving	11.0	5.9
Late Calving	85.7	3.1

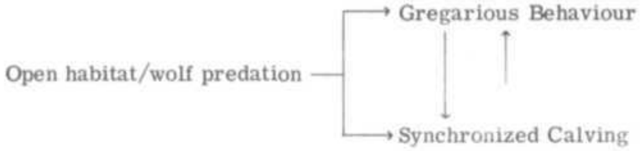
I observed the calving of barren-ground caribou in Keewatin in June 1968. The spring was late and the animals were still south of the traditional calving ground when the first calves were born. The females with these early calves rejoined the moving bands as soon as the calves were able to travel. Young calves were led across lakes with slush and many died. The does of 3 of 8 calves captured deserted their young and rejoined adult groups passing through the area. In contrast, in Newfoundland, we captured 402 young calves in 10 years and had no evidence that any females deserted their young. The Newfoundland herds were stationary following calving until the flies appeared about the first of July.

The Keewatin observations suggest a strong tendency for females to remain with other animals in the spring, at times even at the expense of their young. An alternative explanation for the desertion of young in Keewatin is that the post-parturient females still wanted to reach the calving grounds. However, herd movement can be halted in barren-ground caribou before the calving ground has been reached if a majority of the females calve while *en route* (Skoog, 1968).

The hypothesis that females may leave the area where they lose contact with their calf in order to remain with other adults is implied by Pruitt (1960) and Lent (1966a). Pruitt felt that the period of heightened sensitivity to the calf depended on the presence of other animals in the area—when there are many, the deprived doe does not linger. Lent (1966a) commented on the number of lone calves sighted (also Skoog, 1968; and Kelsall, 1968) and implied that the abandonment might be influenced by the fact that caribou bands at the time are moving extensively and the urge to follow is strong.

Part of the difference in abandonment of calves between the Newfoundland populations and barren-ground races may be due to the larger post-calving herds in the Arctic in which separation would be more likely. However, it does appear that desertion is more general in mobile than in sedentary groups (cf. Estes, these Proceedings, paper no. 8). It would be interesting to compare the frequency of desertion and survival of lone calves between various size post-calving herds. If the rate of desertion and mortality increased with herd size we would have a perfectly density-dependent mortality factor which could be an important check on population increase.

The calf mortality in Keewatin, 1968, was against calves born early. Late calves would also be at a disadvantage in large herds. There may be mutual selective reinforcement between gregarious behaviour and synchronized calving:



Other adaptations of caribou suggest that predation has been an important factor in natural selection during calving. The calves are precocial at birth and have a strong following response. If necessary they are able to follow the dam within a few hours of birth even though the dam probably cannot recognize her calf by scent at this stage. Also calves are cryptic in colour.

Holling (1961) and Salt (1967) argued that predation would favor dispersal rather than aggregating unless the social cooperation of animals in aggregations more than compensated for the increased vulnerability in conspicuous herds. Increased alertness to predators is one way in which animals could benefit from grouping. The alert and flushing distances of doe-calf groups were considerably greater than single does with calves or groups without calves in Newfoundland (Table 5). In fact, does with calves in the spring had greater flushing distances than caribou at any other season. The calving season was the only time of the year when caribou consistently took flight at long distances when alerted by sight stimuli, without verification by scent (Table 6, cf. Lent 1966a). Again the doe-calf herds were the only aggregations in Newfoundland in which many animals fled who had not perceived the danger themselves but only other animals in alarm poses. However, in herds there was often a considerable lag between alert and flushing times. There was some tendency for groups of does and calves to act in unison; the less nervous females seemed to retard the flight of the more nervous. In extremely large herds the few animals that had seen the intruder were sometimes unable to alarm sufficient companions to initiate group flight.

TABLE 5. THE ALERT AND FLUSHING DISTANCE OF DOE WITH AND WITHOUT CALF

Band Composition	No. of Bands	Mean No. of Adults	Distances in Feet		
			To Alert	To Flush	Difference
Does, no Calves	20	2.2	350 ± 39	266 ± 35	84[1]
One Doe and Calf	15	1.0	355 ± 66	332 ± 18	23
Does and Calves	13	3.6	595 ± 177	537 ± 36	58
Total	48	2.3	418	291	127

[1] A significant difference, t = 10.31

Another benefit from aggregating, relative to predation, is that large herds may make it more difficult for a predator to follow and concentrate on one specific animal. Walter (1969) said that the success of a predator depends on its ability to concentrate on a specific animal. Anything that makes an animal more conspicuous, by being alone or in a herd but uniquely marked, would increase its liability.

The functional predator response of wolves may be quite high in large herds. Large herds are known to stampede with calves getting separated when chased by wolves (Crisler, 1956; Kelsall, 1960). However, if predation favours gregariousness it is only necessary to show statistically that survival is better in herds than in isolates (Williams, 1966).

Reinforcement of escape behaviour would be favoured by herding. For example, if 4 animals were together and attacked 3 times and 2 were killed the remaining 2 have gone through the experience 3 times. If the 4 animals were alone and 3 were attacked and 2 were killed the result would be 1 animal with 1 experience and 1 naive animal. Again the handling time of prey by predators would provide reinforcement for escape behaviour of animals in groups.

TABLE 6. COMPARISON OF THE SENSES USED BY DOES WITH AND WITHOUT CALVES TO ALERT AND TAKE FLIGHT IN JUNE

Band Composition and Reaction	No. of Bands	Senses used (% of observations)		
		Sight	Scent	Hearing
Does without calves				
To alert	22	68	14	18
Take flight[1]	23	48	43	9
Does with calves				
To alert	23	56	22	22
Take flight	32	84	16	–

[1] significantly different at 0.05 level (λ^2 test) from does with calves taking flight.

The caribou in the interior of Newfoundland have continued to form calving herds although wolves have been extinct for approximately 50 years. I believe that this is evidence that this behaviour has been selected for and owes at least some of its origin to phylogenic selection.

Another herd in Newfoundland on the Avalon Peninsula does not currently form large calving groups. This population has been isolated for perhaps 100 years. For many years the herd numbered less than 100 animals. Wolves were a component of their environment in the 1800's. I have hypothesized that strong selection by lynx predation since the extinction of wolves could have altered the genetic adaptation of these animals to wolf predation, to that advantageous in lynx encounters (Bergerud, 1971a). Such rapid selection seems possible with such a small gene pool (cf. Ford, 1965).

The herd structure of caribou calving in the forest has not been reported. It is difficult to imagine how such animals could keep in contact; the selection advantages of being scattered seem obvious. In 1959, I studied the rut of the caribou on the Gaspe Peninsula of Quebec that calve in the forest. Breeding occurred over at least a 19 day period. In Newfoundland the breeding lasts 7 days (Bergerud, 1961). Presumably, a similar short breeding sequence occurs in Alaska and Northern Canada since these populations also have brief calving seasons. These contrasting observations lend support to the theory that brief and synchronized breeding and calving are adaptations to a conspicuous place-in-which-to-live.

In Newfoundland the nursery bands continued to coalesce in the post-calving periods; herds of over 50 animals were common (Fig. 3). The animals were more aggregated at this time of year than in any other season (Fig. 2). Barren-ground animals show a similar tendency to aggregate. Post-calving herds numbering 50,000 to 100,000 plus have been reported in the Arctic (Lent, 1966b; and Kelsall, 1968).

Kelsall (1968) listed three factors involved in the formation of these large herds in Northern Canada: (1) the natural tendency of females to progressively form large herds during calving; (2) the fact that barriers were encountered shortly after leaving the calving areas; and (3) the tendency to remain in close-knit groups when harrassed by insects.

In the section on calving I have already argued the importance of the natural tendency of does to aggregate. In Newfoundland, physical barriers were not responsible for the large herds since the animals in the post-calving interval did not travel widely and encounter barriers. Additionally, insects did not appear in Newfoundland until the herds had been formed for two weeks.

Relative to these large herds I think the views of Lent (1966a) on social facilitation are relevant. He argued that individuals that show synchrony in their activities tend to

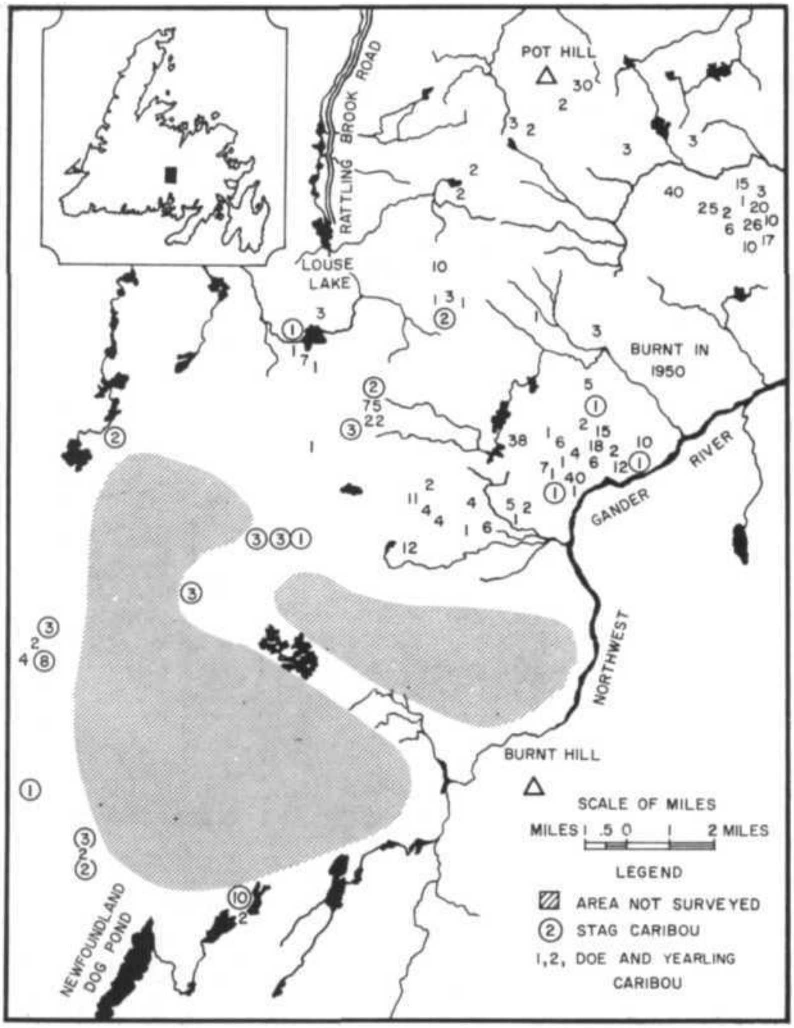


Fig. 3. The distribution of aggregations in the post-calving interval on the Pot Hill Calving ground in June 1958. Many of the caribou were concentrated along the Gander River in a area burned in 1950. Note that most of stags were south of the calving aggregations in the vicinity of Newfoundland Dog Pond where the herd had wintered.

form groups. He noted many occasions during his calving studies when one group reacted to the activity of another group. 'This inter-group facilitation often led to the union of the two groups.' (Lent, 1966a: 736-737). He felt that more commonly a small group will move towards convergence with a large group.

The large post-calving herds can be explained simply as inter-group facilitation between herds resultant from extremely high densities. Caribou females in Alaska, Northern Canada & Newfoundland calve on calving grounds limited in extent—perhaps 50 per cent or more of the population are concentrated at this time of the year. Skoog (1968) documented that the Nelchina Herd continued to use one calving ground from 1955 to 1963, even though the herd increased from 40,000 to 71,000 animals. In contrast, in other seasons the herd divided into an increasing number of subherds as the population expanded.

Another factor that might affect herd sizes is the spring phenology. Frequently, in a late spring, all the females do not reach the calving ground prior to parturition (Lent, 1966b; and Skoog, 1968). Animals are scattered along the migration routes—densities would be lower and post-calving herd sizes likely reduced (Table 4).

The basic question is not the explanation of the large post-calving aggregations but why the same areas, limited in extent, are used year after year as calving sites. This phenomenon automatically leads to high densities and large aggregations.

Fly Season

The large post-calving herds disbanded in Newfoundland at the beginning of July (Table 1). In eastern Newfoundland the animals dispersed into forest cover, probably to seek relief from insects that were less bothersome in the shade rather than to gain relief from the heat. Each year the dispersal coincided with the appearance of the biting flies but not necessarily with hot weather. In May 1960, the animals remained in the open when temperatures were above 85° but the flies had not yet appeared.

In 1958, we studied the behaviour of 3 adult captive caribou to clarify the role of insects vs. heat in the use of forest cover. The animals were visited hourly for 18 days and notes taken on whether the animals were in the open, or under the trees; temperatures were recorded hourly in the open and under the trees and the abundance of insects noted. The results showed that the animals sought shade to escape insects rather than to find cooler temperatures (Table 7). Actually, the mean temperature in the shade averaged only 1.5 degrees cooler than in the open.

TABLE 7. THE CORRELATION OF THE USE OF FOREST COVER (SHADE) WITH FLY ABUNDANCE BASED ON THOSE CAPTIVE CARIBOU OBSERVED HOURLY AUGUST 11-30,1959

	Percentage of Observations	
Fly Abundance	In the Shade	In the Open
None	17	44
Some	26	26
Many	56	31

Statistical Analysis	Number of Observations					
	In Shade			In Open		
Temperature	None	Some	Many	None	Some	Many
cool	5	5	25	109	24	71
warm	7	6	11	113	72	70
hot	0	8	5	21	40	31

shade × heat, x^2 = 4. 68, 2df, n = 623
shade × flies, x^2 = 24.11, 2df, n = 623
flies × temp., x^2 = 53.86, 4df, n = 623

During two summers we observed recognizable wild stags on the Avalon Peninsula from a lookout on a hill. The animals fed in the morning before the flies became numerous and again in the evening after the flies abated (Fig. 4, bottom). The caribou were observed to disappear into the woods at the end of 31 to 40 morning feeding periods. Often the animals would reappear in the same clearing in the evening. The stags reappeared whether it was a warm or cool evening.

The stags had a restricted home range in July and August when flies were common (Fig. 5 and Table 8) but wandered much farther in June and September before and after flies were bothersome (Table 9). The home ranges were not mutually exclusive. Two stags were seen together on 12 occasions (see Fig. 5).

TABLE 8. ACREAGE OCCUPIED BY RECOGNIZABLE STAGS ON THE AVALON PENINSULA IN THE SUMMERS OF 1958 AND 1959

Stag's Identification Number	No. of Times Observed	Uninterrupted Inclusive Dates Observed	Acreage of Habitat Occupied	Cruising Index (Acres/Day)
1	4	5/5-5/29/58	2880	115
1	5	7/22-8/28/58	1000	26
2	23	8/8-9/6/58	480	16
3	0	6/7-6/26/58	3976	199
5	12	6/25-7/2/59	384	48
5	6	8/19-8/27/59	640	71
6	12	6/25-7/2/59	592	99
7	3	6/29-7/3/59	336	67
7	6	8/17-8/26/59	1056	106

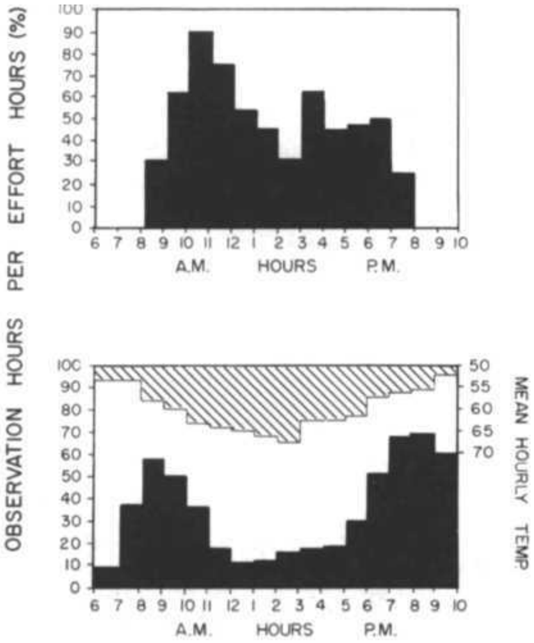


Fig.4. (above) Observations of caribou resting on a beach of a lake in central Newfoundland, caribou observed 51 hours out of 91 effort hours 8/2/59-8/18/59. (below) Observations of four active stags, Avalon Peninsula, caribou observed 133 hours out of 441 effort hours 5/6/59-8/27/59.

TABLE 9. DAILY SUMMER MOVEMENT OF SEVEN RECOGNIZABLE STAGS ON THE AVALON PENINSULA IN 1958 AND 1959

	June and Sept. (few flies)	July and Aug. (fly season)	Entire Summer
Number of observations	11	17	28
Mean distance travelled (yds.)[1]	1736	731	1064
Extreme distances (yds.)	412-3520	138-2022	138-3520
Yards per hour	145	59	90

[1] The straight-line distance between two observations of the same stag seen within a 24-hour period.

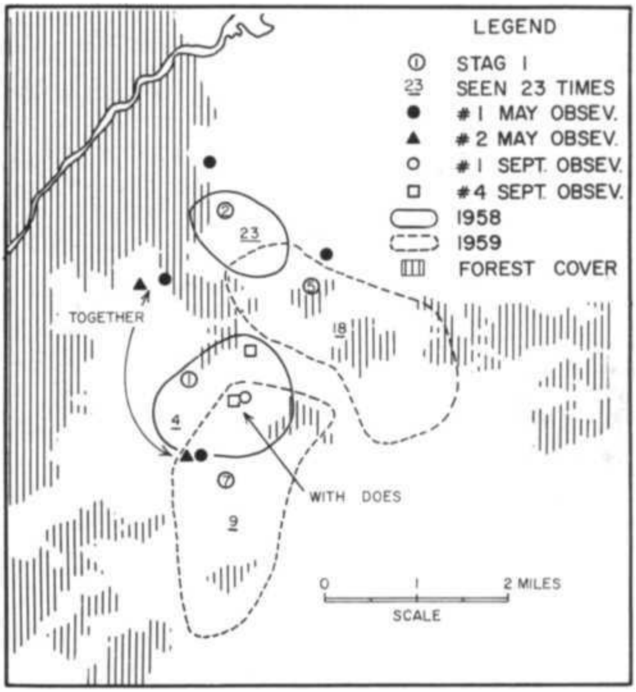


Fig. 5. The summer home range of 4 stags on the Avalon Peninsula.

Two assistants observed caribou using a sandy beach during the middle of the day in central Newfoundland from August 2-18, 1959 (Fig. 4, above). They recognized 5 animals that visited the beach on more than 1 day (Fig. 6). One small stag and doe were in the area at least 14 and 17 days respectively. Three yearlings and three does visited the beach on only one day and were likely transients. These observations again suggest some restriction in movement during the fly season.

In western and southern Newfoundland where tree cover is sparse the large post-calving herds also scattered when the insects appeared but these animals sought wind-swept terrain or snowfields. In these open habitats the aggregations were larger ($\overline{x} = 7.0$) than in the east ($\overline{x} = 1.4$) where the animals moved to the forest cover. Barren-ground caribou also use wind-swept ridges and snowfields to escape insects (Skoog, 1968).

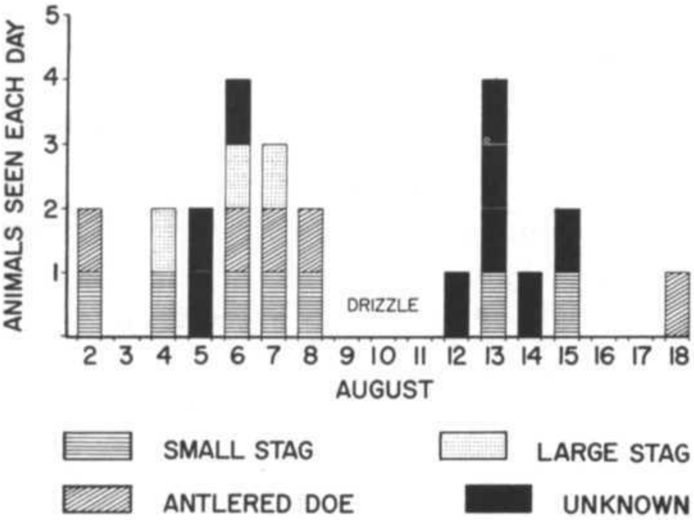


Fig. 6. Observations of recognizable caribou using a sand beach in August 1959.

The grouping aggregation behaviour of these animals in western Newfoundland seemed partly a factor of the discontinuous nature of fly-relief habitats and partly due to social facilitation. There were more animals on certain ridges than would be expected based on the availability of terrain alone. When animals left one hill and headed for another they were more apt to pick a hill that already had animals than one without caribou.

Both Skoog (1968) and Kelsall (1968) felt that animals secured a mutual benefit by sharing their tormentors. The caribou often stood in compact groups with their heads drooping near the ground. Warble and nostril flies seemed to buzz more on the perimeters of such groups.

In the Arctic some caribou herds continue to move during the summer (Kelsall, 1968; and Skoog, 1968). There the terrain was mostly level and open and likely offered little insect-relief-habitat. Thus the animals sought relief by continually moving (Skoog, 1968). One would expect the animals to move more on still days than on windy days.

The significance of the aggregation and movement responses in the fly season is that they were subject to adaptive modification in response to the kind of insect relief habitat available:

forest cover—caribou formed small aggregations and were quite sedentary (cf. Simkin, 1965)

no forest cover but wind-swept ridges—moderate size herds and quite sedentary

no forest cover and discontinuous wind-swept terrain—caribou form large herds that continue to move

Fall Shuffle and Pre-Rut

When the insects abated in mid-September animals in Newfoundland left tree cover and began to move greater distances (Table 9). Aggregation sizes increased and there were more companies with both stags and does (Tables 1 & 2). The most conspicuous movement was that of stags from timber towards females who were more in open habitats. This fall drift of males towards females also takes place in barren-ground caribou (Skoog, 1968; and Kelsall, 1968). Also in some barren-ground caribou herds there is apparently an August dispersal of animals when flies abate (Kelsall, 1968). The animals were widely scattered and in small aggregations. Such a dispersal likely resulted because food was abundant and there was no longer an advantage in seeking fly-relief habitat or other animals to secure relief from insects.

Rut

In October the animals in Newfoundland were highly aggregated for breeding (Fig. 2). Breeding took place either in small companies dominated by one large stag or in larger companies frequently of 50 to 100 animals.

Apparently the sex ratio of adults affected the size of aggregations. In the interior of Newfoundland the sex ratio declined from 32:68 to 24:76 from 1957 to 1966 (Bergerud, 1971b). As the number of males declined the size of aggregations increased (Fig. 7). In contrast the sex ratio remained unchanged in the population on the Avalon Peninsula (40:60, n = 518) from 1956 to 1964 and the size of aggregations were similar between years (Table 10).

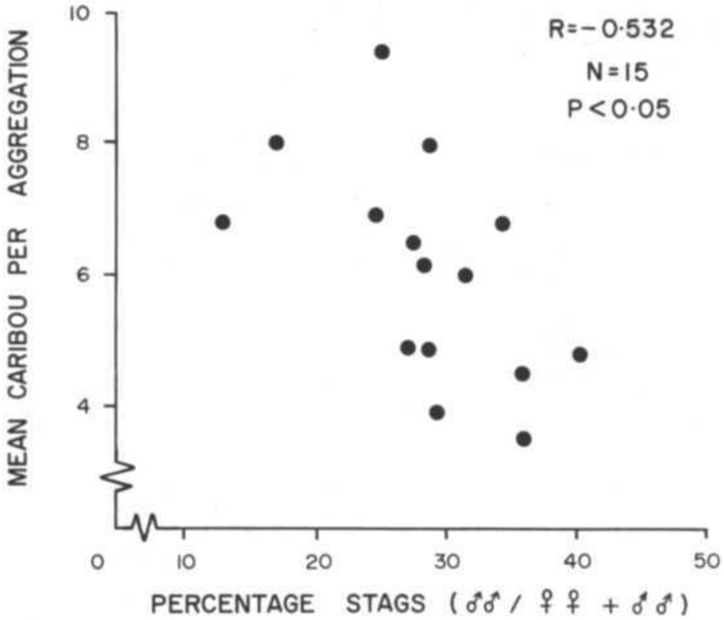


Fig. 7. The regression of the mean aggregation size in October on the adult sex ratio. Each point represents a population of caribou in the Interior herd. The mean number of caribou per point is 166, extremes 49-384.

TABLE 10. COMPARISON OF THE CARIBOU PER AGGREGATION AND PER SQUARE MILE IN THE AVALON PENINSULA HERD IN OCTOBER AS THE HERD INCREASED 1960 TO 1965

	1960	1964	1965
Total caribou in herd	206+	508	518
Caribou per sq. mile	2.4	2.1	2.7
Caribou per aggregation	6.3	5.9	5.0

The Avalon Herd increased from 125 to 720 animals from 1957 to 1966 (Bergerud, 1971a). This increase did not affect the size of the rutting groups, rutting companies or the density of the population (Table 10). As the herd increased the animals occupied a larger area during the rut.

In the large herds of over 40 animals in the interior, many mature stags took part in breeding females. This occurred because many does came into heat during a 7 day period. Dominant stags could not simultaneously expel rivals and court females. Further, when most of the does were in large herds there were fewer solitary males travelling between groups. The increased size of the herds with the decline in males resulted in an economical use of males and assured that all females were bred even though there were fewer males in the population.

Post-Rut

During the post-rut season in Newfoundland aggregations were still quite large. The groups appeared to draw together—many companies in a relatively small area.

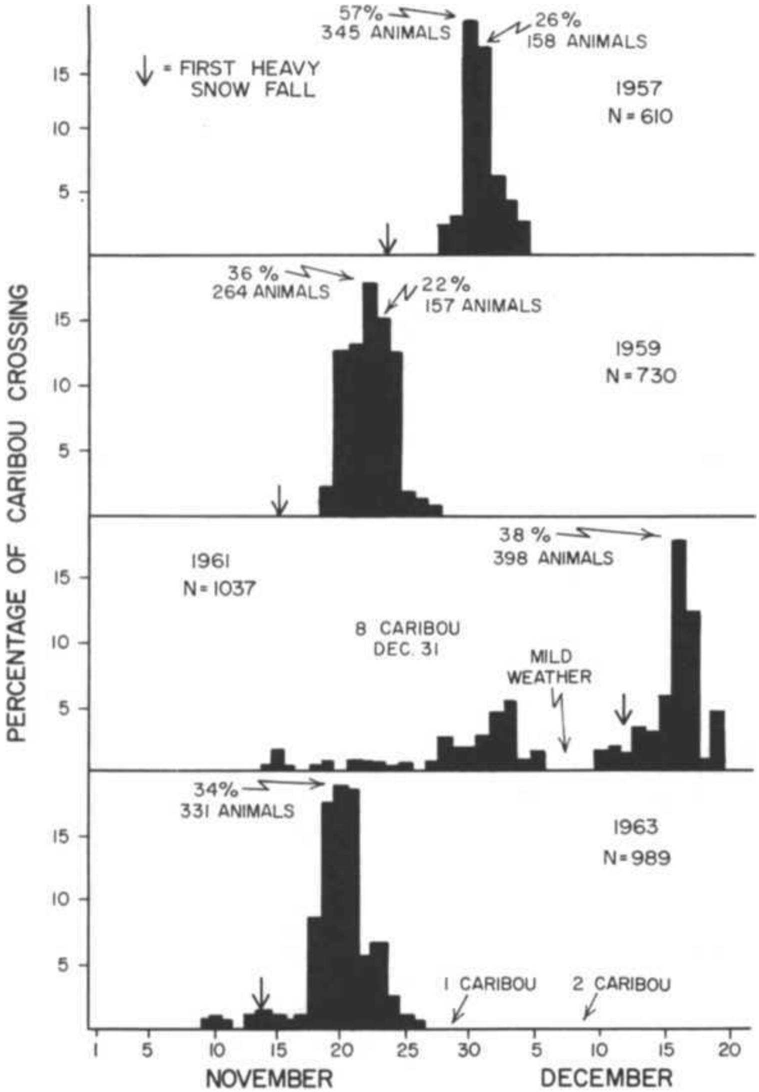


Fig. 8. The number of caribou tracks counted crossing a logging road during the fall migration at Lake Victoria during 4 years.

In November there was a drift of animals in the direction they would later take during migration. The animals seemed 'ready-to-go'. The groups grew larger and left in the proper direction.

Fall Migration

In three years fall migration was initiated in the interior of Newfoundland following the first heavy snowfall of 2 to 4 inches in November (Fig. 8). The migration in a fourth year, 1961, was unusual. Early in November after several minor snowfalls some animals moved south in small groups. Mild weather set in, snow disappeared and the movement halted (Fig. 8). Then a heavy snowfall occurred on December 12 and the animals moved south in a rush.

Another population in Newfoundland, the Humber River Herd (see Bergerud, 1971a; Fig. 1) also migrated following snowstorms. In 1958 the herd started to cross the Trans-Canada Highway 2 days after the first storms, in 1962 they appeared 1 day after snow, and in 1964, 3 days. The proximity of the caribou to the road probably accounted for the difference between years.

The role of photoperiodism and hormonal control of migration is well known. Endogenous factors probably prime the animals physiologically resulting in increased aggregating and pre-migration restlessness. However, there seems little question that the final threshold stimulus is a heavy snowfall. Dugmore (1913), Kelsall (1968) and Skoog (1968) all commented on the correlation between snow and the release of migratory behaviour.

The possibility should be considered that the endogenous and snowfall stimuli must be synchronized for a normal response. In late winter caribou do not migrate following snowstorms. They are probably no longer primed physiologically. If the animals are primed for migration in the autumn but the proper external stimulus fails to appear, the fall movement could be aborted. At times large numbers of caribou in Northern Canada stay out on the tundra in the winter (Kelsall, 1968). Also in Newfoundland some caribou do not migrate in some years. In these situations the timing and/or amount of snow may have been inappropriate to release migration.
Different herds in Newfoundland migrated south, east, or west (Fig. 9). Most of the animals in the interior went south. The Avalon caribou moved southeast to windswept terrain. Caribou on the Northern Peninsula moved southwest. When caribou were abundant in Newfoundland in the early 1900's animals travelled west in the fall to the Lewis Hills, Gregory Plateau and the Anguille Mountains. These shifts had in common that the animals moved to areas containing a relatively greater amount of forage in January and February when snow accumulated (Fig. 9).

Caribou residing in mountainous habitat in British Columbia and Quebec shifted to higher elevations when snows accumulated (Edwards and Ritcey, 1959; and Moisan, 1958). Animals summering in level terrain in southern Labrador went north and to the Mealy Mountains in the autumn (Bergerud, 1967). In general, barren-ground caribou move in the winter to ranges with more tree cover. These ranges offer more food than the tundra because the snow is softer and because food can be found in three stratas: cryptogam, shrub and arboreal.

Each distinctive directional movement may have a traditional basis. Animals in the past that moved in the prescribed direction have usually found forage more available under normal snow conditions than if they had gone in other directions to other ranges. Certainly at the time of migration food is still plentiful in the areas they vacate. It is unlikely that topography or snow cover funnel their movements since the animals frequently move at right angles to numerous barriers and move in such a variety of directions.

This fall movement appears to be an anticipatory adaptation (*sensu* Lack, 1954) based on the relative abundance of forage. Relative abundance is used in the sense of Andrewartha and Birch (1954); that is, food that is actually available because it can be detected through snow cover.

Recently the transplanting of caribou has shed some light on the relative roles of phylogenic and ontogenic considerations in migratory behaviour. In Sweden reindeer that were transported by truck to the winter ranges often failed to make the return

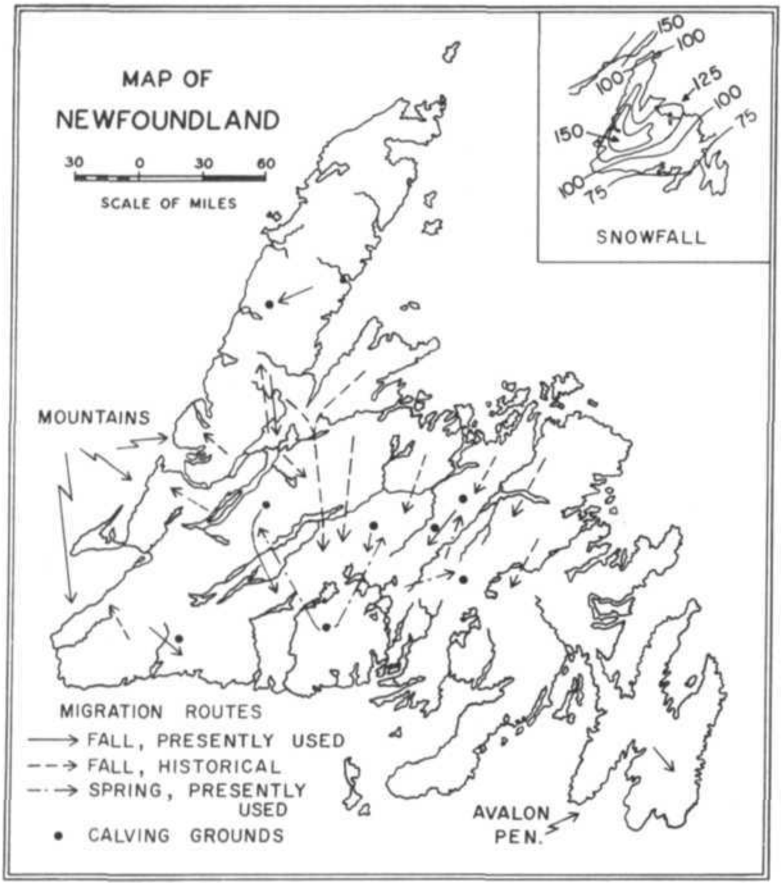


Fig. 9. The major fall and spring migration routes used in the past and presently in Newfoundland.

migration in the spring (Espmark, 1970). He suggested the failure might reflect: (1) destruction of the herd's social organization—animals without an established social hierarchy were shipped together and upon release scattered to reduce social interactions; (2) the importance of uninterrupted learning of the migratory route; (3) disorientation caused by unfamiliar winter areas; and (4) the large proportion of inexperienced animals in the herds-few leaders to lead the return migration. Espmark also felt there was a minimum herd size sufficient to release the migratory stimulus.

Relative to Espmark's first point (1), Lent (1966a) demonstrated in free-ranging caribou that threat encounters are brief and that there was a high degree of tolerance in herds for strangers. Adult caribou introduced into Maine and captured from different bands in Newfoundland travelled together throughout their first winter in Maine but dispersed in April and did not return (Dunn, 1965). During transplanting operations in Newfoundland, we frequently held up to 80 caribou from different bands together in one corral; social dominance was evident but strife was minimal.

A minimum herd size sufficient to release migratory behaviour seems unlikely for free-ranging caribou. Animals in Newfoundland frequently migrated as singles or in small groups of less than 5 (Fig. 8).

Espmark's view that animals may not migrate in the absence of recent reinforcement or because they are inexperienced is supported by transplanting studies of Newfoundland animals. From 1961 to 1965 we transplanted 226 animals to 18 new sites where caribou had not been in recent times. In releases that involved wild adults the animals generally dispersed from the sites unless the release areas were islands 7 miles or more from shore (Table 11). Conversely, hand-reared or wild calves released without wild adults remained at the release sites. For example, 17 hand-reared calves were released on Sound Island in 1961; the Island is only 300 yards from the mainland. The animals remained on the island and produced young in 1964. On a few occasions animals left the island and visited the mainland only to return.

The transfer experiments in Sweden, Maine and Newfoundland suggest that ontogenic experiences may be important for migratory behaviour. The deprivation experiments of hand-reared calves in Newfoundland do not disprove the possibility of a phylogenic basis for migration behaviour (see Lorenz, 1965) but at least suggest that either the releasing stimulus to migrate is absent without adult leaders, or that the operant conditioning secured by following adults is an important reinforcement for retention of the tradition.

TABLE 11. COMPARISON OF THE SEDENTARY HABITS OF ADULTS AND CALVES INTRODUCED INTO NEW HABITATS

Introduction Sites and Age of Animals Introduced	No. of Animals that Staged of Total Released
Islands	
Wild Adults (7+ miles)[1]	31 of 31
Wild Adults (1-6 miles)	6-8 of 20
Hand-reared Calves (< 1 to 4 miles)	45 of 45
Wild Calves (6 miles)	6 of 6
Peninsulas	
Wild Adults [2]	9 of 15
Wild Calves	13 of 13
Mainland Newfoundland	
Wild Adults	0-2 of 17

[1] 7 or more miles from Mainland

[2] Stock taken from Avalon Peninsula herd which may be more sedentary than from the Interior

TABLE 12. AREA OF OCCUPIED RANGE, CARIBOU DENSITIES AND MEAN AGGREGATION SIZE OF THE INTERIOR HERD COMPARED TO THE SEVERITY OF WINTER SNOW CONDITIONS

Year of Census	Winter Condition	Square Miles Occupied	Caribou per Sq. Mile	Mean Caribou Per Aggregation
1957	mild	1400±	4.2	4.7 (2038)[1]
1959	hard	350	11.9	4.6 (2518)
1961	hard	600	8.2	4.8 (3617)
1966	average	1400	4.4	4.0 (752)

[1] Caribou in sample

Winter

The density of caribou in the winter in Newfoundland depended on the size of available food patches. Animals congregated, if food was available, only on wind-swept ridges in winters of deep snow. Animals were more dispersed if the winter was mild with food everywhere abundant (Table 11). These changes in distribution and densities were not reflected in changes in aggregation sizes (Table 12).

Pruitt (1959) stressed the hindrance of nival conditions on snow wading of barren-ground caribou. He felt that caribou in northern Saskatchewan were herded about the countryside by a snow fence of greater nival hindrance characteristics. This hypothesis possibly skirts the main issue. In my view snow cover affects distribution, movement and range use by altering the relative availability of food—animals are moving primarily to seek food and not to avoid snow difficult to travel through.

Nearctic caribou show a wide diversity of major winter movements between snow gradients that suggest food seeking. Caribou in southern Labrador left lichen woodlands in winters of deep snow and travelled to wind-swept slopes in the Mealy Mountains to feed in shallower snows (Bergerud, 1967). The Humber River herd in Newfoundland, in several winters, vacated its winter range in January when snows were deep and soft; they went north to large bogs where snow was harder but shallower. The Avalon Peninsula herd used the wind-swept 'Red Ground' from November to January, but when snows became deeper and uniform, covering the ground and shrub plant strata, some animals returned to the summer range where snows were softer and deeper but where more contacts could be made with tree cover. The Mount Albert, Quebec, caribou did likewise; they abandoned Mt. Albert when the vegetation became glazed in late winter. Mountain caribou in British Columbia did the reverse—they shifted to higher slopes in late winter where snow was both deeper and harder. This movement was directed at securing more tree lichens (Edwards & Ritcey, 1959). The common rationale for these different responses to snow cover is that the animals were moving to a relatively more available food supply.

The location of relative food supplies affected the winter movement and range utilization of the Interior herd. The animals were quite stationary in December and January when the snow was soft and deep and they cratered for a living. Barren-ground caribou showed a similar restriction of movement during mid-winter when they dug craters (Kelsall, 1968; and Skoog, 1968). The Newfoundland animals were more mobile when crusts formed in late winter sufficient to support their weight; they were then free to seek out tree lichens and snow-emergent shrubs.

Local movements of the Interior herd occurred throughout the winter following snow and ice storms and thaws that altered snow gradients so that food became more available elsewhere. For example, after a snowstorm with winds 50 miles-per-hour, on February 15-16, 1959, animals shifted from lichen woodlands to Subalpine habitats that had been wind-swept exposing vegetation. A thaw in March 1961, which enlarged bare ground in craters previously dug, caused the animals to revisit their former feeding sites. Millais (1907) described an impressive exodus from Eastern Newfoundland in December 1898, 'A glitter [ice storm] came on suddenly and the whole of deer moved in a single night to the west at full speed'. The animals moved at least as far as Conn River (50 miles).

Detailed notes were taken of caribou movement during the spring break-up in the interior of Newfoundland in 1961. Prior to the general thaw that commenced on March 25, caribou were scattered cratering the shallowest snows available. Snows were deep and hard from March 22 to 25 and animals were in motion seeking new cratering sites and emergent vegetation (Table 13). When the 'mild' set in, on March 25, the snow strength collapsed. The only animals that could travel during the middle of the day were those able to flounder to lake ice. Other animals moved early or late in the day when temporary crusts formed. After bare ground appeared on March 30, movement slackened (Table 13) even though snows became harder and more dense.

Snow gradients may change so rapidly that caribou can become trapped and severely handicapped in seeking food. Notes of March 27, 1961, illustrate this: 'Snow in whole area is saturated to a depth of at least 27 inches after two days rain and mild weather. Crusts are very rotten and in many places it is not unusual to sink 12-14

Month and Day	Temperature Mini- mum	Maxi- mum	Snow Depth (inches)	Per Cent Snow Cover	Depth Caribou Tracks (in)	Per Cent Caribou Travelling*	Caribou Travelling Across Granite Lake
3/22	16	26	42	100	2½	18(22)	2
3/23	23	28	42	100	½	33(55)	10
3/24	20	28	41½	100	¾	10(49)	10
3/25	18	38	40	100	¾	27(11)	30
3/26	26	30	46½	100	12+	——	—
3/27	32	34	43½	100	12+	43(7)†	3
3/28	31	34	38½	100	12+	33(3)†	—
3/29	30	38	37	100	6½	42(105)	—
3/30	32	44	35	98	—	7(141)	—
3/31	31	42	33	95	—	0(4)	5
4/1	30	38	33	95	4	0(78)	—
4/2	32	52	32	90	—	——	—
4/3	30	36	31	90	1¾	0(4)	16
4/4	24	43	30	87	¾	9(22)	—
4/5	30	46	30	87	¾	——	—
4/6	28	36	30	87	—	——	—
4/7	30	36	29½	87	—	0(3)	—
4/8	26	35	29½	87	—	——	—
4/9	16	36	28½	87	—	——	—
4/10	30	38	28	87	—	11(66)	—
4/11	22	44	28	90	2¾	3(36)	—
4/12	26	34	28	90	—	—	—
4/13	26	31	28	—	—	0(52)	—

* recorded on four binocular scans of the surrounding hills per day.
Figures in parenthesis are the total animals seen on the horizon scans.

† Actually few animals were travelling, hence the small sample size.

inches on snowshoes. Caribou do not appear to be moving. One doe was watched for ½-hour and moved less than 20 yards.... This animal spent most of her time standing. When she did move, a few steps at a time, she appeared to be going to the ground with each step. The animal fell once while watched and took almost a minute to regain her feet. The few animals seen feeding today were feeding on lichens on rocks along the lake shore'.

In both 1959 and 1961, animals were noted that appeared restricted to travelling around the perimeters of small lakes, feeding on the shore lip. They were unable or reluctant to leave the solid surface of the lake yard. Such yard isolation occurred more commonly with solitary animals; groups of animals waded to more trackable snow by walking single file. Animals were noted walking single file when sinking as little as 12 inches and as much as 25 inches in the snow.

Caribou in Labrador are frequently in yards when snow depths reach 4-6 feet. These animals are probably snowed-in by the tremendous soft snowfalls that occur in that area (Hare, 1951). Mountain caribou may also be temporarily immobilized by deep soft snow (Edwards and Ritcey, 1959).

Spring Migration

In North America female caribou usually initiate movement from the winter range to the calving grounds in late March or April (Fig. 10;Skoog, 1968; and Kelsall, 1968). The annual timing of these movements varies between years and appears correlated with the disappearance of snow cover (Skoogs, 1968).

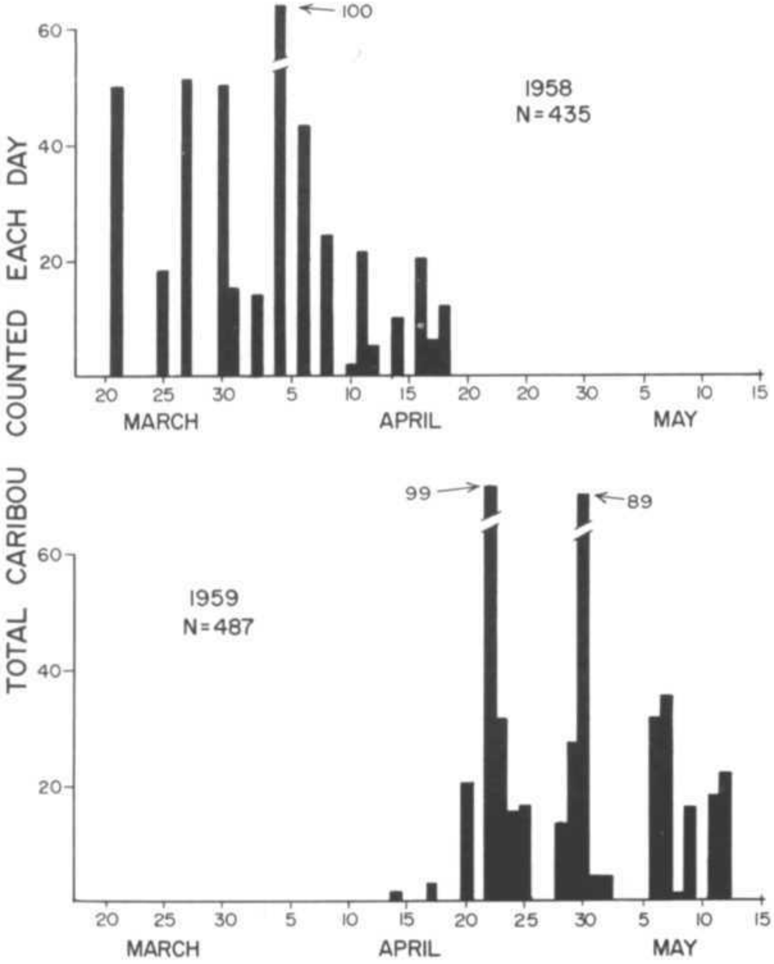


Fig. 10. The number of caribou tracks counted crossing a logging road at Lake Victoria during the spring migration in 2 years.

In the spring of 1961 we tried to isolate what extrinsic factors might release this behaviour. We camped with the caribou and recorded daily snow depths, relative snow hardness, percentage of the ground free of snow, and temperatures; four times daily the activity of the caribou was recorded by binocular sweeps of the horizon. The caribou became more mobile when bare areas appeared but there was no direction in their movements nor decrease in numbers indicating animals had left (Table 13). Possibly there is no single extrinsic stimulus in the spring as in the fall.

Undoubtedly, a physiological drive associated with parturition is a major factor in this migration since pregnant females lead the way back. Perhaps we should consider that the animals are ready-to-go in late March and April but are inhibited by con-

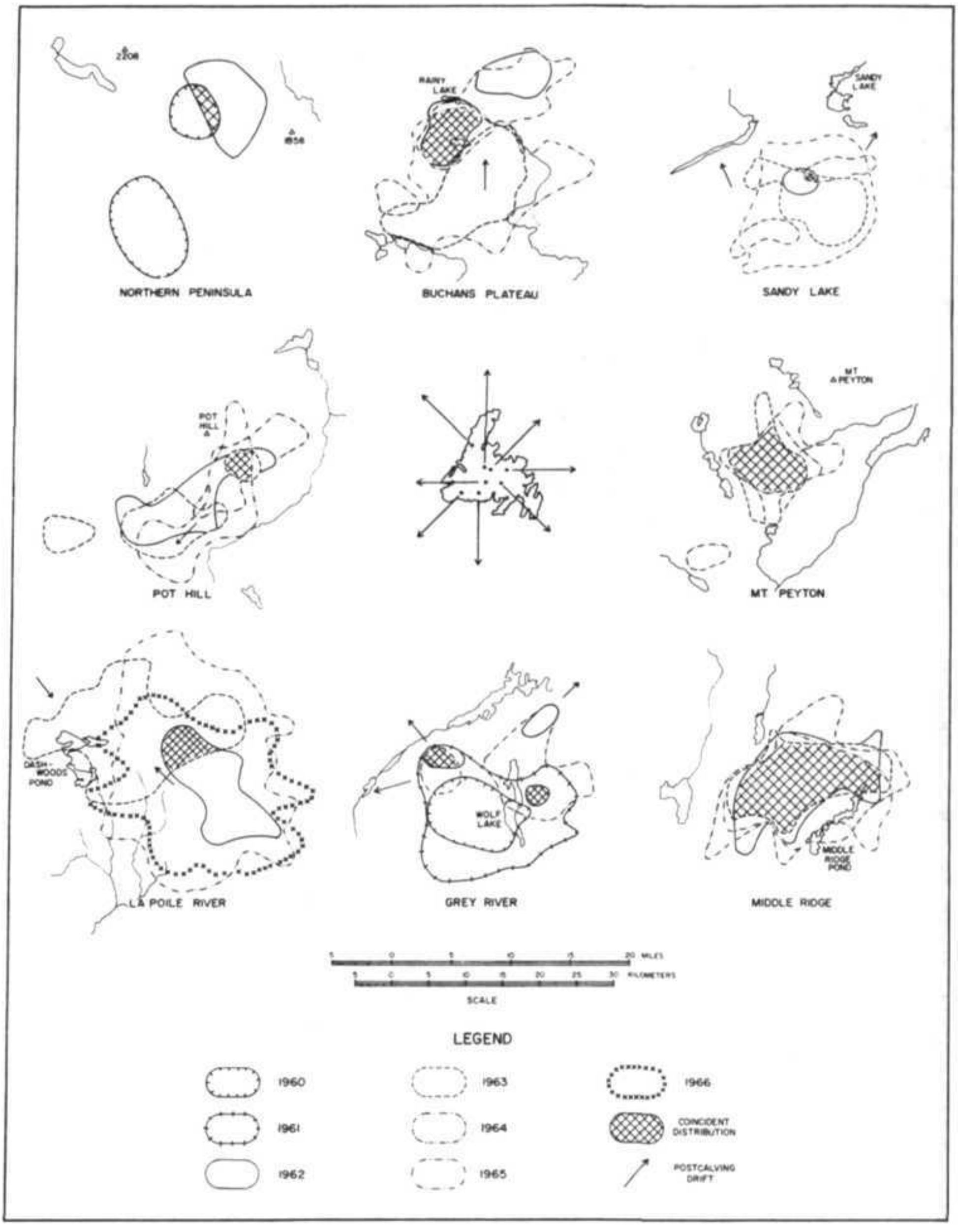


Fig. 11. Comparison of the distribution of caribou on calving grounds in June. The counts were made on one day. If the distribution was shown for the entire spring there would likely be complete overlap of areas used between years.

tinuous snow cover. Kelsall (1968) mentions that the spring migration may be halted or even temporarily reversed by unseasonal snow.

Caribou herds residing in open habitats consistently return to specific areas each year to give birth to young (Fig. 11) (Lent, 1966a; Kelsall, 1968; Skoog, 1968; and Bergerud, 1971a). These calving grounds seem to be the most regularly visited areas in the wanderings of the herds. Our understanding of movement and aggregating behaviour would be greatly enhanced if we knew how the herds returned to these specific locations. Three hypotheses, which may not be mutually exclusive suggest themselves: (1) that animals home to a specific area, learning and tradition involved; (2) that animals are funnelled by topographical features and recognize the calving grounds based on phylogenic imprinting; and (3) that animals have an orientation direction which often results in the animal reaching the same general area.

The information available is not sufficient to decide between these hypotheses. For example, recent tagging studies of caribou (Miller and Robertson, 1967; and Bergerud, 1971a) showed that most animals resighted return to the same calving ground the next year, which is consistent with both a homing to an area and an orientation direction. Also, the results are biased. An animal is more likely to return in two adjacent years, even if topographical funnelling is involved rather than a traditional homing response. The funnel idea presumes that animals would travel to a new calving ground if, during the winter, movement caused the herd to be shifted far enough laterally so that it pointed at a new calving ground when migration commenced. Extreme lateral shifts are less likely between consecutive years than over a greater time span. But by the time several years have elapsed the tags on the animals are usually lost.

Again there is considerable evidence pro and con concerning animals following routes of least resistance. Animals migrate along eskers and travel down frozen lakes and usually cross lakes at their narrowest point. At other times they move at right angles to topographical features. One herd in Newfoundland annually crossed through 10 miles of closed-canopy forest where logging was in progress. Presumably with a homing explanation animals could still follow routes of least resistance. In Newfoundland, walking was extremely difficult because of stunted mats of conifers; the easiest and fastest way to reach a destination was to follow caribou trails that meandered in all directions—always picking a trail that lead in the right direction when a choice was available.

One difficulty with the hypothesis of topographical funnelling and phylogenic imprinting is that the physiography of the calving grounds in North America varies tremendously. Such variability would make imprinting less likely. The Buchans Plateau calving ground in Newfoundland is in a valley at an elevation of 1500 feet. The terrain is open and composed of dry uplands burned 40 years previously and marshes dominated by *Scirpus cespilosus.* The Middle Ridge calving ground is on a low rounded hill where large marshes of *Scirpus cespitosus* predominate. The Pot Hill calving ground is a string of bogs laced among 'islands' of closed-canopy spruce forests. Caribou on the Brooks Range, Alaska calve on rolling slopes dominated by *Eriophorum* (Lent, 1966b). Animals in northern Canada seek rough uplands; apparently sedges are more common elsewhere (Kelsall, 1968). All these sites are open and all have some sedges but most of the North is open and sedges are abundant in many areas.

I tried to determine if calving populations in the Interior Herd of Newfoundland were discrete in order to better understand the population dynamics of the herd (Bergerud, 1971a). If populations that calved at different calving grounds were discrete homing would be suggested. Census results of the caribou on the calving grounds showed large differences between years (Table 14) that are difficult to rationalize with universal homing. Against this I found a significant difference in the percentage of females that possessed visible antlers between those females that calved at two calving grounds on the winter range (no migration involved) vs. the percentage of females with antlers that migrated to four other calving grounds (Bergerud, 1971a).

A homing response to an area is suggested by some further observations in Newfoundland that showed that animals that used the same winter range separated in April and went to different calving grounds (Fig. 9). One group that wintered on the south coast migrated northwest to the Buchans Plateau calving ground; another group moved

TABLE 14. JUNE AERIAL COUNTS OF DOES, YEARLINGS, AND SOME STAGS ON THE CALVING GROUNDS

	Total Caribou Counted by Calving Grounds						
Year	La Poile River	Buchans Plateau	Grey River	Sandy Lake	Pot Hill	Middle Ridge	Mount Peyton
1958	—[1]	—	—	—	600	550	20
1959	—	—	—	100	250	450	80
1960	500	450+	1200	75	250	200	—
1962	650	1000	1300	73	544	502	178
1963	692	643	1800	212	420	265	165
1964	—	1341	1772	123	275	358	257
1965	800	892	2400	161	333	560	253

[1] Accurate counts not secured in years for which no figures are given.

northeast to the Sandy Lake calving ground (Fig. 9). Most significantly, one group did not migrate at all but remained on the winter range and calved at Grey River (Table 14). In 1963 we observed the Sandy Lake group to leave at least a week before the Buchans group. When the Sandy Lake group left snow had disappeared at Sandy Lake, their destination, but was still present on the Buchans Plateau, the destination of the group that waited a week.

The hypothesis of an orientation direction is suggested by the observations that several herds in North America appeared to follow essentially straight line courses to the calving grounds (Fig. 9 and Kelsall, 1968: Map 22). Kelsall reported that animals maintained their courses even on large lakes out-of-sight of land.

I have argued that the directions taken in the fall migration could be based on past movement patterns that led animals to areas where they normally encountered less snow later in the season. The directions taken in the spring migration could be based on traditions but involve the initiation of females who are shifting to areas where their calves have an increased chance of survival. One important survival factor for calves could be the density of wolves. Wolves are present with the herds on the winter range but are less common on the calving grounds on the tundra (Kelsall, 1968).

Such an explanation might partially account for the two populations in Newfoundland that have calving grounds on the winter range. It would have been impossible to reduce contact with wolves by migrating in an island the size of Newfoundland.

If the animals had a migration direction they might normally halt for calving in an area along this route which had less snow cover than surrounding locales. Most of the calving grounds in North America are on exposed, wind-swept terrain and some are on sloping uplands where snow might disappear slightly earlier.

We know that in a late spring barren-ground caribou can calve en route. The locations of the calving grounds could result from a compromise—the furthest areas of reduced snow cover which the animals can normally reach.

If the animals consistently reached the same general area by moving in a specific direction this familiarity could establish a tradition for an area. Calving grounds locations then would depend on both an orientation direction and homing to an area.

Animals initiate migration earlier in some years than others and have further to go in some years. But if homing to an area is involved the animals might vary their rate-of-speed to partly compensate for annual differences in timing and distance. Hence they could still usually reach the same general area.

The data on the return of animals to specific calving grounds are hard to reconcile. The preponderance of the evidence suggests many animals return. Nevertheless, Skoog (1968) clearly documented that major long-term population shifts occur between regions with different calving grounds and the Newfoundland studies suggest differences in the number of animals that return between adjacent years. The return response is not invariable. One possibility that warrants further consideration is that smaller groups can get picked-up and swamped by larger groups and follow the route of the latter (Kelsall, 1968). There seems to be some random-chance-factor interacting with a homing and/or orientation tradition. Social facilitation may be this factor and outweigh individual predilections if the two tendencies are contrary.

Most species of vertebrates have means of spacing themselves across the habitat; territorial behaviour is the most consistent mechanism. Caribou are not territorial and travel in large herds. However, the spring migration and the return of animals to specific calving grounds may be of value in spacing animals or populations. The calving grounds in Newfoundland are widely scattered across the province (Fig. 9). From these loci the animals disperse in July throughout the interior of Newfoundland in the summer. The calving grounds that Kelsall (1968: Map 22) located for barren-ground animals seem to be centrally located in the tundra summer range and are ideally suited to act as centres from which animals can radiate-out across the range.

Unusual Movements

In the past there have been major shifts in the distribution of animals in Alaska and Canada (Skoog, 1968; and Kelsall, 1968). Skoog showed that major shifts have occurred between caribou in central Alaska and those on the Arctic slope. It has been recognized for years that as herds decreased in size their movements became less pronounced. Now Skoog has shown the converse: as densities of the Nelchina Herd have increased from 40,000 to 86,000 animals (1955 to 1964) the movement of the herd has become more pronounced, erratic and less predictable. Skoog (1968) has also documented that in the past when threshold densities of between 5 and 10 animals per square mile have been reached in Alaska, major distributional shifts have resulted and new ranges have been occupied. He argues that these distributional shifts are a social phenomena and have occurred when there was still ample forage. Kelsall (1968) argued the converse of Skoog that unusual distribution shifts occurred at low densities—animals were able to travel in unusual directions for longer distances before encountering other animals and being deflected. Kelsall's theory is based primarily on one observation; Skoog's data seem more extensive and in agreement with findings for most species in which emigration is more frequent at high densities.
However, Kelsall's idea of large groups meeting and being deflected in their movement pattern has merit. Skoog does not indicate what the social stimulus for these unusual movements might be and discounted food, which most biologists might have supposed to be a factor. Possibly, herds increased simply until interherd groups met and one group became the followers and the other the leaders and a range shift resulted.

Caribou fluctuated in numbers in Newfoundland reaching 'highs' perhaps in 1941, 1951 and 1961 (Bergerud, 1971a). When these increases occurred caribou appeared in areas from which they had been absent for years. The animals were usually first noted in the new areas in the fall when they moved out from tree cover. Apparently the dispersal took place during the fly season or fall shuffle. This dispersal seems at odds with the sedentary pattern discussed earlier. My belief is that females and young travel more widely than males and that males make the major shift during the fall shuffle to find females.

Interestingly, when these caribou migrated in the fall they followed routes that had been used during other high populations. Records were secured of animals travelling migration routes that had not been used in the fall for 40 years. Animals may have learned these routes in their summer wandering or perhaps the topography or directional orientation pointed the way.

Resumé of Aggregation and Movement Behaviour

The caribou in Newfoundland were most gregarious during the two seasons when reproductive activities were their main concern, the calving and rutting seasons

(Fig. 2). In both instances the components of the environment which I feel favored grouping were other animals and a place in which to live, the open habitat (Fig. 1). With calving, an interspecific relation is suspected between caribou and wolves; with fall breeding, the relationship is obviously intraspecific. The gregarious behaviour at both times I believe is due primarily to phylogenic contingencies operative through natural selection. To lose one's calf is to fail in contributing to posterity. Similarly failure to breed is to fail in leaving one's genotype in future generations.

Caribou had smaller aggregations at other times of the year (Fig. 2). All the components of the environment were involved, especially the interaction of a place in which to live with insects and the interaction of food with weather (Fig. 1). These environmental responses are variable and the animals appeared capable of showing adaptive modification.

A summary of the movement pattern of caribou is given in Table 15. This pause-shift sequence is taken from Skoog (1968). Skoog apparently felt that caribou were nomadic rather than migratory. I have continued to use the term migratory since some animals do return to the calving grounds, thus fulfilling Heape's (1932) basic definition of migration.

TABLE 15. THE ANNUAL CYCLE OF MOVEMENT IN CARIBOU

Pause-shift Schedule [1]	Factors Involved
Calving Pause	Reproduction of calves
Post-calving Shift	Move to insect relief habitat, also large herd sizes require movement relative to forage
Fly season Pause	Discontinuous insect-relief habitat—not seen if habitat uniform. Also would move more if there is little wind.
Summer Shift	Move to better feeding areas than fly season pause—not seen if food adjacent to fly relief habitat
Summer Pause	Lack of flies plus good forage
Fall Shift	Move to bring sexes together
Rut Pause	Breeding—may not occur if snow becomes general
Early Winter Shift (Fall Migration)	Move to better feeding areas—not seen when animals summer where good relation to availability of winter food
Winter Pause	Discontinuous areas that have a high relative abundance of food; continue to move if relative abundance changes with time.
Spring Shift (Spring Migration)	Move to familiar areas to produce young ?—traditions ?

[1] Taken from Skoog, 1968

Most of the contingencies that affect movement seem to relate to environmental factors that vary and the animals show plasticity in their responses. Hand-reared calves were sedentary, suggesting that the longer movements in spring and fall involved some learning.

Clearly food is the most important contingency in movement. The nomadic behaviour and great variability of facultative responses to food suggest a variable past history of amount and kinds.

Movement patterns tend to remain consistent but not permanent (Skoog, 1968). Possibly the most we can say is that movement is in response to a fine mix of the use of familiar areas, social facilitation and facultative responses to a variable extrinsic environment.

The spring migration and homing tradition are the least understood and will probably require experimental studies rather than further simple tag and release procedures. One crucial test (*sensu* of Hempel, 1966) that might predict conflicting outcomes between the rival hypotheses, of topographical funnelling, directional orientation and homing to an area, would be to capture females from two calving grounds and place them together on the winter range. If both groups returned to their traditional calving ground homing to an area would be supported. If upon release they migrated in the directions they normally take in the spring in contrast to topographical features, an orientation direction could be suspected. A major difficulty would be the possibility of social facilitation in regard to groups which the experimental animals might encounter.

DISTURBANCE BEHAVIOUR

Important factors that have influenced perceptive and escape behaviour have been the open habitat, gregarious herd structure and the predation of wolves. Animals that respond inappropriately to wolves were selected against and thus these disturbance mannerisms appear due to phylogenic contingencies (Fig. 1).

Caribou are adapted to perceive motion but have difficulty detecting motionless objects. Wolves most often approach caribou in the open (Mech, 1970). Wolves must have been an integral part of their perceptive environment since caribou in large herds tolerate the close approach of wolves and flight is commonly not released until the intention movements of the predators are recognized. The speed of caribou and wolves are closely matched so that a caribou can perhaps afford to wait for a close approach in order to gain more information on the intent of the predator.

When an intruder is sighted but not scented caribou frequently approach or circle. This may result, not from curiosity, but from an inability to recognize objects at long distances and the stimulus to identify the object by scent. Again such approach behaviour would argue against the need for healthy caribou to have a long head start in a chase. Studies of wolves showed that chases were usually short and often unsuccessful (review by Mech, 1970).

Scent seems to be the most discerning sense which can release flight behaviour. A strong scent received, prior to visual contact, commonly will cause immediate flight—often the excitation leap is seen. When an object is seen the animals can possibly relate to distance and await further developments; scent may offer less clues to the proximity of danger.

Noise disturbances in the absence of sight or scent usually have little impact (cf. Kelsall, 1968). I studied a herd in Newfoundland that wintered 1 mile from the Canadian National Railway and 2 miles from the Trans-Canada Highway. The sounds of trains, cars, chainsaws, and dynamite produced no visible reaction.

When caribou take flight they normally move to open habitat, in winter they often run out on frozen lakes. This sequence applies to woodland caribou that I have seen in Labrador, Quebec and Newfoundland. D. Simkin (pers. comm.) reported a similar escape reaction for animals in Ontario.

The caribou on the Avalon Peninsula have much greater flushing distances than animals in the interior of the province. Both populations once were associated with wolves and have been heavily hunted by Newfoundlanders. I attribute the difference to the fact that the Avalon herd was reduced to less than 100 animals after wolves became extinct and have argued elsewhere that natural selection could proceed rapidly with such a small gene pool. In the absence of counterselection by wolves the caribou could have developed more effective escape reactions to man.

Female caribou are considerably more wary than males. Females with young are especially wary. For a female to contribute to future generations it is necessary that she successfully rear her young; adequate escape behaviour for herself and calf is essential. The Darwinian fitness of males depends on his successfully siring which depends on dominance in the rut (Bergerud, unpublished). Size and physical condition are important as well as perseverance and attentiveness to females in courtship. These characteristics may be at odds or override interspecific wariness.

Caribou are generally considered unwary by our standards. We consider deer and moose more adept. These species must be able to detect and respond properly to predators in the woods at short distances. This more rapid response makes them appear more wary to us. However, the wolf-caribou interaction forged in open habitats need not be as rapid but still entirely effective for escape against wolves. It is perhaps inappropriate to claim that caribou are not wary in unnatural man-caribou interactions and to argue that deer and moose are more wary because their man interaction more closely resembles their natural predator interaction in forest cover.

MANAGEMENT IMPLICATIONS

Concept That Caribou are Wilderness Animals

The caribou has frequently been called a wilderness animal. Management plans often start with this premise, which we substitute for our lack of specific knowledge of the behaviour and habitat requirements of caribou.[1] Three ideas seem intertwined in the concept: (1) caribou need undisturbed lichen plant communities as part of their habitat; (2) caribou have an inherent adversion to man and his activities and cannot live near civilization; and (3) caribou are unwary and susceptible to overhunting.

However, in the first place, caribou do not require climax plant communities nor do they need lichens. Populations in Alaska and on South Georgia Island live mostly on sedges (see review by Skoog, 1968). Caribou will also use habitat that has been logged or burned. Much of north-central Newfoundland has been logged and burned since 1940 (Bergerud, 1971c: see Fig. 1). Caribou are found throughout these areas in summer. For example, in June 1958, I noted 10 of 41 stag groups and 24 of 181 doe groups in disturbed habitats (see also Fig. 3). What these animals did seek in the fly season was habitat to gain relief from insects. Small patches of timber can provide that habitat. Logging and forest fires in Newfoundland often resulted in a patchwork of denuded areas and small patches of closed-canopy conifers. The caribou used the forest islands to gain relief from insects and the disturbed areas for feeding on deciduous shrubs.

The seriousness of human disturbance should be considered in the light of perceptive and escape adaptations which caribou have evolved in association with wolves. For example, a road or a building are not factors that have been prior phylogenic contingencies. Caribou have no aversion to roads or railroads in Newfoundland (cf. Klein, 1971); they are more open tundra to travel upon. Animals in Newfoundland even detour to be able to walk along roads. Further, the noise of a car is cause for only a temporary alert. However, the motion of a car is a stimulus for flight. A road could be a barrier if the vehicle activity is such that strange moving objects are perceived continuously. Many caribou in Newfoundland cross the Trans-Canada Highway in the early morning hours prior to traffic. Airplanes again provide motion; the helicopter more so than fixed wing. Again caribou pay little heed to high flying planes when the noise is heard but the motion not perceived.

Caribou can live close to civilization. The Avalon herd in Newfoundland uses ranges within a mile of a well-travelled highway. The Humber herd winters on ranges where cars and trains are heard daily. Caribou in the Gaspe Peninsula, Quebec, feed in the winter on arboreal lichens on trees recently cut by loggers. The behaviour of barren-ground caribou of crossing roads and railroads and even passing through communities is well documented.

The use by caribou of open habitats plus their gregarious herd structure and inability to perceive motionless objects makes them extremely vulnerable to hunting. Caribou probably often do not live near man because adjacent populations have been over-exploited. Phylogenically there appears little aversion to man—caribou can live near man if we permit it.

Caribou are wilderness animals in one sense; large herds need vast areas to wander in. The gregarious herd structure superimposed on the slow-growing fragile Arctic flora requires continuous wandering and vast areas if populations are large.

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[1] See also Geist, 1971, in Duffey and Watt (eds.) The Scientific Management of Animal and Plant Communities for Conservation. Blackwell, London.

In summary, I suggest that the open habitat-wolf-caribou interaction has consequences not liable to rapid modification. We might expect caribou to continue to be unwary towards man, gregarious and vulnerable to hunting, as long as wolves are part of their environment and breeding populations are large. In situations in which food, insects or weather are important considerations in behaviour, a plastic response might be expected. We might expect adaptive modification to human activities that affect these latter components of the natural environment of caribou.

Predation

It has been suggested at this conference that when we harvest ungulates which no longer have natural predators we should attempt to remove animals that are behaviourally and demographically similar to those a natural predator would take. This view is not necessarily correct because it presupposes that behavioural adaptations that provide fitness are the same in habitats with and without predators. Selection by predators will favor nothing but fitness to that particular type of predation and will not necessarily make succeeding generations more fit to meet circumstances other than those of predation.

Predator A selects for adaptive fitness in prey B only and wholly in the context of the presence of predator A as an environmental contingency. For example, wolves interacting with caribou in open habitats may have favoured the ability of caribou to detect motion. In an environment without wolves this ability may no longer be needed. It has been my argument that caribou might be more wary to man in a wolf-free habitat; in the absence of wolves they might develop better visual acuity to recognize the shapes of men. Their inability to recognize hunters that are motionless— to be unwary to man— has contributed to their overexploitation.

We often assume, uncritically, that predation is 'good' for a prey population. In essence predation selects against conspicuous animals. Predation results in prey population being more uniform in response to predators. Hence predation reduces behavioural plasticity and conceivably could reduce the ability of species to respond to other environmental components.

Wildlife managers will have to decide what behaviour patterns they want their populations lacking natural predators to possess. If they want animals less liable to overexploitation they should harvest those that have poor escape patterns interacting with man. If they desire unwary animals, perhaps a population that can be seen in a park, they should harvest the more wary.

Restocking of Caribou

Until quite recently there has been a hesitancy on the part of wildlife managers to restock caribou on depleted ranges. This reluctance stemmed in part from the concept that caribou are wilderness animals requiring undisturbed lichen pastures far removed from man's activity, and that caribou would leave the introduction sites.

I believe caribou can be successfully introduced to many former ranges. Firstly, I argue that the decline of caribou in most of North America in the late 1800's and early 1900's resulted from increased mortality from hunting and possibly predation and not from range destruction *per se* (in preparation). If this is valid, local populations and their tradition for local areas were eliminated. Secondly, caribou do not require climax lichen pastures in remote areas. Suitable areas are available for re-establishment.

What is required is to find procedures that will increase the likelihood that the released animals will remain where released. One program that appeared successful in Newfoundland was to release hand-reared calves. These calves remained at the release site (Table 11). The following year wild calves were released at one site. The wild calves followed the leadership of the tame animals, now yearlings, and remained in the area. With such a program, the hand-reared animals could be removed from the population if they became dangerous as tame adults, thus leaving the wild component with an established tradition. Another possibility that may suffice, is simply to release wild calves that have not migrated. Certainly the stock least likely to remain in the area and become established are adults captured in the wild (cf. Dunn, 1965).

At the present time re-establishment programs are in progress in Quebec, Nova Scotia, Newfoundland and Southhampton Island, Canada. Hopefully, these studies will provide more information on how to establish traditions for restocking purposes.

CONCLUSIONS

The Arctic environment is characterized as relatively simple and uniform (cf. Dymond, 1947; Solomon, 1949; and Odum, 1953). Heterogeneity is to a considerable extent provided by changes in time—daily and seasonal weather patterns. The resources of such an eco-system would be fine-grain (*sensu* of MacArthur and Connell, 1966) relative to the needs of the animals. Caribou could not stay within habitats and specialize. Mobility permitted the animals to optimize their contacts with this uniform pattern in space yet take advantage of variability in time.

I would argue that the basic adaptation caribou have to their extrinsic environment is their continuous movement. If this is so we might ask relative to the more specific—annual pause—shift schedule (Table 15), not why they shift but why they pause.

They pause because at this moment in time it is relatively more favourable in their interaction with the extrinsic environment to be where they are than elsewhere. However, this temporal-space optimum will soon be altered and it will be more advantageous to be elsewhere. Hence, caribou always seem ready to go and can take advantage of a variable weather regime superimposed on a simple physical regime.

Social facilitation appears to be an important aspect of the ability of caribou to optimize patterns in time and space. Caribou groups show a degree of openness, permeability (Lent, 1966a). Animals can join groups with ease. An animal can take advantage of a local food supply or insect-relief habitats located by others. Again animals frequently leave groups and groups separate. Lent (1966a) speaks of the temporary nature of a specific group and of the continued dynamic process of group formation. There is a strong following response among adults yet no lack of individuals to initiate action. Perhaps a compromise was needed between taking advantage of what others were doing and being able to take independent action when numbers were too large for fine-grain habitats or when moving herds encountered adverse topographical features.

Klopfer (1969) has distinguished between adaptation and adaptability in behavioural responses. He argues that adaptation and adaptability may be inversely proportional in some species. Caribou, on the contrary, seem to be both highly adapted and highly adaptable. The harsh but simple Arctic ecosystem would require adaptation. The equally important weather variability would suggest a premium on adaptability to optimize changes with time. The major adaptation that caribou may have is their adaptability.

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Paper No. 30

Comparison of Ungulate Adaptations in the New World and Old World Tropical Forests with Special Reference to Ceylon and the Rainforests of Central America

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ABSTRACT

Ungulate feeding niches are compared and contrasted for the Old World and New World tropics. Ungulate evolution has shown a trend toward increasing specialization for the exploitation of open areas supporting herbaceous vegetation. Exploitation of open areas by ungulates has involved the evolution of morphological adaptations permitting speed as a means of predator avoidance. Movement in cohesive social groupings is a characteristic behavioral attribute of ungulates adapted for savanna life. With the exception of swine, forest adapted ungulates tend to be semi-solitary.

Ungulate species which have remained adapted to forest life have the benefit of increased cover as a means of avoiding predators but they must sustain populations in the face of reduced availability of food, since the bulk of the vegetation in the forest is unavailable for direct exploitation by terrestrial ungulates. Mature rainforest for both the New World and Old World tropics has a less diverse and less dense terrestrial ungulate fauna when compared with the savanna. In both the New World and Old World forests, arboreal herbivores show a high density and a high diversity. Tropical grasslands support the highest biomass of terrestrial ungulates.

Ungulates, either forest adapted or savanna adapted, have a variety of anti-predator strategies which are outlined. Responses of savanna-adapted and forest-adapted ungulates to predators are compared and contrasted. It is suggested that forest ungulates take advantage of the cover in the forest and remain inconspicuous as a major means of anti-predator behavior. Furthermore, forest ungulates usually live at low densities. A small social group or solitary behavior may be a combined adaptation to (1) reduce competition for food and (2) remain inconspicuous thus avoiding predator detection.

It is concluded that a remarkable convergence can be demonstrated when forest adapted ungulates of the Neotropics are compared with ungulates of the Old World tropics, especially with respect to anti-predator mechanisms, coloration and size.

I. INTRODUCTION

This symposium is concerned with the behavior and ecology of ungulates. The term 'ungulate' in its extended form includes the following extant mammalian superorders: (1) Protungulata, Order Tubulidentata; (2) Paenungulata Orders Hyracoidea, Proboscidea, and Sirenia; (3) Mesaxonia, Order Perissodactyla; and (4) Paraxonia, Order Artiodactyla. These ordinal taxa show a great variety in morphology but, with the exception of the Tubulidentata, all show within their ordinal radiation a uniform tendency toward the utilization of plants and plant products for their primary food resources (Simpson, 1945). Differences in morphology reflect in part different specializations for procuring and processing plant material. Differences in gut morphology reflect (within the Perissodactyla and Artiodactyla) greater and greater dependency on bacterial and/or protozoan symbionts for the fermentation and breakdown of plant bi-products within specialized portions of the digestive tract; thus allowing the 'host' to utilize the bi-products of microbial metabolism and, in many cases, the surplus productivity of the microbial symbionts themselves (Hungate, 1960). Our concentration in this symposium then is with several Orders of mammals which have evolved methods of feeding and metabolizing plant parts. Many differences in morphology among the species of these herbivorous Orders are attributable not only to differences in procuring food but also to differences in predator avoidance and differences in social and breeding systems. Because our primary focus is on the terrestrially adapted herbivores, we are in essence dealing with Orders (especially the Artiodactyla and Perissodactyla) which have shown increased adaptations for speed; and one can conclude that a digitigrade mode of locomotion and the accompanying skeletal and muscle changes have been to a large extent in response to continual selection by predators (Howell, 1965).

The tropical rainforest is not a habitat type that encourages either a high density or a high diversity of large, terrestrial herbivores. Typically most species of Artiodactyla and Perissodactyla are adapted to an open savanna condition, either a tall grass savanna or in more arid climates a short grass steppe. Foraging on grasses in the open requires an adequate predator avoidance technique which for the most part involves reliance on early detection of the predator and avoidance through speed. In the short grass prairies and steppe country, the ungulate can hardly avoid being conspicuous to some extent. Mature forest provides cover to an extent but it does not offer low stature herbaceous vegetation at a high cover density which, if it were available, would be within easy reach of most mammals for feeding. Mature forest generally contains a rather thin undergrowth which allows for some grazing, but most herbivores have to supplement their diet with fruits and nuts. Within a forest the bulk of the plant material is locked in the form of cellulose contained in the trunks of trees or available together with more easily digested plant materials in the leaves which are beyond the reach of terrestrial ungulates (Fig. 1). Thus, the carrying capacity of a mature forest region is reduced for the terrestrial herbivores. In order to effectively graze and browse in a forest, a terrestrial herbivore is obliged to live at thin densities and, if the species is non-migratory, then intraspecific spacing mechanisms become important. An open forest condition or an interface between forest and grassland allows for the maximum in diversity and density of herbivores for the tropical regions but the true forest itself supports a *less diverse* ungulate fauna at *thinner* densities.

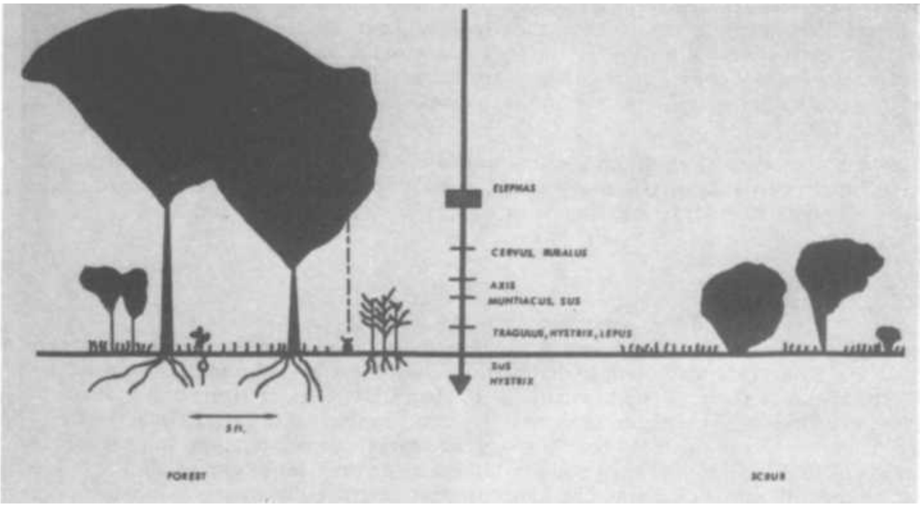

Fig. 1. Feeding heights of herbivorous mammals found in the Ceylon dry zone. The elephant has the tallest reach and can utilize forested habitats to a greater extent than any other ungulate. All things being equal, grazing ungulates are favored by discontinuous forest or discontinuous scrub and least favored in a continuously forested habitat with maximal shade and a minimum of herbaceous vegetation.

This is not to say that the herbivorous mammal diversity is low in the tropical rainforest, quite to the contrary. Diversity is low only with respect to terrestrial herbivores but the equally important plant feeders which are arboreal, show a high diversity of forms and exist at significant densities. The arboreal niches achieve tremendous importance in the tropics where, in contrast to the temperate zone, deciduous trees and broad-leafed evergreen trees may collectively present an almost unbroken stage of foliation; thus providing arboreal herbivores with a food reserve accessible

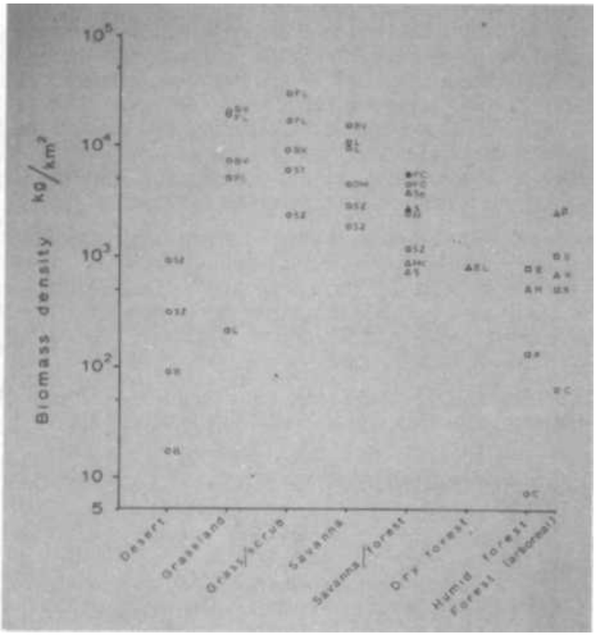

Fig. 2. Biomass comparisons for seven tropical habitat types. Biomasses are plotted on a log scale. All plots include only mammalian herbivores. The extreme right hand series is restricted to arboreal herbivores; the remaining vertical series include only terrestrial herbivores. Terrestrial herbivores show the highest concentrations in grassland, grass scrub, and savanna biomes, and show the lowest levels in the desert and humid forest habitats. Arboreal herbivore biomasses are significant in humid forest habitats. Blackened symbols include domestic livestock with wild ungulate estimates. Open symbols refer to wild populations only.

○ = Africa; △ = Asia; □ = Neotropics.

Sources: B (Bourliere, 1963); BV. (Bourliere and Verschuren, 1960); C (Collins, 1959); DM (Dasmann and Mossman, 1961); E (Eisenberg, unpublished estimates for Barro Colorado Island); EL (Eisenberg and Lockhart, 1972); FL (Field and Laws, 1970); FC (Foster and Coe, 1968); L (Lamprey, 1964); H (Hoogewerf, 1970); M (Mentis, 1970); Mc (McKay, in press); P (unpublished estimate for Polonnaruwa, Ceylon-Eisenberg, Muckenhirn and Dittus); S (Schaller, 1967); ST (Stewart and Talbot, 1961); SZ (Stewart and Zaphiro, 1963); Sp (Spillet, 1966); R (Rudran, 1970); X (Eisenberg computations for Gwamba, British Guiana, adapted from data for Operation Gwamba assuming 15. 5 km^2 sample size).

the year round. It is not surprising, then, in an area that does not experience synchronous deciduation of broad-leafed trees that we find among strictly arboreal animals a multiplicity of adaptations for the utilization of plant parts and especially cellulose. In the tropics and subtropics arboreal members of the mammalian orders Rodentia, Edentata, Primates, and Marsupialia are equivalent to the higher ungulates with respect to their abilities to graze, browse, and utilize cellulose (Bauchop and Martucci, 1968;Denis *et al.*, 1967). These arboreal forms have been under different types of predator selection than their terrestrial counterparts and their adaptive strategies often seem somewhat bizarre (e.g., the sloth, *Bradypus*).

A comparison of biomass levels achieved by the larger herbivores in tropical rainforest and in savanna situations is revealing (Fig. 2). Previous treatments of biomass data have demonstrated the reduced carrying capacity for ungulates within tropical forest biomes (Bourliere, 1963). However, the biomass of arboreal herbivores was largely neglected. Although the wet savanna undoubtedly will support the highest biomass of herbivores, Fig. 2 illustrates that when the biomass of herbivorous arboreal forms is included with that of terrestrial forms, the biomass of herbivores in the tropical forest is comparable with that found in some savanna estimates.

In correspondence with the reduced density of terrestrial forest ungulates, one also notes a corresponding decrease in the number of species when the forest biomes are compared to the savanna (see Table 1). This is true only if the biomes are kept conceptually separate; of course, ecotone areas or forest/savanna interfaces exhibit the maximum diversity for any given geographical area (Dasman, 1966; Leopold, 1934; Eisenberg and Lockhart, 1972).

To sum up, then, regardless of the geographical area the tropical forest biomes at moderate to low elevations will exhibit, in contrast to the savanna, an increased di-

TABLE 1A. TERRESTRIAL HERBIVORE GENERA*–A GEOGRAPHICAL COMPARISON

Number of Genera for Geographical Areas	High Altitude Steppe	Temperate Forest	Sub-tropical Gallery Forest	Tall Grass Steppe	Short Grass Scrub Steppe	Arid Steppe
South America 32° S						
Cervidae	1 (?)	2	1	1		
Camelidae	1				1	1
Tayassuidae			1			
Chinchillidae				1		
Cavidae					1	
	2	2	2	2	2	1
India- Pakistan 30° N						
Bovidae	3	2			1	1
Cervidae		2	2	2	1	
Suidae		1	1	1		
Leporidae					1	1
	3	5	3	3	3	2

* Hare size or larger. See Table 2 for reference

TABLE 1B.

	Tropical Evergreen Forest	Semi-deciduous Tropical Forest (with grassland	Dry Deciduous Forest (with grassland)	Semi-arid** Savanna
Central and South America 10° N				
Cervidae	1	2	1	
Tayassuidae	1	1	1	
Tapiridae	1	1	1	
Dasyproctidae	2	2	1	
Cuniculidae	1	1		
Hydrochoeridae	1	1		
Leporidae		1	1	
	7	9	4	
India 15° N				
Bovidae	1	4	3	
Cervidae	2(3)	3	3	1
Tragulidae	1	1	1	
Suidae	1	1	1	
Elephantidae	1	1	1	
Hystricidae		1	1	1
Leporidae			1	1
	6 (7)	11	11	6

** Almost non-existent at this latitude in Neotropics.

versity and biomass of arboreal herbivores, a decreased biomass of terrestrial herbivores, and a decreased diversity in the number of species of terrestrial herbivores. A comparison of biomass for Ceylon and Barro Colorado Island in Panama substantiates the statements made in the previous sentences with respect to herbivore diversity, terrestrial forms, arboreal forms, and biomass (see Fig. 3).

II. CONVERGENT AND PARALLEL EVOLUTION IN THE RAINFORESTS

This brings us to our first topic of consideration, namely the case for convergence and/or parallelism. The Neotropical Realm is confined almost entirely to the continent of South America which underwent prolonged geological isolation. The history of land mammalian fauna in South America has been amply reviewed by Simpson (1969) and Patterson arid Pascual (1968), while the present distribution of genera within the Neotropics has been reviewed by Hershkovitz (1958, 1969). When we compare the Paleotropics with the Neotropics, the terrestrial herbivore diversity is low for the Neotropics (Table 1). This is a uniform generalization for all habitat types. Herbivores had a fantastic diversity in the Neotropics before the Pliocene and the story of the rise and fall of the terrestrial mammals in the Neotropics has been well documented by Simpson (1969). A comparison of trophic exploitation for the Neotropics and Paleotropics (Table 2) will indicate however that niches are occupied in a convergent fashion and that the herbivorous terrestrial niches of the Neotropics have been

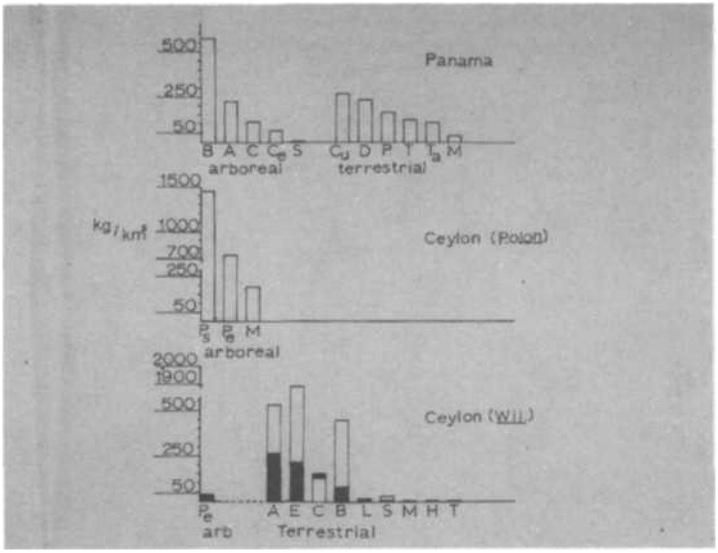

Fig. 3 Biomass comparisons for Panama and Ceylon. Two graphs for Ceylon are presented since the Wilpattu census was carried out in arid zone, scrub forest or low stature forest which does not support high primate densities; and the Polonnaruwa census includes a small block of mature forest supporting a low, wild ungulate density. The data for Panama were obtained from Barro Colorado Island which supports an artificially low level of larger forest ungulates. Given these limitations, the following inferences are possible. Arboreal herbivore biomasses are favored in forested habitats. Terrestrial herbivore concentrations are not spectacular in forested habitats. The Ceylon (Wilpattu) calculations portray both crude biomass (black bars) and biomass at concentration density (white bars).

Legend: Panama: B (*Bradypus*); A (*Alouatta*); C (*Choloepus*). Ce (*Cebus*); S (*Saguinus*); Cu (*Cuniculus*); D (*Dasyprocta*); P (*Proechimys*); T (*Tayassu*); Ta. (*Tapirus*); M (*Mazama*). Ceylon: Ps (*Presbytis senex*); Pe (*Presbytis entellus*): M (*Macaca sinica*); A (*Axis*); E (*Elephas*); C (*Cervus*); B (*Bubalus*); L (*Lepus*), S (*SuS*); M (*Muntiacus*); H (*Hystrix*); T (*Tragulus*).

occupied in part by rodents of the suborder Caviomorpha (Dubost, 1968). In both the Old World and the New World, the arboreal browsing niche is occupied in a convergent fashion.

An inspection of Table 2 will acquaint the reader with the manner in which the various feeding niches are filled for three tropical forested areas: Ceylon, Panama and Ghana. Arboreal browsers and grazers in the tropics belong primarily to the Orders Primates and Edentata. The browsing edentates, *Bradypus* and *Choloepus,* are a unique relict stock which appear to occupy the Neotropical arboreal browsing niche to a degree unparalleled in the Paleotropics, where Primates of the genera *Colobus* and *Presbytis* exploit the foliage to varying degrees but are not as highly evolved herbivores as are the sloths (Bauchop and Martucci, 1968;denis *et al.*, 1967).

In a recent article Dubost (1968) pointed out that a remarkable convergence exists when the form and ecology of the Cervidae and Caviomorph rodents of South America

TABLE 2. SOME TROPHIC COMPARISONS

	Myrmecophagous	Frugivore/Granivore (Carnivore)			Frugivore/ Browser		Browser/Grazer
Arboreal							
Ceylon		*Macaca radiata* *Ratufa macrura*			*Presbytis entellus* *Petaurista*		*Presbytis senex*
Panama	*Cyclopes* *Tamandua*	*Cebus capucinus* *Ateles geoffroyi* *Sciurus* sp.			*Alouatta villosa* *Choloepus hoffmctnni* *Coendou prehensalis*		*Bradypus infuscatus*
Ghana	*Manis longicaudata* *Manis tricuspis*	*Cercopithecus diana* *Cercopithecus mona* *Cercocebus torquatus* [Various Sciuridae]	*Pan troglodytes*			*Colobus polykomos* *Colobus badius* *Colobus verus*	
Terrestrial							
Ceylon	*Manis crassicaiudata*	*Hystrix indica*	*Sus*	*Tragulus*			*Muntiacus* *Lepus nigricollis* *Elephas maximus* *Axis axis* *Bubalus bubalis* *Cervus* (*Rusa*) *unicolor*
Panama	*Myrmecophaga*	*Dasyprocta* (*H*) (*Myoprocta*)		*Cuniculus*		*Tapirus bairdii* (*Hydrochoerus*}	*Sylvilagus* *Mazama* *Odocoileus*
Ghana	*Manis gigantea*	*Hystrix cristata*	(*Potamochoerus*)	*Hyemoschus*		(*Hippopotamus*) *Neotragus pygmaeus*	(*Loxodonta africana*) *Philantomba maxwelli* *Cephalophus dorsalis* (+ 4 other species) *Tragelaphus* (2 species)

H = Hoarder

Note: General information concerning the distribution, habitat preferences, and feeding behavior of the individual species was obtained in part from: Eisenberg and McKay (1970) and Phillips (1935) for Ceylon; Prater (1965) and Schaller (1967) for India and Pakistan; Cabrera and Yepes (1960) and Hershkovitz (1958, 1969) for South America; Goldman (1920), Handley (1966) and Enders (1935) for Panama; Leopold (1959) for Mexico;Dubost (1968) and Dorst and Dandelot (1970) for West Africa. In addition, the status and distribution of the South American Cervidae and Camelidae were assessed from Osgood (1934), Krumbiegel (1942), MacDonagh (1940), Krieg (1925) and Jungius (1971).

are compared with the Tragulidae and Bovidae of Gabon. At this point it is convenient to re-examine some of the suggestions made by Dubost and to compare quite closely the Neotropical herbivorous niches with those of India and Ceylon. Some reference will be made to West Africa in the course of the discussion but in the main our focus will be on the Asian and Neotropical forms.

In his article, Dubost made careful comparison between the external morphology of the Neotropical Caviomorphs and the smaller forest ungulates of Gabon. That a remarkable morphological convergence exists cannot be denied. Extending his observations to the Indian subcontinent, it is fair to say that the following similarities in external morphology can be noted when the three areas are compared. The Neotropical Cervid genus, *Mazama,* which shows a strong correspondence with some species of the bovine genus *Cephalophus* from West Africa, shows a similar correspondence in morphology with the Asiatic genus *Muntiacus.* The Asiatic genus *Tragulus* (*Moschiola*) *meminna* shows a convergence with the Neotropical *Cuniculus,* as does the West African Traguline genus *Hyemoschus.* The Neotropical genus *Dasyprocta* shows a strong morphological convergence toward the West African bovine genus *Neotragus* and superficially resembles the Asiatic chevrotains, *Tragulus napu* and *T. javanicus.*

In size, coloration, and general body form the Neotropical rodent genera *Dasyprocta* and *Myoprocta* bear some resemblance to the African genus *Neotragus* and the smaller species of the genus *Cephalophus.* These small caviomorphs are, however, not ruminants as are their African and Asian counterparts. The agouti and acouchi must obtain their food in the form of fruits, seeds, and nuts. In addition, both of these species share with many other rodents in the characteristic of food hoarding, a trait unknown in any of the ungulates (Enders, 1935; Morris, 1962; Smythe, 1970a).

The Neotropical caviomorph genus *Cuniculus,* on the other hand, is not a food hoarder and the elaborate development of its caecum suggests that the animal can harbor bacterial symbionts which permit it to effectively use cellulose in its diet. *Cuniculus,* although a frugivore,is also a browser at certain seasons of the year (Smythe, 1970a) and exploits in a manner more reminiscent of the Old World smaller ungulates than is the case with the sympatric *Dasyprocta.* Hence, *Cuniculus* is occupying a trophic niche somewhat similar to that of its Old World counterparts, the mousedeer *Tragulus meminna* and *Hyemoschus aquaticus,* than is the case when the trophic comparison is made between *Dasyprocta* and *Neotragus.*

III. SOME COMPARISONS

An inspection of Table 3 will indicate that most forest ungulates are characterized by a dispersed form of social organization. Occasional groups will assemble at prime grazing areas or at water holes but the only cohesive, mobile social unit is either the mother and her young or a temporary courting pair. Most species appear to show an antipredator strategy which involves freezing or fleeing while emitting a characteristic warning cry. The swine are notable exceptions to the above generalizations.

Leaving aside the larger forest herbivores of West Africa, such as *Boocerus* and *Tragelaphus,*[1] with their Asian counterparts, *Cervus* (*Rusa*), we may turn to the smaller herbivores of Asia and the Neotropics for some close comparisons of functionally related behavior patterns.

(a) The Cervidae

Unfortunately detailed field studies on the behavior of deer are only now underway. The communication system for *Odocoileus* can in part be pieced together from general descriptive accounts (Cowan, 1956; Severinghaus and Cheatum, 1956; Linsdale and Tomich, 1935; Geist, 1966). Recently Muller-Schwarze (1971) has published on the

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[1] The larger forest antelopes as well as the genus *Cervus* may well represent secondary adaptations to the forest, and the cervid genera *Odocoileus, Mazama, Muntiacus,* as well as the Cephalophinae, Suidae, and Tragulidae, probably represent a phylogenetically 'old' forest adaptation.

TABLE 3. COMPARISONS OF FOREST ADAPTED TERRESTRIAL HERBIVORES

Species	Study Area	Grouping Tendency	Major Anti-Predator Strategies	Remarks	Authority
Bovidae:					
Tragelaphus spekei	Kenya	1-2	–	–	Owen, 1970
Tragelaphus scriptus	Botswana	1-2	–	Occasionally larger groupings	Elder & Elder, 1970
Cephalophus silvicultor	Gabon	1-2	Flight with whistle	–	Dubost, 1968
Cephalophus (Philantomba) maxwelli	Gabon, Congo	1-2	Flight with whistle	–	Dubost, 1968; Aeschleman, 1963
Neotragus pygmaeus	Gabon	1-2	Flight with warning cry	–	Dubost, 1968
Tragulidae:					
Hyemoschus aquaticus	Gabon	1-2	–	–	Dubost, 1968
Suidae:					
Polamochoerus porcus	Congo	6-20	May show group attack; warning grunts and flight	Large home range, highly mobile	Shortridge, 1934 Roberts, 1951
Cervidae:					
Cervus (Rusa) unicolor	Ceylon	1-7 (Av. 1-3)	Flight with warning cry	–	Eisenberg & Lockhart, 1972
Muntiacus muntjac	Ceylon	1-2	Flight with warning bark	–	Eisenberg & Lockhart, 1972
Tragulidae:					
Tragulus meminna	Ceylon	1-2	Flight with warning cry	–	Eisenberg & Lockhart, 1972
Suidae:					
Sus scrofa	Ceylon	1-30 (Av. 1-7)	May show group attack; warning grunts and flight	–	Eisenberg & Lockhart, 1972
Cervidae:					
Odocoileus virginiana	Panama, Mexico	1-5	Flight and tail flagging	–	Leopold, 1959
Mazama americana	Panama, Mexico	1-3	Flight without a sound	–	Leopold, 1959
Dasyproctidae:					
Dasyprocta punctata	Panama	1-2	Flight with warning cry	–	Smythe, 1970a
Cuniculus paca	Panama	1-2 (3)	Flight with warning bark	–	Smythe, 1970a
Tayassuidae:					
Tayassu tajacu	Panama	3-20 (Av. 8-12)	May show group attack or flight with warning bark	–	Smythe, 1970a; Enders, 1935

chemical communication system of *O. hemionus.* Our understanding of the muntjac is less complete (see Dubost, 1970; Eisenberg and Lockhart, 1972) and the behavior of *Mazama* is still anecdotal.

Although *Odocoileus* can exhibit large social groupings at winter feeding areas, especially in areas which have seen the extermination of natural predators, it is fair to say that under less disturbed conditions these deer do not exhibit cohesive social groupings beyond the mother family. Chemical traces apparently provide different types of information to conspecifics. This form of indirect communication may in part be responsible for spacing as well as attracting members of the opposite sex. The problem is given an excellent review by Müller-Scharze (1971).

Antipredator behavior involves snorting with or without stamping followed by flight. Slow flight characteristically involves raising the tail and displaying the white underside. This tail display with a slow bounding gait may be considered an 'attraction display' which will be discussed later.

The muntjac (*Muntiacus muntjac*) is also quite solitary in its habits. Adult males are well spaced and marking bushes with the preorbital gland secretions may well be involved in the spacing phenomenon. Adult females may show tolerance toward their own daughters and share a home range with them but strange adult females maintain spacing. Anti-predator behavior involves raising the tail and erecting the white rump hairs. Flight may be accompanied by growls but the characteristic warning bark is generally delivered when the animal is motionless facing the disturbance and at a reasonable distance from the potential predator.

The brocket (*Mazama americana*) is 'solitary' to the extent described for the muntjac. Adults appear to live in small, permanent home ranges (Hall and Dalquest, 1963; Leopold, 1959). It tends to flee silently when disturbed and may slip away almost unnoticed by a human observer; however, we have noted flight behavior where the white underside of the tail was prominently displayed. The preorbital glands are poorly developed and its marking behavior remains to be investigated.

(b) The Tragulidae

Tragulus meminna is crepuscular or nocturnal in its activity rhythm. The dorsal pelage exhibits longitudinal rows of spots which may fuse to form stripes. The animal appears to be solitary in its movements but there is good evidence that several animals (3-4) may be in auditory contact with one another (Eisenberg and Lockhart, 1972). They emit a reedy grunt as a warning cry, which may be produced while running away. The male of *T. javanicus* and *T. napu* possess a chin gland with which they mark their environment, but the functional significance remains to be studied.

Dubost (1968) has outlined some of the behavior patterns shown by *Hyemoschus* in Gabon. Interestingly enough, *Hyemoschus* frequently takes refuge in water during escape behavior—a trait shared with the paca (*Cuniculus paca*) of the Neotropics; but seeking refuge in water is not characteristic of *Tragulus. Tragulus meminna, Hyemoschus aquaticus,* and *Cuniculus paca* are all nocturnal in their habits and all three exhibit a spotted coat which suggests some common camouflage function in response to predator selection.[1]

(c) The Wild Swine

Compared to the preceding species, the swine (Tayassuidae and Suidae) are somewhat exceptional. These species are not ruminants and, although they may browse or graze at some seasons of the year, they tend to feed as general omnivores often seeking subterranean roots, corms, bulbs and fungi. Typically swine form 'sounders' which consist of one to four adult females and their progeny. The sounder is essentially a matriarchy which is joined at various intervals by adult males which are often semi-solitary for part of the year. Group size and cohesiveness will vary in swine depending on the habitat and predation pressure, but the point to be made is that groups of swine can and do exhibit active, offensive behaviors toward predators. This is not to

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[1] *Tragulus javanicus* does not exhibit a spotted coat, and may be more diurnal in its habits.

imply that swine fail to exhibit flight behavior when disturbed. Quite to the contrary, flight is a normal response to a predator; however, the possibility for group or individual attack remains. Flight behavior generally involves emitting a bark-like grunt, wheeling and running off. Several short grunts may be produced while running away.

Swine may produce low contact grunts while moving as a sounder; thus cohesion can be maintained. Chemical communication is of definite importance since the urine of estrous females is attractive to males. In addition, rolling in special communal wallows and rubbing the body on certain trees all contribute to the maintenance of a group odor as well as impregnating the sounder's home range with such odors.

The Tayassuidae have a specialized cutaneous gland in the posterior mid-dorsal region. The gland will emit a musky odor when the animal is aroused while exhibiting mid-dorsal piloerection. In addition, secretions of this gland are smeared on the cheeks of a partner whenever the two animals engage in mutual 'cheek rubbing'. This latter behavior occurs when two animals align their body axes in opposite directions while rubbing their cheeks on the partner's side or back. The dorsal gland secretions of individual members can thus be spread throughout the sounder, creating the possibility for a group odor (Enders, 1935; personal observations).

As one might suspect, given the omnivorous diet and larger social grouping, swine sounders may have large home ranges compared to other forest ungulates of comparable size (see Smythe, 1970a; Enders, 1935; and Leopold, 1959 for *Tayassu;* Eisenberg and Lockhart, 1972, and Gründlach, 1968 for *Sus scrofa;* Roberts, 1951, and Shortridge, 1934 for *Potomochoerus*).

(d) The Tapirs

The Central American tapir (*Tapirus bairdii*) and related New World species have an Old World counterpart, the Malay tapir (*Tapirus indicus*). Unfortunately the latter species has not been studied in any detail but what little we know suggests that its behavior is similar to that of *T. bairdii.* Baird's tapir is generally found in heavy forest near permanent water. It is a grazer and a browser with a nocturnal activity pattern (Enders, 1935). In contrast to the swine, this forest-adapted perissodactylan does not form a cohesive group. The home ranges of adults overlap extensively but the female and her young of the year comprise the only cohesive social unit. Resident tapirs will use the same trails in common and occasionally feeding aggregations will develop in prime grazing areas. Young and nursing female tapirs produce a monosyllabic note which serves to maintain auditory contact between them while moving in the forest. A similar low grunt can serve to localize and perhaps identify adult tapirs who are near one another but are out of visual contact (Hunsaker and Hahn, 1965). Unfortunately almost nothing is known concerning the role of chemical communication in this species.

(e) The Cursorial Caviomorph Rodents

Field studies by Smythe (1970a) have revealed some important features concerning the behavior of *Dasyprocta* and *Cuniculus.* Captive studies on *Myoprocta* (Kleiman, 1971) have allowed us some insight into the mechanisms of communication employed by the Dasyproctidae.

Dasyprocta and *Myoprocta* employ chemical communication in coordinating the activities of a resident population. Urine marking is involved in courtship and mating, whereas territorial scent marking is accomplished with anal gland secretions. The male scent-marks more frequently than the female and he marks most heavily at the boundaries of his territory (Smythe, 1970a).

During antipredator behavior, auditory communication by *Dasyprocta* involves thumping with the hind feet. This thumping may attract other members of the 'community' which will join in a mobbing response toward a slow moving terrestrial predator, such as a snake. An alarm bark is also produced when the animal is startled and flees. This call is generally given when the animal is in full flight. The acouchi (*Myoprocta*) thumps while uttering a screeching call in circumstances much like those which elicit thumping in agoutis. Other aspects of alarm behavior in the acouchi have not been studied in the field. The paca (*Cuniculus*) has a thumping response also, but mobbing behavior does not result. Pacas will often utter a short growl while fleeing.

The agouti exhibits a strong spacing behavior so that a territorial system appears to be the rule. In general the territory of a male overlaps that of a female and the male will attempt to drive out any strange agoutis encountered in his 'patrol' area. The male is most aggressive toward other males and, although the female is less involved in aggressive interactions, she is quite aggressive toward alien females (Smythe, 1970a). It would appear that the paca has a similar land tenure system.

All of the Neotropical caviomorphs studied to date produce rather precocial young. This is evidentally a phylogenetically ancient trait (Dieterlen, 1963). The cursorial caviomorphs of the forest (*Cuniculus, Dasyprocta,* and *Myoprocta*) produce small litters (1-3) and have extremely precocial young. The courtship and mating behavior as well as the maternal neonatal interaction patterns show strong convergences toward the patterns of ungulates (Kleiman, 1971).

(f) Generalizations

The forest Caviomorph rodents of the Neotropics, *Cuniculus* and *Dasyprocta,* the Neotropical cervid genus. *Mazama,* the West African duikers, *Cephalophus* and *Philantomba,* and the Asiatic genera, *Tragulus* and *Muntiacus,* all appear to be solitary to semi-solitary in their habits. They feed, drink and rest separately from other members of their species. All species apparently show a similar home range utilization pattern in that a small permanent home range is maintained from year to year. Spacing behavior is indicated since adult females are less tolerant of the presence of other adult females within their home range and adult males are very intolerant of alien adult males. All species tend to mark their home ranges with glandular secretions and/or urine. The modes of marking are quite different when the rodent genera of the Neotropics are compared with the cervid and bovine species.

The animals comprising a given 'community' do come together at various intervals during the annual cycle for mating, and intermittent daily contact is maintained between the mother and her young. During early life, the young is left in a secure resting place and the mother returns to it to nurse it. Following, on the part of the young animal, probably starts at the age at which the youngster can escape on its own if necessary. It would appear that the male can contact the female at the time she comes into estrus. Partial or complete overlap of male and female home ranges appears to be the rule.

In captivity, *Dasyprocta, Tragulus,* and *Muntiacus* can show varying degrees of social tolerance, although some sort of spacing among males and females is carried out. This has been well described for captive *Muntiacus reevesi* (Dubost, 1970).

IV. COMMUNICATION AND ANTI-PREDATOR BEHAVIOR

(a) Communication Mechanisms—A Review

In the preceding section we have not attempted to be exhaustive in our analyses of the communication mechanisms shown by the forest ungulates and their neotropical counterparts. Rather we have highlighted some aspects of chemical and auditory communication mechanisms in representative species. Tactile communication, an important component of close intraspecific communication, has been left out almost completely. Similarly the components of visual communication have been glossed over in order to focus attention on communication by auditory and chemical signals. These latter two methods of conveying information are ideal for a forest-adapted species, since the potential receiver need not be either close or visible to the sender.

Two functional classes of communication have been outlined: (a) interspecific involving a prey animal and its predator; (b) intraspecific involving members of a reproductive mit. We may note that chemical communication is extremely important in the integration of male-female interactions and appears to function in spacing phenomena. The role of chemical communication in the life of the mule deer (*Odocoileus hermionus*) has been discussed by Müller-Schwarze (1971) and for *Cephalophus* (*Philantomba*) *maxwelli* by Rails (1971). Auditory communication involves the production of contact notes which serve to maintain cohesion among group members or a mother and her offspring. Warning cries or mobbing calls are involved in predator prey interaction and serve the dual function of alerting conspecifics as well as attracting and focusing the attention of predators on the presumptive prey. This form of interaction between predator and prey has been long neglected in the biological literature.

(b) Anti-predator Strategies—An Hypothesis

The smaller cursorial mammals of the tropical rainforests bear morphological similarities and behavior similarities, not so much through identity of mode of exploitation (i.e., trophic level) as perhaps from the fact that they are under similar predation pressures. Becoming larger (than let us say, a rat) entails a certain burden of conspicuousness. When a species adapts to an open environment, especially a short grass environment, conspicuousness is a risk which must be borne without any major recourse. An animal adapting to the exploitation of open habitats may then come under significant predator selection for greater speed and perhaps becoming larger in size is one of the consequences of adapting to the demands of predators since, as Howell (1965) points out, greater size confers greater potential speed. A smaller cursorial mammal in a rainforest habitat, however, has an option to remain cryptic or inconspicuous while still being reasonably large, if it undergoes selection to increase its camouflage ability and if it remains relatively solitary in its movements. A further strategy not taken by most cursorial herbivores is to become extremely slow moving, thus increasing inconspicuousness. This is an option, however, which has been taken by many arboreal herbivores (e.g. the sloths).

The basic social system, then, for a terrestrial forest-adapted form is a system predicated on overlapping home ranges of an adult male and an adult female but retaining individual movements. Contact can be re-established on a daily basis at selected points in the home range. Each 'pair' or 'polygynous' territory must supply the requisite amount of food. If remaining inconspicuous is a premium and food is not limiting then predator pressure alone could enhance the selective value of a dispersed or semi-solitary social system.

Possible anti-predator strategies for cursorial herbivores are outlined in Fig. 4. One can consider that either a generalized stimulus contrast phenomenon in the sense of Andrew (1964) or a specific stimulus input reminiscent of a releaser phenomenon **can**

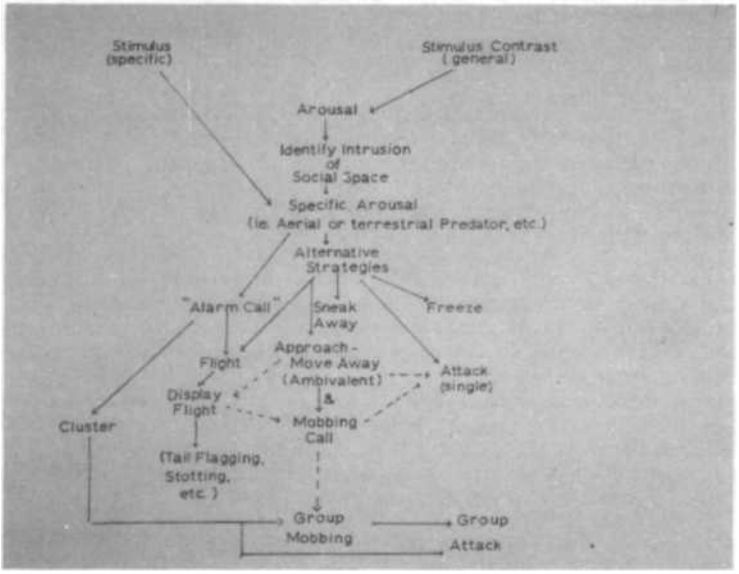

Fig. 4. Antipredator Strategies. The flow diagram presents a sequence of events and their alternatives which may be followed by a terrestrial herbivore upon perceiving a predator. The term 'stimulus contrast' is adapted from Andrew (1964). See text for discussion.

both lead to arousal in the general case. A general arousal or in the specific case a specific arousal leads to the identification of the novel stimulus. Several strategies are open to the animal once the identity of the intruding object is noted.

Alternative strategies will depend on whether the predator is aerial or terrestrial, whether it is a specialized predator, such as a snake, or a relatively unspecialized one, such as a generalized small carnivore. Detection of the potential predator can lead to orientation toward the predator followed by several classes of activity. These may include freezing, sneaking away, or emitting an alarm call. The emission of an alarm call in a solitary species is generally followed by flight behavior or a specialized form of flight behavior involving a display which may promote an attack upon the prey by the presumptive predator. Smythe (1970b) suggests that the display flight movement is deliberately contrived to elicit an attack maneuver and is only performed when the presumptive prey is in a position to avoid an elicited chase.

Options generally not open to the solitary species include mobbing the predator or attacking the predator outright in a group formation. These options appear to be emergent phenomena found in group-living species of a sufficiently large size such as the swine (Eisenberg and Lockhart, 1972).

V. CONCLUSIONS

One can conceive of the small forest ungulates and cursorial caviomorph rodents as living in auditory and chemical contact with each other. The home ranges of males and females overlap. The home ranges of related females may overlap in part (e.g. muntjac; Dubost, 1970) and something similar to the extended mother-family of the larger, savanna ungulates may be maintained in a more dispersed pattern. If this is the case, then the pattern approximates the social structure shown by the small, solitary cervid, *Capreolus*, as reported by Kurt (1968). Hence, although these animals are dispersed, they are to some extent in communication with one another.

This dispersed social structure would help to explain the role of the alarm call so characteristic of these small forest forms which at first sight would seem to be unrelated to a social function. Nevertheless, if home ranges do overlap and individuals in a 'community' are in auditory contact, then the loud warning cry can serve to alert not only the young but neighbors as well. This behavior need not be considered as altruistic since the thesis developed by Smythe (1970b) would indicate that the original selective advantage for alarm cries and conspicuous markings, such as white rump patches, is to attract the predator's attention toward the prey and induce the predator to chase, when, all things being equal, a healthy animal should be able to outdistance a predator if the predator is outside its escape distance at the time of the chase. For an extended discussion of this and its implications, see Smythe (1970b). All altruistic derivatives of such warning cries are secondary rather than primary to the original selective advantage which remains with the individual.

The behavior of forest ungulates does not appear to differ radically from the behavior of their savanna adapted counterparts. The elegant studies by Walther (1964, 1968, 1969) on the behavior of *Gazella* clearly demonstrate some of the range of variation shown by two species adapted to the short grass savannas of East Africa. Spacing behavior is demonstrable among adult males; marking by urine, feces, and pre-orbital gland secretions effect spacing; females are more tolerant and can form herds. Non-territorial or subadult males form bachelor groups distinct from the females. Distraction displays involve a peculiar and conspicuous gait (stotting) and a warning cry is emitted upon detecting predators. Mass movements of these highly mobile species may occur in response to seasonal climatic changes.

In a behavioral sense what distinguishes the forest adapted ungulates from the savanna adapted forms is really a matter of degree rather than any absolute difference. The forest adapted forms appear to have a more permanent home range with little seasonal movement; this is especially true within the tropical evergreen forest characteristic of zones with climatic stability. Home range stability may demand intraspecific spacing thus reducing competition for food resources. Yet the forest swine do show cohesive group formation, although each group possesses a correspondingly large home range. Group formation for the swine may render them somewhat conspicuous but their size and offensive weapons (tusks and hooves) permit active group offensive action toward predators. It would seem then that the smaller forest ungulates and the cursorial, New World caviomorphs may exhibit intraspecific spacing for at least two reasons:

(1) competition for food within permanent home ranges is reduced; and

(2) large predators are avoided by remaining solitary and relatively inconspicuous.

We conclude that the superficial resemblance in morphology between these small forest adapted African and Asiatic ungulates and the Neotropical caviomorph rodents is due in part to the primary selection of predators; that there has been a strong convergence in anti-predator behavior on the part of these forms which is tied in with their mode of environmental exploitation. An increase in size leads to relative potential for conspicuousness which alters the selective advantage of dispersed social systems. We maintain that in adaptation for open country feeding, selection favoring increase in size has consequences in also favoring more extended social groupings. The solitary, dispersed pattern of the forest forms is in part related to the premium placed on remaining inconspicuous and the degree of solitary behavior displayed by these forms is in part related to the need for remaining inconspicuous.

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Paper No 31

Behavioural Problems of Some Captive and Domestic Ungulates[1]

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ABSTRACT

This paper reviews behavioural problems encountered in grazing and confining domestic ungulates. Grazing is not only affected by the availability of herbage, its phenology, structure and species composition. It is also affected by such factors as the presence of disliked species in the sward, the contamination of herbage by the species' feces, the animal's own characteristics such as its age, sex, experience during early life, whether it is pregnant or not, the presence of companions on the pasture, the frequency of disturbances such as herding, availability of pastures during the night, the severity of the weather and availability of water. From a knowledge of such factors one can construct an effective grazing system. Confinement of domestic animals can lead to a great variety of behavioural abnormalities detrimental to production. This includes a rise in aggression with many negative secondary consequences, and reproductive defects which decrease natality as well as the survival of offspring. A number of remedies are discussed.

INTRODUCTION

The emphasis of the programme of this conference is on the behaviour, management and ecology of wild rather than agricultural ungulates. In the past 18 months I have become convinced of the similarity in the management problems facing agriculturalists and conservationists. Thus I shall attempt to point out this similarity by considering certain behavioural problems which are common to both. Certain points must be borne in mind in an approach of this sort.

Firstly, although little of what is said may be relevant to truly wild populations, it may nevertheless be relevant to many populations of ungulates since wild ones are becoming increasingly difficult to find. As a result of human population growth even the arctic and desert populations are becoming confined. As confinement increases, so behavioural problems become more evident. Let us remember that many of the problems that are confronting the agriculturalist today may well be confronting the conservationist tomorrow.

It is possible to look at the development of these problems as a continuum; at one end of the scale the ecologist and conservationist work, at the other are the agriculturalists. Since agricultural research pre-dates conservational research, there is in some respects a greater wealth of information at that end of the scale. However, traditionally speaking, if one is an agriculturalist, behavioural problems are those with which one lives, not those on which one does research. Hence there is a dearth of experimental work, and this review will serve mainly to point out fields in which it would be most profitable to work in the future.

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[1] This paper is an extract from a report written for the British Agricultural Research Council in 1972, entitled 'The behavioural problems of agricultural animals'.

There are a host of problems that could be discussed; however, this paper will be confined to considering two topics and their behavioural problems of particular relevance in the present context. These are:

(1) An outside ecological behavioural problem, grazing behaviour.

(2) Behavioural responses to crowding. This is a physiological/behavioural problem more characteristic today of the indoor environment.

In consideration of both of these topics certain management policies will be suggested which might help towards their solution. Although these are advanced from the point of view of an ethologist, economic pressures and conflicting interests in land use have been taken into account.

Discussions with park managers, farmers, research ecologists, conservationists, agriculturalist psychologists and physiologists, plus visits to farms, personal observational and experimental work on wild and agricultural ungulates and a fairly broad, but not comprehensive, search of the relevant literature from these disciplines are the sources of information.

GRAZING

This is essentially a behavioural problem an understanding of which would lead to more successful management of the grazing animals and their various dependents, as well as of the grassland. Thus it is a behavioural problem that interferes with management not only in an intensive farm or wildlife park, but also on a more extensive scale. There have been several reviews on the grazing behaviour of agricultural animals (e.g. Tribe, 1950a; Hancock, 1953; Arnold, 1962); however, to justify a further review let me say that these works are somewhat out of date now, and secondly as far as I know there has not been one attempted by an ethologist.

Selectivity in Grazing

This has been known at least since Linneaus (1749) did a series of preference tests of different species; we do not know a great deal more in 1971.

As Stapeldon (1948) pointed out, the degree of grazing selection is to some extent related to availability. Thus the more food available the more selective the animal will be. Another group of workers headed by Blaxter are convinced that digestibility is primarily important in selection (Blaxter, 1962). There is no doubt that availability and digestibility are of great importance in selection by the grazing animal, but they are by no means the only considerations; other behavioural factors of sometimes equal importance are very often over-looked.

That selection in grazing was a real problem in cattle was perhaps finally accepted following the publication of a paper by Hardison *et al.* in 1954. They showed that there was a greater selection by the *grazing* cow for crude protein, either extract or ash, than by the stalled animal fed on clippings from the same area. Wier and Torell (1959) using oesophagal-fistulated sheep showed a similar result. This should serve as a warning to wildlife ecologists who tend to do preference tests with penned animals fed on clippings.

On what grounds then are the animals making their selection? 'Nutritional wisdom' is often assumed and movement of groups of animals to different areas is often explained on this basis. However, taste, physical form of the plant, learning and other factors confound any innate preferences that may exist; and they may or may not be related to the nutrient value of the grazed material.

Although we are far from understanding the complete mechanism controlling such behaviour rays of light are falling on it, mainly from detailed work with the rat (Booth, 1971). Thus all we can do at this stage is to indicate the variables which do effect selection in a grazing situation. Of course different species and even different individuals make their selection on varying grounds. Selection on grounds of taste was demonstrated by Roe and Materstead (1962) who made an extract of a palatable strain of *Phalaris* and sprayed it on an unpalatable one. The sheep thereafter preferred the sprayed strain. Selection on grounds of stage of growth has been demonstrated; for example Bell (1970) found that Serengeti herbivores selected on stage of growth and locality. Milton (1956) similarly found that sheep in the Welsh hills would take species normally unpalatable when they had some succulent growth.

Specific parts of the plant may be selected. For example Johnstone and Wallace (1937) found that cattle preferred leaves to stems. The length of the plant is also important as Johnstone, Wallace and Kennedy (1944) pointed out. Cattle prefer the grass to be 4-5 inches high whereas sheep and horses prefer it shorter.

Techniques for making these assessments have remained relatively crude and it is more likely to be nearer the truth to say that all these factors are important in selection by the grazing animals, the emphasis changing amongst species.

In addition plant selection is to some extent dependent on the age of the animal. Leaver (1970) showed that heifers selected the tops of the grass, while the pregnant cows grazed the whole plant. Lambs and foals also tend to select the tops and seed heads, partly no doubt due to inefficiency of grazing.

The sex of the animal may equally have an effect on selection. It has been shown that testosterone affects the method of feeding in chicks (Rogers, 1971). Testosterone treated animals search more persistently for a particular cue on which they have been trained; perhaps male grazing animals do the same. Certainly there is some evidence to suggest sexual differences in grazing behaviour of sheep (Foot and Doney, 1971, pers. comm.).

Selectivity is to some extent conditioned by the variety and type of floral species available. Thus the catholic tastes of sheep shown by Linnaeus were confirmed by Doran (1943) on the high aspen ranges of America. However, Meyer (1957) found that on ley pasture, sheep are more selective than cattle. In addition, Milton (1956) found that the mere presence of a disliked species can strongly influence the utilization of a liked species.

Individual variations in time spent grazing was shown by Hancock (1954) with pairs of identical twins compared to the herd, which suggests that selection and amount grazed may also show considerable individual variation as production does (e.g. milk yield).

Learning is also important in grazing. Dove (1935) suggests that young horses, swine, goats and rabbits learn what to select from their mothers and Tribe (1950), reinforcing such a view, showed that mortality in sheep was increased when they had no opportunity to learn selection from their mothers.

Social facilitation

Social facilitation of intake has of course been demonstrated in the rat. There is considerable anecdotal evidence of social facilitation of grazing, lying and possibly ruminating in herds of ungulates (Hardison *et al.*, 1956; Dove, 1935; Tribe, 1950; personal observation), but the extent of this has not been measured, even though this would be a very useful thing to know. Bouts of these activities tend to occur in the grazing mammals, but to some extent this may be confounded by circadian rhythms.

Time spent grazing and circadian rhythms

Hardison *et al.* (1956) showed that the time spent grazing was inversely related to availability of herbage. Time spent grazing may also be related to total dry matter intake (Castle *et al.*, 1950), cellulose content (Lancashire and Keogh,1966) and such factors as the weather. However, there is a maximum limit to the time that will be spent grazing even when herbage is scarce. From the management point of view particularly of marginal or overgrazed land, it would be useful to know where that maximum is for each species. It would then be possible to prevent loss of weight of animals while ensuring maximum usage of the pasture.

More important for the management of intensive systems is that there is very likely a minimum grazing time. Thus the animal may be able to consume all it requires for both maintenance and growth in a very short time on a good ley pasture, but it will continue to graze, thus wasting food, in the same way as happens with concentrate feeding.

Time grazing may be a very rough estimate of herbage availability at the extreme ends of the scale, but it is too gross and inaccurate a measure where availability is adequate. Intake and time grazing will be influenced in addition by the efficiency of grazing, for example the number of bites per minute, size of mouthful and so on.

Earlier than the 1950's it was assumed that cattle did not graze at night. Thereafter Castle *et al.* (1950) and others, as a result of observing animals through the full 24 hours, found that they grazed almost as much at night as they did during the day (60% during the day, 40% at night). This discovery profoundly affected management as thereafter cattle were placed on good grazing at night as well as during the day. With more detailed investigation it became apparent that there were circadian rhythms in grazing. Thus cattle for example tend to graze in the evenings and often late at night, early morning and possibly mid-morning.

Monotony Factor

It has been observed by several workers (e.g. Stapeldon, 1948; Greenhalgh, 1971; personal observation) that cattle, sheep and horses, at least, frequently graze hedgerows and rough pastures some of the time in preference to rich leys. It is possible that leys consisting of one, two or three species heavily treated with fertilizer or slurry become monotonous in taste, and a change is sought, even if the chosen herbage is less succulent and less easily digestible. The effect of this possible monotony factor on intake is another interesting topic for research.

The weather and topography

Hunter (1954) points out that the amount of grazing and resting time in sheep is largely controlled by the weather, as are the movement of groups of hill sheep. Hardison *et al.* (1956) showed that time spent grazing, lying, ruminating, and loafing depends to some extent on the temperature and location in cattle. However, the amount cattle graze is generally considered to be less controlled by the weather than that of sheep. But this has not been recorded, to my knowledge, under equally inclement conditions.

Sheep will not eat if this involves going out of sheltered zones to graze in bad weather (Foot and Doney, pers. comm.). The steepness of the slope is also of particular importance as to whether the sheep graze or not. Thus sheltered less-steep slopes are often overgrazed. This could well be a considerable problem in conservation areas where weather conditions are extreme.

The availability of water in arid areas frequently determines the grazing patterns of cattle, sheep and goats. The area around the waterhole tends to be grossly overgrazed with consequent erosion whereas this happens to a less extent where indigenous ungulates are grazed, as many of them are capable of going for prolonged periods without water (Lamprey, 1963).

Defaecation

This factor must be considered here as soiling by faeces strongly influences the selection of grazing areas. Although it is becoming a very considerable problem in the intensively managed grazing areas, very little work has been done on the individual defaecation habits of any species. It has been estimated by Johnstone and Wallace (1944) that one cow produces 46 lbs of faeces covering 8 square feet during 24 hours. Cattle, horses and to a lesser extent sheep will not graze over their own defaecations, hence in a large herd of dairy cows for example, a large amount of grass will become essentially unavailable as a result of faecal contamination. With successive grazings during the same season the amount of grass of a ley actually utilized will decline. Proctor *et al.* (1950) measured this and found that 81% utilization declined to only 43% on the third grazing of the season. Greenhalgh (1971) found that the area affected by the faeces in terms of rejection of the grass around the faeces was not due to any change in chemical composition of this grass, but rather to the continued presence of the faeces.

Various animals will, however, graze over other species defaecations so that a rotation of animals (e.g. cows followed by sheep and horses) would reduce the wastage factor. If we knew more about the different species' defaecation habits and how this affects selection, more efficient management would result.

Parasites

The faeces are of course the main source of infection or reinfection by intestinal parasites in grazing animals, particularly young ones. Thus the avoidance by individual species of their own faeces has a beneficial effect on them, particularly because, as Rose (1963) and others showed, many of these parasites migrate only a very short distance from the faeces. Again we want more information on the behaviour of the parasites before we can work out really effective grazing schemes.

Social organization

Social organization interferes with grazing considerably and this can be a particularly important problem for conservationists. A good example of this is to be found in Hunter and Milner's work (1963) with South Cheviot sheep. These animals stayed in their own home areas (as do most hill sheep), although some of the animals were in areas which supported more palatable sward than the rest. Sheep from other groups did not migrate to those areas. Even when the animals were shepherded into folds and were released after several days, they returned to their own home areas.

Home areas, territorial areas, formation of harems and associations between individuals are bound to affect the free movement of individuals to graze. It is clear that, particularly in close-folded animals, dominance relationships may well affect the ability of certain animals to obtain the supplementary feed or the new grass at the electric fence, or to approach the water trough.

The net effect of such behaviours, particularly on an extensive scale, is that to increase or decrease stocking rate will not necessarily lead to improved production on an area, although from the floral point of view it should. This is because of the non-random spread of the grazing animals in the area, which makes some sectors virtually psychologically unavailable to some individuals.

Herding

The herding of animals clearly affects grazing; a classic example of this is to be seen in dairy cows who are herded around two or three times per day. Even on an extensive scale on the range the intake of sheep can be substantially influenced by shepherding. Doran (1943) found that it reduced selection, and even caused an increased intake of poisonous plants. Herding also decreased eating time and increased resting time as compared to non-shepherded animals on a similar area (cf. observations by Baskin and Gauthier-Pilters in papers 27 and 28 of this volume).

If these behavioural factors of grazing are considered, then certain types of management clearly suggest themselves. It is apparent that grazing is essentially a behavioural phenomenon, and to develop management techniques without considering most of the aspects of grazing that have been mentioned will probably result in unsuccessful policies. Of course the controls are not so rigid on an extensive scale, but as the land becomes further enclosed, management becomes more essential. Many of these problems that agriculturalists are struggling with become relevant suddenly to the conservationist and safari park manager. If we take into account these behavioural factors, plus the economic effects, feasibility, and conflicting interests of, for example, agriculturalists and conservationists, can we suggest methods of increasing production from grasslands both on an extensive and intensive scale ?

Intensive grazing management

We have demonstrated selectivity in grazing of different floral species, growth stage of the plant, or part of the plant. Different faunal species and different age-groups of animals have been shown to select different floral species, and even different sexes and individuals may show varying preferences. Thus it would seem logical to plant a ley relatively rich in floral species, of relevant types for the stock that will graze it, and then to graze such a ley by a fair variety of different species, age-groups and sexes of animals.

Let us take a test area in South-East England to see how an approach of this type could be integrated with increasing production. South-East England is an area of very high amenity value; every inch of land is tended and watched with care by various sections of the community with varying interests. Agricultural interest at present is orientated towards digging up the hedges and making vast fields out of the patchwork countryside. This, needless to say, destroys the traditional pattern of the countryside and reduces its amenity value. Can we suggest a management policy that will increase production on such areas, while keeping the wealth of amenity value?

Proctor *et al.* (1950) have suggested that maximum production can be gained off a ley or permanent pasture by paddock grazing in rotation. At the end of the grazing the ley must be close grazed, as this encourages growth. The grass should be topped by a mower just before the end of each grazing season so that the defaecation tufts of grass are removed from the presence of the faeces and the animals will consume them. Thereafter, in order to prevent reduction in utilization due to faecal contamination, the ley should be grown for hay or silage before being grazed again.

An appropriate rich ley should be planted and, in addition, different species grazed. There is some evidence that mixed grazing (in agricultural parlance this indicates cattle and sheep) increases production of a ley. Hamilton and Bath (1970) showed that production from a grass ley increased in 3 out of 4 years with mixed grazing at 3 different stocking rates, compared with sheep only or cattle only. Culpin, Evans and Francis (1964) also found that production was increased when cattle and sheep were grazed together on ley pastures. Leaver (1970) found that production was increased when heifers and calves were grazed as compared with either one or the other. In all these experiments, higher stocking rates increased production, as the two species, age-groups or sexes grazing allowed for differences in food selection, thereby reducing the amount of wastage.

In addition, a mixed grazing scheme would allow for the inclusion of amenity animals (such as donkeys and horses) in a useful way. In South-East England these are numerous and the demand for them is increasing.

Therefore, the following policy is suggested: to start with, because the tops of grass contain the highest percentage of digestible matter and protein, animals which are required to grow quickly, are lactating or are in the last stages of pregnancy should be rotated first on the ley (e.g. dairy cattle, quick-growing young beef animals, mares and foals, ewes in late pregnancy and early after parturition). Next, animals requiring maintainance only and/or able to close graze should be placed on the ley. These would be breeding males, riding horses and ponies, dairy herd replacements and dry cows, and perhaps geese.

The problem is to work out equivalences to ensure the correct number of each species. Although there are detailed figures on intake in a grazing situation in cattle and sheep, there are none for the less conventional species such as horses and geese. However with some thought these can be calculated as a guide line (a calculation along these lines done for me by Mr. Bob Large of the Grassland Research Institute, Hurley, indicated that a similar area could support one cow, or 185 geese).

Such a scheme would not be suitable for all areas, and the species managed would of course depend largely on the area. In the South East of England, an area of high amenity use and where production must also be high, perhaps such an approach would help to reduce the conflict between agriculturalists and conservationists. Small fields and a varied countryside would be necessary to such management, and production could be very high if correctly managed.

Extensive Grazing systems

In this context we will take the upland moorland areas of Scotland which present difficulties for farming and conservation alike. This marginal land has traditionally been grazed by sheep, and as a result has suffered considerable deterioration in the last 100 years or so (Hunter, 1960; Ratcliffe, 1965).

The germinating woodland and *Erica* spp. are systematically destroyed by the sheep and a system of management involving too frequent burning. Thus there is a loss of primary production, reduction in soil fertility and the formation of screes (Ratcliffe, 1965). These developments are clearly detrimental to wild-life (including the grouse and red deer which account for a substantial amount of the income from such areas) and result in further loss of production in sheep. As a result sheep farming in the hills has today become generally unprofitable and is maintained largely by government subsidy.

Large scale improvement of the hills by ploughing and reseeding is in general neither successful nor economically viable except on easily accessible lower slopes. In addition as Tribe (1950b) points out a mixed flora must be maintained if year round subsistence is required. Similarly Dale (1965) in Snowdonia showed that a varied flora allows for better production in bad years as well as good.

Mixed species grazing of agricultural animals can increase production on an extensive scale as well. This has been shown by Peart (1962) who found that the addition of cattle to traditional sheep hill pastures increased production from 26 lbs/acre to 54 lbs/acre.' Clarke (1963) found that not only was total production increased when cattle were introduced to traditional sheep grazing, but that the sheep also benefited. It therefore seems logical to extend such thinking to include, for example, red deer, goats and ponies, as well as sheep and cattle. The hardy highland ponies of various breeds in Britain have hardly been considered in this way, although irrespective of their possible use for meat, there is a growing market in America and the Continent for such animals for amenity use.

PROBLEMS OF THE INDOOR ENVIRONMENT

Let us now consider behavioural problems that are the result of intensive husbandry, usually involving confining the animals indoors.

Agricultural effort over the past half century has concentrated on understanding nutrition and animal breeding. Although the fact that external conditions such as temperature and ventilation can interfere with production has been recognized, farm building design for the most part has concentrated on cutting costs and on labour saving devices. In addition there has been a strong emphasis on hygiene. The same is often true of zoo management, with the addition that the economic controls on zoo buildings are less stringent. These are frequently required to be status symbols and thus aesthetic considerations may hold sway. This is certainly not the case with farm buildings, frequently with disastrously unaesthetic results. Agriculturalists have believed that provided the animal is clean, kept in draughtless, ventilated environments, and fed a balanced diet suitable to its requirements, it should show maximum productivity.

Little attention is given to such factors as the animals' social environment—for example, the optimum size and composition of the group, or the effects of overcrowding or deprived environments. Even if such factors are considered, as for example by enlightened zoo management, we have a partial answer at best.

With the increasing intensification of agriculture it is becoming apparent that not to consider such physio/pshychological needs of the animal can reflect in substantial loss in production. Although profits may remain reasonably high in agricultural enterprises, this is often by virtue of increasing the number of animals raised or very generous subsidies from the government, in Britain at least. There is some evidence to suggest that where very large numbers of animals are kept in either dairy herds, pig units or beef units, production per individual is decreased.

Thus in order to avoid very large capital investment in buildings which may prove uneconomic because they do not make allowances for the animals' physio/psychological needs, we must begin to try and answer such questions as the optimum stocking rate, size and composition of group and so on. However, although these questions can no doubt be answered by suitable laboratory experiment, we must always consider, in particular, two things, when working in the laboratory with agricultural animals: firstly, their cost (a dairy cow in Britain today costs around £200) and, secondly, the fact that the results from the laboratory environment may not be applicable on the farm; each farm is different and buildings and management vary enormously. This may render such laboratory findings inapplicable. An example of this which has occurred concerns feeding. The amount and type of voluntary food intake has been worked on in detail in controlled laboratory situations, with the animal in isolation. This makes the measurement of intake easier and the statistics more respectable.

When the conclusions of such experiments are applied to the farm situation (where the animals are in groups in far less controlled environments) social facilitation of feeding or dominance relationships may affect intake to such a degree that the laboratory results are rendered irrelevant.

Our first task therefore is to try and identify what all these different conditions are that can affect behaviour, and the types of behaviour that result from their extremes. Many abnormal behaviours, or normal behaviours that interfere with management, have many possible causations. But since it is not possible to discuss them all in the space available, one condition only has been selected for attention, on which there is a considerable volume of work in rodents, namely overcrowding.

This condition is central to intensive husbandry. Economic controls are such that it is likely to increase in the future. It is not possible to define crowding merely in terms of insufficient space per individual. Firstly, we do not know what 'sufficient space' is. It is not as simple as the agriculturalists would have us believe, that you must have X number of square feet per lb. live weight (Brambell report, 1965).

Overcrowding clearly depends on the species and the balance of other factors such as group size and composition, temperature, ventilation, shape of pen, size of the feeding trough, type of food and so on.

Thus we are forced to define crowding in terms of the psycho-pathologies to which it gives rise. These are, in particular, as pointed out by Christian (1963) and others, in the case of rodents:

(1) An increase in aggression.

(2) Reproductive defects: a drop in fertility, deficient maternal behaviour, non-recognition of oestrus, and drop in male libido.

However, it is evident that these behaviours occur under other conditions as well, so we are unable to define crowding in terms of the behaviours it produces. Nevertheless, it remains a useful descriptive term. Like dominance and territory it must be considered a dynamic and relative concept; thus from season to season it may change depending on the individuals in the groups, the hormonal states of the animals and changes in the physical environment.

Physiological effects of crowding

Let us consider briefly the physiological effects of crowding. These have been examined by Christian and Davis (1964), Welsh (1964), Thiessen (1964) and others in rodents. They include an increase in cortico-steroids, adrenal hyperactivity,gonadotrophic changes and so on. There is little information to date on these responses in large mammals.

The physiological responses are similar to those described by Selye (1950, 1956) which are caused by many types of 'stressors'. More evidence suggests that such physiological changes are not confined to crowding any more than are the behavioural changes we will now consider.

Behaviour responses to crowding

In rodents there are several behavioural responses to over-population; these have been reviewed by Thiessen (1964), Christian (1963), Myers (1966), and Archer (1970). Similar types of behavioural problems occur in intensive husbandry units. The most obvious of them is an increase in aggression.

Increase in aggression

This is particularly a problem in pig and poultry units where tail and ear biting in pigs and worrying of sore spots and feather-pecking in hens and turkeys can end in cannabalism. In addition to crowded conditions, feather pecking appears to be related to high temperatures and lack of adequate sand-bathing material. In intensive barley beef rearing units, bunting of individuals by others may result in injury to the bunted animal. More commonly it has an indirect effect, as the bunted animal will subsequently stay away from the feeding troughs. It must be emphasised that this behaviour may be intensified by the lack of bedding or roughage material (a modern agricultural economic trend), which severely restricts lying and ruminating.

There may also be a rapid increase in aggression in crowded units if there is a sudden environmental change, for example, a loud noise or a bright light. This is so pronounced a response that it has been found, for example, that pig rearing units near an occasionally used airport were uneconomic whereas a unit near an airport in constant use does not suffer the same disadvantages (the frequent rather than occasional or sudden loud noise resulting in the pigs becoming habituated).

Changes in the social environment also induce outbreaks of aggression in crowded pigs and poultry; thus, the introduction of new animals to the pen causes loss in weight gain for some weeks in piglets (Teague and Griefe, 1961). If the group size is too large aggression again tends to increase. Thus, many farmers will not keep sows in pens of more than five, although on free range, a score or more can be kept paddocked together.

Many other factors in addition to crowding can clearly affect an increase in aggression. For instance, it might be expected on hormonal grounds. However, possibly just as important is the social disorganization resulting from over-population as pointed out by Archer (1970).

There is accumulating evidence from work on rodents and primates to suggest that the idea of a constant stable dominance hierarchy giving priority of access to certain individuals in many situations is incorrect. Again this is not the place to present this argument in detail, but suffice it to say that it may be more appropriate to consider the social organization of various species in terms of role structure (cf. Gartlan, 1968), or at least to bear in mind the dynamic property of dominance and its situatibnal changes, as shown by Bernstein (1970).

What does seem clear is that in penned environments the normal organization of the society is totally disrupted: individuals cannot get away from the aggressor and as a result a more rigid dominance hierarchy emerges, as an artifact of captivity (Gartlan, 1968).

Furthermore, although the establishment of a rigid dominance hierarchy initially may reduce fighting and injury, it can have secondary deleterious effects—such as inferior animals not daring to approach the food or water dish, and hence ending up as runts (Ewbank and Bryant, 1969). In very crowded conditions, even this breaks down. Ewbank (1969) found that the rigid social dominance hierarchy set up in a pen of pigs broke down with further increases in populations. One may believe hierarchies to be controlled to some extent by the action of the submissive animal as well as by aggression from the dominant (as Rowell, 1966, shows in baboons), and that this action is in general for the submissive animal to get away from the aggressor. Then clearly, if populations are very dense and environments without hide-away areas, the submissive animal will be unable to get away. Since pain may induce aggression (Ulrich, 1966), the submissive animal may fight back when attacked; thus aggression will increase further.

Effects of over-population on reproduction

There is a drop in fertility, particularly in dairy cows where A.I. is used, due to two established factors:

(1) Non-recognition of oestrus. This depends of course on the ability of the stockman to recognize oestrus and act on it. However it becomes increasingly difficult in large herds and some cows have silent heats which makes it virtually impossible to notice by today's methods of observing one animal mounting another.

(2) The absence of the male. It has been established by Russian workers (1958 and after) that the presence of a vasectomized male increases fertility to A.I. This has been shown also in sheep by Frazer (1968). Edgar (1965) showed that the introduction of rams to the ewes would induce oestrus. Whether it is an olfactory, visual or auditory stimulus that effects ovulation or conception in these animals has not been ascertained. It has been shown though that both olfactory and auditory cues from the boar affect conception in the pig (Signoret *et al.*, 1960 and 1962).

Another reproductive problem attributable in a way to over-population is loss of libido in rams. In modern agricultural practice ewes are brought into oestrus by artificially increasing the day length, plus injections of pregnant mare serum. The effect of this is that the ewes come into oestrus in synchrony and the ram cannot cope with so many ewes all at once.. . he may as a result give up sex entirely.'

Hypersexuality, which has been reported in captive primates in particular (Morris, 1963) also occurs, but less frequently, in cattle. Oestrous cows may induce bouts of mounting in the pregnant cows of the herd. When the animals are yarded or in a confined space, oestral riding seriously disturbs the herd with a resultant drop in milk yield and possible injury to individuals. The disruptive effect of oestrous females in yarded barley beef was so great that they were latterly excluded from the unit (Hastie, 1969).

Maternal behaviour

The deficient maternal behaviour that is directly attributable to crowding is the inability of the mother to recognize and attend to her own young. Where sheep are lambed in crowded pens, and more often than not have twins or triplets, the mother and lambs are frequently separated soon after birth. The process of mutual imprinting which depends on visual, olfactory and at a later stage auditory stimuli, is consequently disrupted. Firm recognition of each other is not established with a consequent non-acceptance of the young by the mother.

Cattle that calve in a field which is tight grazed, with an electric fence for example, may have the calf trampled on or adopted by a cow that is not the mother, as the animals mill around in an over-solicitous or curious way. One farmer, it was reported to me, lost 25% of his calves in this way.

Mason (1960) showed with rhesus monkeys that the experience of having a mother affects how good a mother the individual becomes. It is quite possible that a similar phenomenon occurs in ungulates. Thus dairy cattle which have been mother-isolated as calves in general make worse mothers than mother-reared individuals, and they are less likely to adopt a second calf successfully. After having one or two calves isolated from them at birth, they are more likely to reject their own young when they are left with them. Thus learning clearly has a considerable part to play in maternal behaviour of these animals.

Non-suckling of the young is another problem that confronts the agriculturalist and zoo keeper. Up to 25% of lambs born may die from not suckling. Thoroughbred foals often have to be manipulated to suck from the mother, who may kick and prevent them from doing so.

Bucket group reared calves however will suck each other. This is a relatively common phenomenon in other species who are raised in groups apart from their mothers. It is a particularly economically disastrous problem in calves as they may swallow hair balls and urine and thereafter grow slowly. In addition the suckled umbilicus and scrotum often become inflamed. Inter-suckling is clearly habit-forming and may continue into adulthood. One dairy herd of Friesians had to be disbanded as the cows learnt to suckle each other, confronting the dairy man with beatific milk-sodden smiles and empty udders at milking time! (Wood *et al.*, 1967).

Remedies and solutions

The farmer's approach to these problems, since his day to day living depends on it, must be pragmatic. Thus his response to restricted animals injuring each other is to restrict them further, rather than to consider what might have caused the problem in the first place. The zoo keeper will consult his veterinarian, scratch his head and respond similarly. The managerial results of this approach in agriculture are sow stalls, stalled dairy cattle, crated farrowing sows, and crated veal calves. There are of course other advantages from the farmer's point of view of having the animals so packaged. However let us consider what the effect of this packaging is likely to be on the animal. Firstly there is little doubt that isolation will further increase aggression. In psychological work, it is used as a research technique to increase aggression (e.g. Janssen *et al.*, 1960; Fredericson, 1950; Banerjee, 1971)

Another result of this further restriction of the animals is that they may develop stereotypic behaviour, as well as continue to have the reproductive and aggressive problems outlined. Indeed it is predictable that these problems may also become pronounced under these more extreme conditions. Stereotypic behaviour is of course best exhibited by zoo and other captive animals. It is characteristic of conditions where locomotion is restricted and where the environment is monotonous (see Kiley, 1969).

A stereotypic movement is a movement that is often repeated in a constant form and appears to be non-goal orientated. Examples are pacing in caged cats and ungulates; crib-biting in cattle and horses; windsucking in horses; wool-licking and rubbing in dogs and sheep; weaving in camels, horses and elephants; pen licking or chewing; intersuckling; thumb-suckling (and rocking) in children; hair twirling in adults. Many of these actions are not pathological but may become so, like for example paw licking in the dog which may result in open wounds. Three particular points emerge from a review of the literature to date. These are:

(1) There is some evidence to suggest that these actions are imitative; others may learn them from seeing one individual perform them, particulary young animals, as I noted in horses.

(2) Once established, such actions are habit forming; in effect the more they are performed, the more they are likely to be performed, and therefore cannot be cured by correcting the conditions that give rise to them (Meyer-Holzapfel, 1968, in bears).

These established stereotypes can be sparked off by a large variety of situations, in particular either when the animal is 'bored' (insufficient environmental stimuli) or when there is an environmental change, or when the animals are agitated in some way (e.g. separated from young or social partner, or scared by something).

(3) It appears that stereotypes could be considered as a cut-off mechanism to divert attention from an unacceptable environment to self-stimulation. If this is so, then an argument could be made for encouraging stereotypes that were not pathological in these restricted environments. The performance of these might help to prevent the performance of other behaviours that would interfere more drastically with production.

Thus one can, for example, conjure up a picture of 400 tie stalled sows, stereotypically nodding their heads or chewing on a chewing bracket. However it is preferable to consider stereotypes as a symptom of environmental inadequacy, rather than a therapy.

Many of these problems are either ignored or overcome today by the use of surgery—for example, dehorning of cattle, debeaking of chickens, docking of tails in pigs, castration of males, etc.; or by use of drugs—particularly tranquilizers and hormonal treatments. Many of these methods are unlikely to be economically viable on a large scale or aesthetically acceptable. It would seem more rational to try and understand the cause of these behavioural problems and thereafter use behavioural knowledge to design buildings and management techniques appropriate to prevent their establishment, or to cure them.

This does not necessarily mean that more space must be provided per animal, but that the space provided must be thought about in more detail and measures taken to bring the environment into the realms of acceptability. One of the main problems here is boredom and monotony of oversimplified environments which will increase as present building trends continue. If the animal had the opportunity of performing as many activities for itself as possible it would not only help the animal, but also cut down labour costs. Thus pigs have been shown to adequately control their own temperature (Baldwin and Ingram, 1967) and they could also control their own feed dispensation (Hafez *et al.,* 1962) and cooling system. Cattle could similarly control their own feed dispensation. In zoo animals the possibilities of occupational therapy are innumerable. Some enlightened zoo managements have trainers teaching the animals to perform certain actions for their own and the public's benefit. A clear extra source of income can be seen here.

It might help in some situations to increase environmental stimulation. Dairy cows are said to let down milk faster and be more 'relaxed' when music is played to them at milking time. Auditory stimulus in general might help in other units, since pigs in pens separated by metal partitions will bang the partitions apparently to hear the noise. Increasing visual stimuli in many units would be a comparatively simple thing by providing ground level windows which could be suitably double-glassed to prevent substantial heat loss. Changing visual stimuli with light shows might hold the animals' attention and reduce these problems also.

A two-level pig house to allow the aggressed animal to get out of sight of the aggressor would help without increasing erection costs greatly.

We have attempted to point out some of the various behavioural problems that result from management and confinement of ungulates. What is needed at this stage is more research on the normal behaviour of agricultural and wild ungulates at an analytical level, as well as experimental work on the effects of different environments on this behaviour. Meanwhile certain pragmatic solutions towards helping the farmer, zoo keeper, safari-park owner or rancher and game manager solve these problems have been proposed.

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Paper No. 32

Remarks on the Social Structure and Ecology of the Ceylon Elephant in the Yala National Park

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ABSTRACT

Asiatic elephants live semi-solitarily (bulls) or in open groups (cows with their offspring) of 2 to 22 individuals. A study herd observed in the Yala National Park (Sri Lanka) for 11 months (April 1968-February 1969) contained 70 individually known animals. It was found that cows with infants (calves up to 1½ years of age) form nursing units concentrating in optimum biotopes, whereas cows with juveniles (calves older than 1½ years) form juvenile units which range in less suitable biotopes in the vicinity of nursing units. Bulls in musth were seen in herds more often than bulls not in musth. Musth, a period of characteristic, often aggressive, behaviour when the temporal gland is active, and lasting from 1 to 34 days in bulls 15 years old and older, was seen in a momentary social role which functions as a spacing mechanism between adult bulls. Analysis of the population structure of the study herd suggests that reproduction rates are low and that population growth, if it occurs at all, is slow. Yet the elephant population in the Yala National Park is increasing due to jungle clearings in the surrounding areas and to well-enforced conservation laws. The elephants' environment is threatened by their increasing numbers and by the large population of feral water buffaloes. Buffaloes are found to pollute waterholes making them unfit for elephant use. To guarantee the long range conservation of the local subspecies of elephant, which is believed to be endangered, management plans which include provision for the limitation of buffalo numbers are essential.

INTRODUCTION

The present status of the Ceylonese elephant reflects the history of elephant trading and catching in Ceylon and India: the taming and training of the Asiatic elephant in the middle of the 6th century B. C., their export in classical times down on through the Middle Ages, and the monopolies of the elephant trade, by the Portuguese in the 17th century, followed by the Dutch, who introduced the kraal system of catching elephants, and the British, who continued with the system into the 20th century. Before 1800, Ceylon led in elephant exports; between 1863 and 1894 a yearly average of 66 elephants left the island, but only about 9 per year were exported between 1925 and 1930. Today the number of elephants exported is practically nil.

Kraaling was highly successful in the 18th and 19th centuries, according to the historians and naturalists, LaCombe (1681), Strachan (1690), Pieris (1918) and Deraniyagala (1955), who mention Kraal quotas up to several hundred animals. In Ceylon mortality rates were high as well, with less than half the animals surviving the capturing operations. Analysis of mortality rates from the Khedda method, as kraaling is known in India, indicate that in the 19th century the British were less interested in having tame elephants for work and export than in eliminating elephants from areas where new plantations had been established and where the wild herds had been responsible for enormous crop damage.

Kraaling, which developed from a simple catching operation into a royal spectacle costing huge sums, and elephant hunting, which became the sport of British big game hunters and Ceylonese nobles in the late 19th century, took a toll of thousands of wild elephants (Baker, 1966). Around the turn of the century, Storey (1907), the elephant expert, estimated there were some 2000 elephants in Ceylon. C.E.Norris (1959) estimated that several decades later there were some 1600 to 1700 elephants in the south and south-east of the island. Conservation movements begun by Norris and Spittel resulted in the creation of several reserves for the dwindling elephant population.

A new threat faced the elephant in 1948, when Ceylon became independent and began developing huge areas in the process of making the country self-sufficient. However, a re-intensified drive to protect the Ceylonese elephant was reflected in the decreasing number of licences issued for capturing elephants (the last was issued in 1960), partly as a result of a report to the IUCN General Assembly in Edinburgh in 1956, on the status of the Ceylonese elephant. The subsequent request for an expert to study elephant problems in Ceylon eventually brought about the joint Smithsonian Institution and WWF Survey of 1967-1969, under Program P1 480, of the ecology of the endangered Ceylonese elephant. The program was headed by Dr. H. K. Buechner, Department of Ecology at the Smithsonian Institution, assisted by Dr. J. F. Eisenberg, of the National Zoological Park, Washington, D.C., who undertook the research for the project in the Wilpatu National Park in 1968. George McKay worked in the Gal Oya Reserve, and I collected data for two years in the Yala National Park, with the assistance of Anil Jayasuriya and A. P. W. Nettasinghe.

Conservation of the Ceylonese elephant faces two problems in particular: the annual crop damage by elephants, and the concentration of surviving herds in national parks and reserves. The first problem can be solved with well-equipped control teams of Ceylonese rangers, but the solution to the second consists of enforced management plans based upon ecological research.

This paper outlines some aspects of the sociology and the ecology of the Ceylonese elephant and their meaning for the management and conservation of the species and its habitat.

POPULATION

Laws (1966) estimated the age of wild living African elephants from the shoulder height. This was a convenient method to follow because elephant growth is gradual until after 20 years of age and because shoulder height can easily be determined from the forefoot print measurements. In asiatic elephants the circumference of the forefoot, which is larger than the hindfoot, is exactly half the length of the shoulder height. The shoulder height method has been used accordingly to determine population struc-

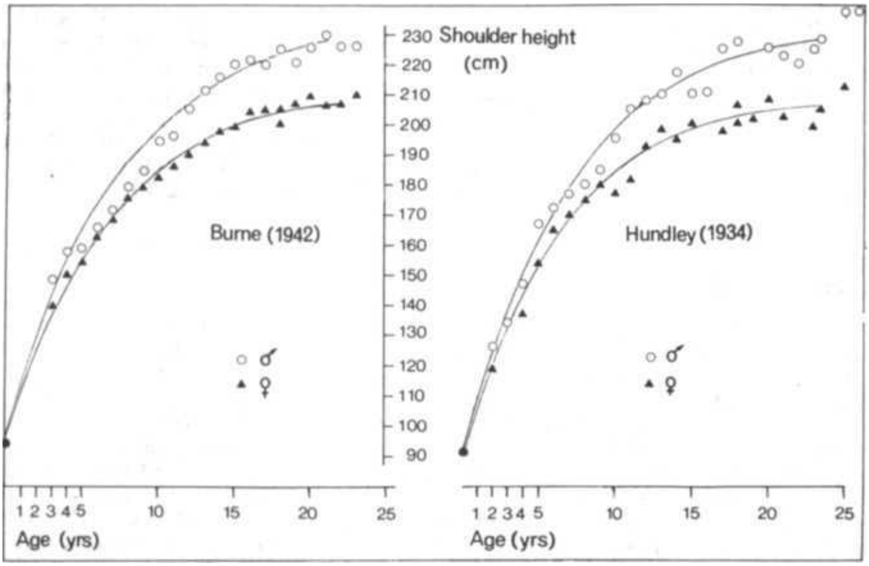

Fig. 1. Growth of tame Asiatic elephants according to shoulder height measurements taken by Burne (1942) and Hundley (1935).

ture in the Asiatic elephant. I distinguished 9 size classes based on the data published by Burne (1942) and Hundley (1934) on 108 and 51 elephants respectively (Fig. 1). These data are unique since they reflect the growth of 159 captive-born elephants up to the age of about 25 years. The 88 captive elephants measured by us in Ceylon showed a similar growth curve but with larger deviations, most probably due to the fact that the age of these animals could not be so precisely determined.

Full-grown cows reach their maximum height after the 24th year. They were considered as age class 8. Newborns, which are recognizable the first few weeks by a red rim around the eyes and dense lanugo hair, were considered as age class 1. Newborns can stand between the front legs of cows, more or less touching their bellies. Six more classes were established in between (classes 2-7). Class 9 consisted of bulls larger than full-grown cows (Fig. 2).

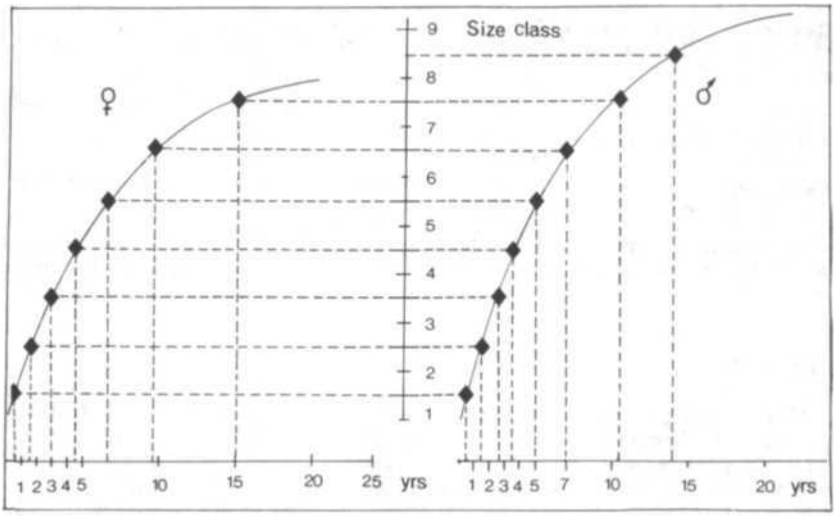

Fig. 2. Size classes of Asiatic elephants based on shoulder height.

The population structure of 89 elephants individually known by scars, tail and other distinguishing marks, is given in Table 1. These 70 elephants of the south herd (study herd) and 19 of the north herd do not reflect the total population of elephants usually observed in Block 1 of the Yala National Park. There were at least 15 other males belonging to age classes 7, 8 and 9, and 3 cows with offspring that could not be described individually; a few of these belonged to the north herd. About half of the population consisted of adults, the others were infants, juveniles and subadults. The sex ratio was calculated for each of the 4 main age classes distinguished in Table 1. In each of the 4 classes there were more females than males.

REPRODUCTION

Captive elephant cows can bear offspring when still subadult. Cases have been reported of 9 and 10 year old females bearing calves (Kurt. 1970). Since the gestation period lasts some 21 months, the mating therefore took place when the cows were 7 and 8 respectively. Of the 36 females 6 years old or older captured in the Mysore Khedda (South India) in 1968, all animals 10 years old or older had well developed mammary glands, seemed pregnant, or had a calf at heel. Among the 6 to 10 year olds, only one had developed breasts, and she gave birth one month after Khedda. Five cows of the study herd were of size class 7, i.e. having an estimated age of 9. 5 to 15 years. Two were without calves but considered pregnant (♀ 16 and ♀ 17), and one (♀ 4) gave birth at the end of February 1969. One (♀ 5) had a newborn and one (♀ 2) had a calf of size class 2 at heel. These few data lead to the assumption that first parturition takes place around the age of 10 or older and the first mating around 8 or later.

TABLE 1. SIZE AND AGE CLASSES IN THE SOUTH HERD (1) AND NORTH HERD (2) OF THE YALA NATIONAL PARK

	Size class	1	2	3	4	5	6	7	8	9	Total
♀♀	Age group (yrs)	0-0. 5	0.5-1.5	1. 5-3.0	3.0-4.5	4.5-6.5	6.5-9.5	9. 5-15	15- ±40		
	1 South	2	3	3	4	3	4	5	17		41
	2 North	–	2	1	1	3	2	2	2		15
	1 + 2	2	5	4	5	6	6	7	19		54
♂♂	Age group	0-0.5	0. 5-1. 5	1.5-2.5	2.5-3.5	3.5-5.0	5.0-7.0	7.0-10. 5	10.5-14	14- ±40	
	1 South	3	2	2	2	1	3	3	2	11	29
	2 North	–	1	–	–	1	–	–	1	3	6
	1 + 2	3	3	2	2	2	3	3	3	14	35

	Age group	infants	juveniles	subadults	adults	Total
♀♀	Size class	1,2	3,4,5	6	7,8	
	Number	7	15	6	26	54
♂♂	Size class	1,2	3,4, 5,6	7	8,9	
	Number	6	9	3	17	35
Total	Number	13 (14.8%)	24 (27.3)	9(.10.2)	42 (47.7)	89 (100%)
	♀ : ♂	1:0.86	1:0.60	1:0.50	1:0.65	1:0.65

Of the 22 elephant cows of the study herd between April 1968 and February 1969, 5 had 2 calves of different ages at heel. In April 1968, ♀ 22 had a ♀ of size class 2 as well as a ♂ (tusker) of size class 6 at heel. Later in the year the smaller calf was not seen; most probably it died. Female 4 gave birth to a calf in January 1969, and ♀ 13 in February 1969. By comparing the ages of these calves, the time span between two consecutive, successful births could be determined (see Fig. 3). The time span was estimated between 3 and 5 years; in 3 cases the time span was approximately 4 years.

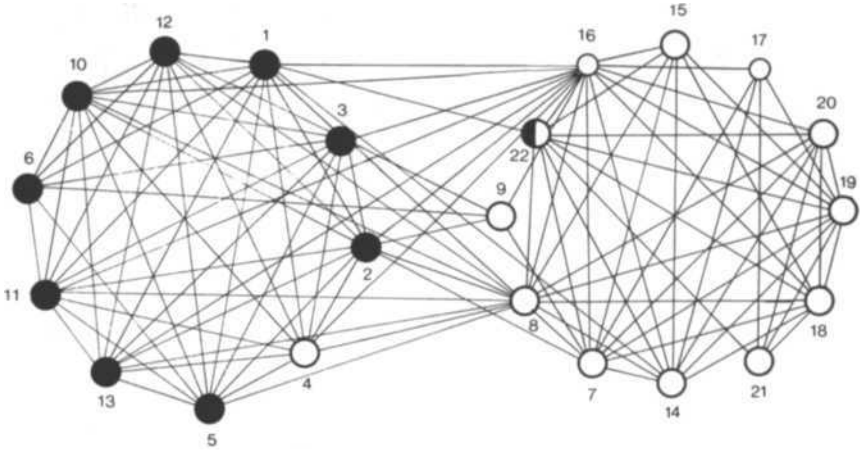

Fig. 3. Group contacts (represented by lines) of 22 cows of the study herd between Sept. 1968 and Feb. 1969. Blacked-in circles: cows with infants. Large circles: cows with juveniles. Small circles: cows of size class 7, considered pregnant. Half-blacked circle: cow which lost infant.

Mating therefore occurs about 2 years after giving birth. Data collected on elephants in captivity giving birth to more than one calf have been compared (Kurt, 1970). In all cases in which the calf was kept with its mother, the time span between 2 births was 47 months on the average, with extremes of 36 and 50 months, respectively. In all cases in which the calf died or was removed immediately after birth, the next birth took place after 23 months.

Counts of rather small populations with a few hundred animals whose ages were estimated by limited field criteria such as shoulder height do not allow as accurate a description of reproductive rates and turnover as was possible with large populations of cropped African elephants, whose ages were determined from the analysis of molars. By studying the group composition of several herds in the Yala National Park and in Lahugala (East Ceylon), I found that between 25 and nearly 50 percent of females born reach puberty. If one assumes that each of them reaches the age of about 40 years, the oldest age from the analysis of molars in some 47 skulls collected in the National Park, the reproduction period (first mating through last parturition) lasted some 32 years. If there is a calfing interval of 4 years, 8 calves could be born, 4 of which are females, and 2 of these females could be assumed to reach puberty. The pattern of herds in the Yala National Park falls short of this estimate. Only about 1 female per year reaches puberty (28 adult cows between 9.5 and some 40 years of age), i.e. only 1 out of every 4 calves estimated to be born every year (Table 1). I therefore assume that population size does not increase markedly by reproduction.

GROUPING PATTERNS

I defined an elephant group as any number of elephants observed together and showing distances from one elephant to the next of less than 100 meters. Sizes of these groups ranged from 2 to 22 animals. Large herds of 70 to 150 animals were seen in other areas of Ceylon, but never in the Yala National Park. Herds were composed mainly of females, juveniles, and infants. Bulls of age classes 8 and 9 appear in small bull groups of 2 to 4 animals or remain solitary. Bulls are often found in herds, but usually only a single one or at most with two other bulls.

Groups defined by the above-mentioned method are not stable in size or in composition. For example, between September 1968, and February 1969, ♀ 7 was seen 31 times in groups of which all members could be identified individually. The size of these groups varied from 4 to 18 animals. Altogether she had group contact with 12 different adult females, 1 infant, 11 juveniles, and 4 subadult and 5 adult males.

I was particularly interested in the partnership of cows of age classes 7 and 8. I wanted to find out, first of all, who the partners of one particular cow were and how often they were with this cow in the same herd. For this I had to select an observation period in which I could be certain that I knew all the elephants living at this time in the southern part of the Yala National Park. I also had to limit myself to samples of groups of which all members could be identified individually. The best observation period was between September 1968, and February 1969, in which I concentrated on elephants for five periods of some 10 days each. When 2 cows were observed together at least once in the same herd they were said to have group contact. In Fig. 3 the group contacts of the 22 cows of the study herd are summarized. Females with infants at heel seem to associate more with females with infants than with females with juveniles, and vice versa.

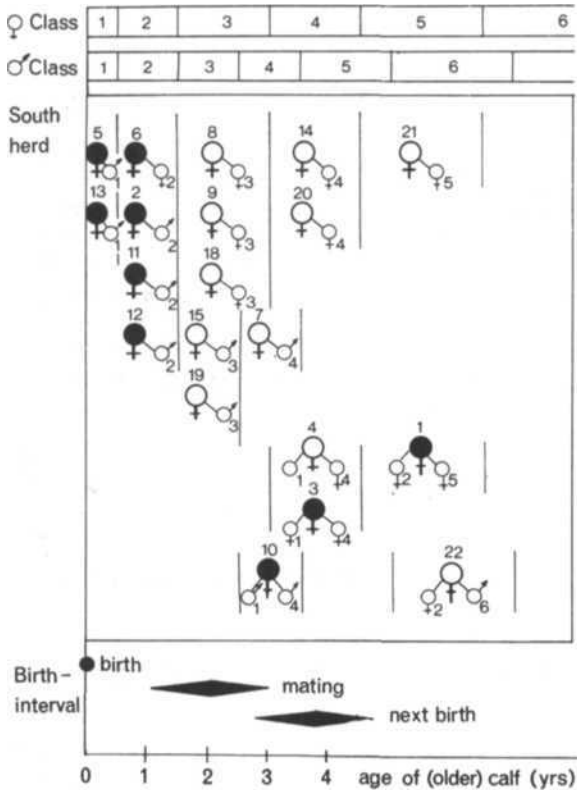

Fig. 4. Cow-calf-units of study herd plotted according to estimated age of (youngest) calves. Black dots: cows with infants. Circles: cows with juveniles. Numbers above females correspond with female number. Numbers below calves represent size class.

TABLE 2. NUMBER AND FREQUENCY OF GROUP CONTACTS BETWEEN 22 COWS OF STUDY HERD (SEPT. 1968-FEB. 1969)

$a = 2b/N_1 + N_2$; 1: female number; 2: number of observations; 3: number of females with infants as partners; 4: number of female partners pregnant and/or with juveniles.

					(a) for female partners with infants		(a) for female partners with juv. and/or preg.		T_1	P(2a) <
	1	2	3	4	Var.	$\bar{x}$	Var.	$\bar{x}$	Wilcoxen-Test	
Females with infants:	1	19	8	3	0.15-0.72	0.32	0.00-0.44	0.05	133	0.01
	2	14	8	5	0.18-0.53	0.31	0.00-0.27	0.06	134	0.01
	3	20	8	4	0.14-0.72	0.44	0.00-0.50	0.10	134	0.01
	5	5	8	3	0.15-0.40	0.26	0.00-0.46	0.04	132	0.01
	6	8	7	1	0.00-0.25	0.16	0.00-0.08	0.00	127	0.01
	10	17	8	3	0.16-0.56	0.31	0.00-0.32	0.03	137	0.01
	11	16	7	5	0.20-0.64	0.34	0.00-0.08	0.02	140	0.01
	12	9	8	2	0.24-0.64	0.34	0.00-0.24	0.02	132	0.01
	13	5	7	3	0.00-0.40	0.26	0.00-0.27	0.04	125	0.01
Females with juveniles and/or pregnant	4	8	8	2	0.00-0.50	0.29	0.00-0.10	0.02	139	0.01
	7	31	1	11	0.00-0.04	0.00	0.00-0.60	0.22	18	0.01
	8	16	7	9	0.00-0. 13	0.07	0.00-0.60	0. 14	78	
	9	16	3	9	0.00-0.08	0.02	0.00-0.60	0. 14	40	0.01
	14	14	0	10	0.00	0.00	0.00-0.26	0. 11	19	0.01
	15	9	2	7	0.00-0.09	0.01	0.00-0.36	0.12	22	0.01
	16	18	6	11	0.00-0.22	0.08	0.00-0.36	0.15	73	
	17	3	1	6	0.00-0.25	0.03	0.00-0.24	0.07	29	0.01
	18	37	0	10	0.00	0.00	0.00-0.81	0.21	9	0.01
	19	30	0	11	0.00	0.00	0.00-0.81	0.21	9	0.01
	20	29	0	9	0.00	0.00	0.00-0.76	0. 18	9	0.01
	21	6	0	7	0.00	0.00	0.00-0.22	0.08	9	0.01
	22	29	1	10	0.00-0.04	0.00	0.00-0.42	0.20	19	0.01

The above conclusion was reached by the following method. During rhe observation period I saw ♀ 1 (N_1) 19 times, ♀ 2 (N_2) 14 times, and ♀ 1 and ♀ 2 in the same herd at the same time 6 times (b). Applying the formula devised by Dice (1945), $a = \frac{2\ b}{N_1 + N_2}$, I measured mutual attraction (a) and obtained 0. 36 (maximum attraction = 1.0, minimum attraction = 0.0). Cows were grouped according to the size of their older offspring. Mother-child units were defined on the basis of suckling, i.e. one particular cow allows only one particular calf to suck, with the exception of newborns who may drink from more than one cow for the first few days. As shown in Table 2, cows with calves of the same age are seen together more often than cows with calves of different ages. Elephant herds can therefore often be described as juvenile units (calves older than 15 years with their mothers) and nursing units (cows with calves younger than 15 years plus any older offspring—see also Fig. 4).

Females of size class 6 (6.5-9.5 years old) were found to have most of their group contacts with juvenile units and were only rarely seen in nursing units. I therefore assumed that these females were the elder daughters of the cows with juveniles at heel.

Juvenile units consist of pregnant females and females of mating age. One female (♀ 4) with a juvenile at heel was often seen in the nursing unit during the observation period, and she gave birth to a calf at the end of February 1969. Moving from the juvenile unit into the nursing unit therefore seems to take place several months before parturition. The movement from a nursing unit to a juvenile unit was observed twice, between July and September 1968, when ♀ 22 left the nursing unit to lead a juvenile unit in October. Female 19, who had a calf of about 2 years at heel, joined this latter juvenile group about one month later.

Juvenile units also attracted groups of juvenile bulls up to 8 members. It seems that juvenile bulls group together with other males of the same age after their mothers have again given birth. A tusker of size class 6 stayed with its mother (♀ 22) nearly all the time after she lost her one year old calf.

Sector	Nursing - units ●	Juvenile - units ■
A	44	23
B	10	29
C	0	19

Fig. 5. Distribution of nursing and juvenile units of study herd between Sept. 1968 and Feb. 1969. Dots: nursing units. Squares: juvenile units. Scale:- 1 : 33000.

Several socially open groups can be considered as forming a herd or clan. This clan rarely associates with members of other clans but shares parts of their ranges. Clans can be considered as socially closed by non-territorial units.

SPATIAL DISTRIBUTION

In Fig. 5 I plotted the first identification of each herd per day and distinguished whether the herd consisted of cows with juveniles or infant offspring. If the herd had both infants and juveniles, I plotted the groups as if they were 2 separate units. The spatial distribution of juvenile and nursing units differs as follows: nursing units seemed to concentrate more in sectors A and B, while juvenile units were often seen in sectors B and C. The only river in Block 1 (Menikganga) and a number of permanent waterholes were found in Sector A; permanent waterholes were rare in Sector C. It was found that there was more rainfall in Sector A than in Sector C, and that the rain came three weeks earlier in Sector A. Presumably food plants were greener in Sector A. Both woodapple trees and grass, the preferred food of elephants, were found in abundance in Sector A, but were rare in sectors B and C. I therefore considered most parts of Sector A as optimum biotope for elephants and Sectors B and C as less suitable.

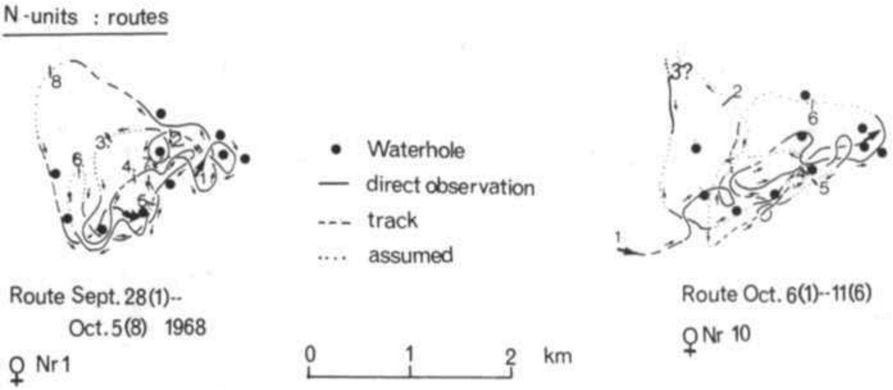

Fig. 6. Routes of 2 different nursing units (Xl. W10) in Block 1 of Yala National Park. Dots represent waterholes visited by members of group.

Nursing units have a smaller home range than juvenile units. Their daily routes measured from 1 to 3.5 km (see Fig. 6), whereas those of juvenile units were found to cover 3 to 8.5 km (Fig. 7). The movements of nursing units seem to have a focus, such as a pattern of neighboring waterholes; juvenile units are more nomadic. Cows with infants at heel change social partners often, whereas juvenile units tend to be more stable. There were contacts between juvenile and nursing units occasionally, but these groups usually disbanded as a result of cows with infants dominating over cows with juveniles. During the dry season 3 different clans shared large parts of their home ranges along the Menikganga, and during the rainy season nursing and juvenile units of the north herd were observed within the ranges of the above groups of the study herd. I never observed social interactions between nursing or juvenile units belonging to neighboring clans which could be interpreted as leading to spacing. Such interactions were, however, found between nursing and juvenile units of the same or different clans. Home ranges of neighboring clans seem to be traditionally rather than socially established.

MUSTH

African and Asiatic elephants have a pair of temporal glands located just over the temporal arch between the ear and the eye. Each gland has a slit-opening of some

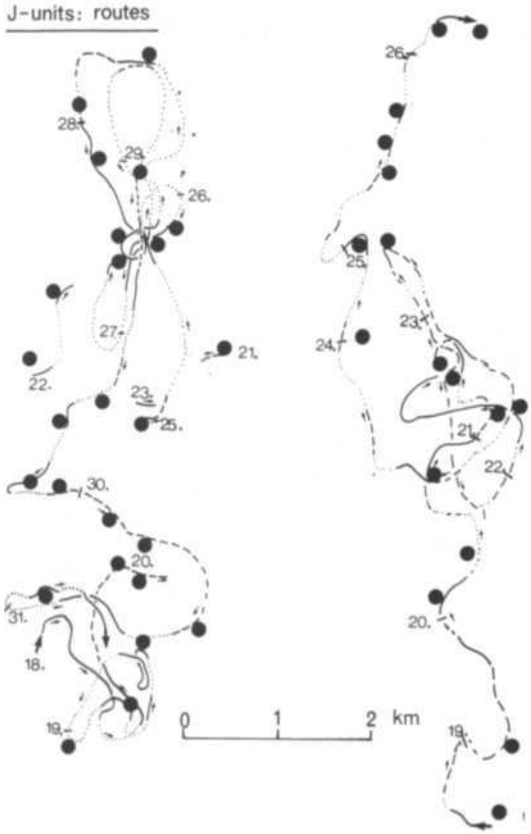

Fig. 7. Routes of 2 different juvenile units (♀ 17, left; ♀ 22 right), in January 1969 (♀ 17) and February 1969 (♀ 22). Dots represent waterholes visited by members of group.

3 cm in length and is periodically active. At the beginning of the active phase the surrounding skin swells until a blackish fluid of tar consistency overflows onto the skin and occasionally even into the mouth. This fluid is said to have a bitter taste (Sanderson, 1966). Both the time span in which the glands are active and the characteristic behaviour during this time are known as musth. The phenomenon occurs in both sexes of the African elephant, but normally only in bulls of the Asiatic, though females in musth have been reported (Deraniyagala, 1955).

All musth periods of 13 adult bulls frequently seen in the study area during the 11 months of observation were measured. Data in Table 3 are based on the time span between the first and last day the musth gland was seen in an active state. In cases where it was not possible to estimate the length of the musth period accurately, e.g. when males left the study area for short periods of time, the minimum length of the musth period is given. The musth period in wild elephants was found to last from one (♂ 11) to 34 days (♂ 12). A male can come into musth more than once a year. Musth periods were observed to last only a few days in 4 old males. old according to their hollow cheeks and temples, paper-thin ear flaps, split nails, and hairless tails. In other males, younger and healthy looking, musth lasts longer. During 11 months of observation, some of them even had 1 or 2 additional short musth periods lasting only a couple of days.

Males in musth were observed more often during the rainy season (September-April) than during the dry season (May-August). These findings seem to support the saying

TABLE 3. NUMBER, MONTHS AND DURATION OF MUSTH PERIODS OF 13 ADULT MALES. APRIL 1968-FEBRUARY 1969.

Male Nr.	Nr. of musth-periods	months	duration (days)
1		April February	>6 1- 9
2	1	April-May	22
3	2	April May	$\geqq 1$ 9-12
4	3	May-June January February	22 1- 4 >7
5	2	June January	>12 21
6	1	June-July	27
7	1	Sept.-Oct.	$\geqq 16$
8	1	Dec.-Jan.	16
	2	July January	>15 2
10	2	April December	$\geqq 1$ $\geqq 1$
11	1	December	1
12	2	June-July August	34 1- 4
13	2	May August	1- 2 1- 2

of elephant owners that males are more likely to come into musth when they are well fed and that reducing the amount of food shortens the musth period. On the other hand, it can also be said that if musth were affected by the presence of herds in the home range of bulls, these data would simply reflect the fact that herds were seen in the observation area less during the dry than during the rainy season.

To determine whether or not there is a correlation between musth and the amount of precipitation, I divided the 12 months of the year into months with more than 50 mm rainfall (8 months, Sept.-April) and with less than 50 mm (4 months, May-Aug.), according to the map of Müller-Dombois (1968). Taking into consideration the fact that the time I spent observing elephants was not spaced evenly over the 11 months of observation, it can be said that there were some 2 to 3 males in musth per month throughout the year. Presumably there is no correlation between males coming into musth and amount of rainfall. Months with optimum food resources may not, of course, coincide directly with months of more rainfall, but I was not able to determine whether or not there was a correlation between musth and food conditions.

I determined whether or not a male was in musth only by the status of the temporal gland, not by any characteristic musth behaviour. Males in musth were usually easy to identify, though sometimes a layer of mud on the gland made it difficult to detect that the gland was active, particularly at the beginning and end of the musth period. When I compared the social and spatial positions of adult males (Table 4), I therefore considered a time span of ten days before the first and after the last positive observation of an active gland as belonging to the musth period (in the following, maximum musth period).

TABLE 4 SOCIAL AND SPATIAL POSITION OF 13 ADULT MALES DURING MAXIMUM MUSTH PERIOD AND WHEN NOT IN MUSTH, APRIL 1968-JANUARY 1969.

$t_{1,2}$: total of observation days
$a_{1,2}$: total of observation days seen with herds
$b_{1,2}$: total of observation days alone
$c_{1,2}$: total of observation days within herd range
$d_{1,2}$: total of observation days out of herd range

	maximum musth period							not in musth						
Male Nr.	t_1	a_1	b_1	c_1	d_1	a_1/t_1	c_1/t_1	t_2	a_2	b_2	c_2	d_2	a_2/t_2	c_2/t_2
1	5	4	1	5	0	0.80	1.00	11	2	9	4	7	0.18	0.36
2	10	4	6	5	5	0.40	0.50	27	2	25	9	18	0.07	0.30
3	9	8	1	9	0	0.88	1.00	7	0	7	1	6	0.00	0.14
4	20	10	10	18	2	0.50	0.90	28	1	27	7	21	0.04	0.25
5	12	66	6	11	1	0.50	0.91	11	5	6	8	3	0.45	0.72
6	5	1	1	5	0	0.80	1.00	7	2	5	2	5	0.28	0.28
7	2	2	0	2	0	1.00	1.00	15	1	14	3	12	0.06	0.20
8	4	1	3	4	0	0.25	1.00	20	5	15	11	9	0.25	0.55
9	10	2	8	2	8	0.20	0.20	9	2	7	1	8	0.22	0.11
10	10	0	10	3	7	0.00	0.30	19	7	12	12	7	0. 41	0.63
11	1	1	0	1	0	1.00	1.00	19	1	18	7	12	0.05	0.41
12	6	3	3	5	1	0.50	0.83	10	3	7	6	4	0.30	0.60
13	11	2	9	1	10	0.18	0.09	12	1	11	7	5	0. 83	0.58

Males 1 to 8 and 12 are considered as young adult males, males 9 to 11 and 13 as old males.

$$a_1/t_1 \ \frac{\text{for young adult males}}{9} = 0.63$$

$$a_2/t_2 \ \frac{\text{for young adult males}}{9} = 0.22, \ T = 36 ^{**} \ P(2\bar{a}) < 0.01$$

$$c_1/t_1 \ \frac{\text{for young adult males}}{9} = 0.90 \ T = 45$$

$$c_2/t_2 \ \frac{\text{for young adult males}}{9} = 0.38 \ P(2\bar{a}) < 0.01$$

** Rank test for 2 matched samples (Wilcoxen Signed-Ranks)

Male 1 was seen on 5 days (t_1) during its maximum musth period, often more than once a day. It was observed alone on 1 day and with the herd at least once on the four other days (a_1) It stayed within the daily range of the herd on all 5 days (c_1). The same male, when not in musth, was observed a total of 11 days (t_2);on 2 days (a_2) it was observed with the herd at least once, and on 9 days alone. In 4 (c_2) of the 11 days the animal stayed within the herd's daily range, but on 7 was outside the range. I compared the number of days seen with herds with the number of observation days (t_1, t_2). The same factor was calculated for the number of days when the male was found to range within the daily range of herds. For 9 young adult males the correlation was found that males frequent herds and stay within the herd's daily range more when in musth than when not in musth. The mean values of the factors (a_1/t_1) and (c_1/t_1) for the maximum musth period were 0.63 and 0.90 respectively, and for not in musth, 0.22 and 0.39 respectively.

In totalling the number of observation days of the 13 adult males, I found that males in musth were within the daily range of a herd 80 times: in 27 cases the range of the herd was that of both nursing and juvenile units; in 36 cases, juvenile units; and in 17 cases, nursing units only. Males were observed to stay within the daily range of herds 78 times when not in musth: 8 times within the daily range of both nursing and juvenile units, 46 times of juvenile units only, and 24 times of nursing units. The fact that males seem to range more in the vicinity of juvenile units, which definitely consist of more females receptive to mating than nursing units do, plus the fact that males in musth are seen with herds more often, lead to the conclusion that most males with juvenile herds are in musth. Males in musth seem to control waterholes, frequently urinating and defaecating, more than males not in musth. Males in musth also control members of the herd more intensively and direct more attention to females. The response of herd members by presenting and urinating is more frequent towards males in musth than males not in musth. In addition, males are more aggressive towards other males when in musth than when not in musth.

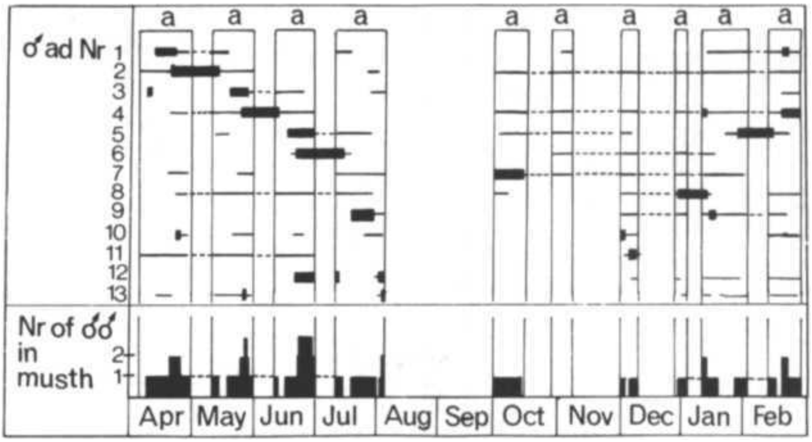

Fig. 8. Musth periods of 13 adult males between April 1968 and February 1969. a: observation periods. Above: thin lines: males not in musth present in the Study area. Thick lines: male in musth present in the study area. Below: number of males in musth at the same period. Nr. 6 left the study area to join the North herd in June. It was therefore not included.

The musth periods of identified males within the study areas are shown in Fig. 8. It was found that musth periods follow each other, e.g. over an observation period of 11 months, only 1 male at a time was in musth. Over-lapping of long musth periods was observed for ♂ 5 and ♂ 6. Male 6 was seen alone near a herd with ♂ 5 in musth. Male 6 was wounded (most probably by the tusker ♂ 5),and it then left the place to head north for about 12 km, where it joined the north herd until the last half of July. It was observed in musth until July 16. Male 13, whose musth period of 1 day overlapped with the long musth period of ♂ 3, was fought by the younger and stronger bull. Male 13 then came out of musth and left the range of the herd. These data, summarized in Tables 3 and 4, can be interpreted as follows: several males may come into musth at the same time and try to associate with herds; the stronger one stays in musth and with the herd, whereas the weaker can leave the place and perhaps stay in musth, or come out of musth immediately and either leave the place or stay within the range of the herd. The latter can especially be said of old adult males which seem to stay within the daily range of herds about the same as when in musth as when not in musth.

Most of the elephant owners of the former East India Company as well as the Ceylonese owners and mahuds believe that musth occurs with puberty. But the fact that most of the fathers of elephant calves born in western zoos had not yet shown symptoms of musth (most were younger than 15 years, the time when the first musth period appears in tame and wild elephants) indicates that this belief is not substantiated.

Eisenberg *et al.* (1971) summarize some observations of wild adult elephants not in musth when mating. Cow 18 of my study herd was mounted on 3 days before the actual mating took place by 3 different males, adults and subadults, who were not in musth. The actual mating, however, took place with a bull in musth. Like Eisenberg *et al.* (1971), I believe that musth has a momentary social role similar to rut, if rut is defined as the period in which a male is not only physiologically able to produce sperms and able to mark important checkpoints of its daily range, such as waterholes, with an active gland, but also socially in a position to dominate other males. Marking by elephant bulls in musth has been described by Sykes (1971), Eisenberg *et al.* (1971), and by myself. Musth can also be considered as a momentary social status in which males contribute enormously to the spacing of the male population, leading to a dispersal in which the strongest bulls range in the most marginal biotopes at the peripheries of the herd's range. Nursing units, surrounded by juvenile units and bulls in musth, range in the ecologically optimum center. It can be said that musth functions to keep social interactions of bulls within the herds at a minimum. It also means that the strongest animals (bulls) are in the position to prepare any new territory for the herd, e.g., by knocking down trees, followed by secondary growth, and by turning wallows into waterholes (Kurt, in prep).

CONSERVATION

Recent conservation measures indicate that the Ceylonese government is concerned about the plight of the remaining wild elephants. Today, for example, clearing companies are co-operating with the Wildlife Department to ensure that jungle clearings are carried out in such a way that herds can retreat to the national parks. This means, of course, that the elephant population in the reserves is increasing rapidly. Population increase of resident populations by reproduction, if it occurs at all, is very low.

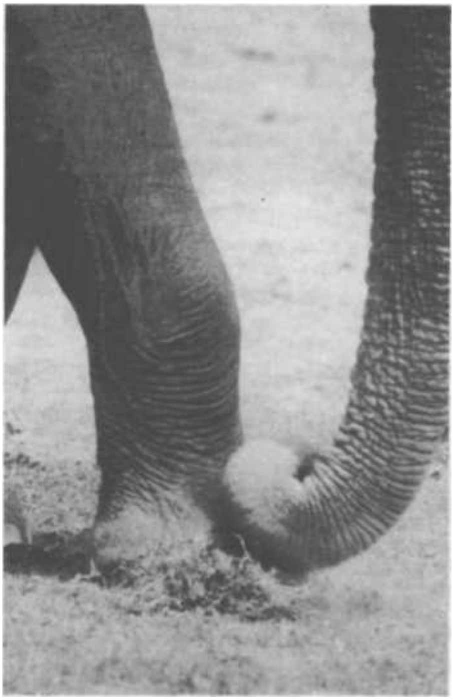

Fig. 9a. Elephant scalping short grass with its front leg.

Since the home ranges of neighboring herds seem to be traditionally rather than socially established, I doubt whether a population increase by immigration would result in behaviour leading to any form of population regulation, but one could assume, first of all, that it would lead to a dense overlapping of home ranges of different herds.

The consequences of more and more elephants depending on the same natural resources are primarily ecological. Even now the elephant population is feeding on grasses faster than the grasses can recover. Grasses, some of them naturally short. are often grazed down to a few millimeters in length by the numerous large ungulates, such as spotted deer, sambar and feral buffalo. Elephants scalp the grass with the forefoot nails (Fig. 9) thus creating the ideal situation for erosion during the rainy season, especially around lagoons on large plains where the soil is very thin. Most of the larger plains now have bare spots. Introduced plants such as *Lantana* and *Cassia* thrive, pushing out food grasses. On several occasions the Wildlife Department has tried to introduce grass from cattle farms, but so far seemingly without success.

Fig. 9b. The erosion caused by the scalping activity of elephants is clearly visible in this photo.

Of the wild ungulates competing for vegetation in the reserve, the buffalo in particular represents a threat to the elephant. As with the elephants, buffaloes immigrating from jungle areas outside the park, as well as tame populations released in the jungle, add to the size of the population in the reserve. But in contrast to the elephant, the buffalo has a high rate of reproduction. The leopard does not even begin to limit the size of the population, and neither do the yearly removals of some dozens of bulls by the Wildlife Department. Rinderpest (the last epidemic was in 1908/09) and drought (1931, 1934, 1948, 1956) take a toll, as does the starvation of a number of bulls during the dry season. Even so, the density of buffaloes in the reserve has been estimated as 70 animals per sq.km, with extremes up to 380 in some parts of the open plains.

Elephants regularly use waterholes for bathing and drinking as well as for social checkpoints. Today many of these waterholes have been taken over by buffaloes for wallowing and urination and defaecation, so that these waterholes are now unfit for elephants. The number of elephants and buffaloes visiting 8 waterholes during a period of 15 days during the dry season (May 12-August 2) was compared. Two waterholes, 1 of them artificially made, and the other situated between two high rocks, were too deep for buffaloes to wallow in. The number of buffaloes visiting these 2 waterholes was estimated as 30 to 40 each. Both waterholes were regularly visited by elephant herds, one on 12, the other on 13 days. Two other waterholes, which were less than 1 meter deep but did not dry up during the dry season, were frequented by 70 to 80 buffaloes each for wallowing: they were used by the herd on 6 and 7 out of 15 days, respectively. There were 4 waterholes which practically dried up at the end of the dry season (beginning of September) because of the wallowing activities of a buffalo population of 60 to 200 animals. The herds stopped visiting 2 of these sometime between May and August. The other 2 were visited once or twice by elephant herds within the 15 day period of observation.

Long-term conservation of elephants in Ceylon cannot be guaranteed simply through more additions to the reserves. It often seems, incidentally, that these additions are granted because they lack water and therefore are not attractive to human settlers; but for the same reason they are not attractive to elephants. The present policy of pushing additional elephant herds into reserves has led to higher densities and to over-utilization of park resources. Feral buffaloes must be considered as competitors for food and water, and they should therefore be reduced. This proposal is not new—it was already suggested at the beginning of this century by pioneers of the Ceylonese conservation movement such as H. F. Thompson in 1925, L. Nicolls in 1928, and J. O. Brown in 1929. But the solution is political in nature and consequently difficult to realize. National parks in Ceylon have been promoted by idealists who are concerned about the survival of individual animals. Shooting has therefore been strictly prohibited, and no efforts have been spared to transplant individual elephants into national parks. This factor, plus the Buddhist ethic of not killing, may inhibit any management plan which seeks to eliminate the cause of the unbalanced ecosystem and not merely its symptoms. It has been suggested that Ceylonese elephants may react with population regulation to the higher density and over-utilized resources of its habitat by means of lower reproduction rates and higher mortality. This, however, would not solve the problems of erosion and of polluted waterholes.

Ceylon's national parks consist mainly of forest areas with only a few open areas where visitors can observe elephants at a distance. Chance meetings in a forest area occur rather rarely, with the elephants taking off immediately and the bulls sometimes charging. As a result, most visitors congregate around waterholes as the one spot where elephants have to appear, even though these crowds may prevent the elephants from appearing for hours at a time. Proper management plans should stipulate that no roads may be made within fifty yards of waterholes so that elephants can drink undisturbed and visitors can still observe under optimum conditions.

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Paper No. 33

Territoriality and Population Regulation in the Uganda Defassa Waterbuck

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ABSTRACT

Details are given of densities, sex ratios, population structure and social organisation, of three contrasted populations of the Uganda defassa Waterbuck *Kobus defassa ugandae* Neumann in the Queen Elizabeth Park, Uganda. Possible functions of territorial behaviour in the male are examined with particular relation to a role in population regulation. A function for territorial behaviour could not be defined with certainty, and changes in sex ratios which have taken place in two of the study populations during the past ten years, suggest that territoriality did not limit the numbers of males compared to females. It is concluded that territorial behaviour in this species is not the ultimate behavioural factor regulating population numbers, which, if such a mechanism exists at all, must rest with the female, who is not territorial.

INTRODUCTION

The Uganda defassa Waterbuck (*Kobus defassa ugandae* Neumann) is a large African antelope, the genus being widely distributed from about 15° N to 30° S. Adult males of the Uganda race stand about 126 cm high at the withers and weigh 236 kg, whilst females stand about 120 cm high and weigh 188 kg. The horns, present only in the male, are imposing bowed structures reaching almost 90 cm in length, with annulations on the anterior face and terminating in sharp points.

Territoriality in this species was first suggested by Verheyen (1951, 1955), and later confirmed by Kiley-Worthington (1965). From October 1964 until May 1967, its social organisation was studied in the Queen Elizabeth Park of western Uganda, at latitudes 15' N to 30' S,and longitudes 29° 45' to 30° 15' E, where it is common, with an overall estimated density of 2. l/km^2. Three main areas in the park were studied in detail. The Mweya Peninsula, almost an island of 4.4 km^2, with a density of 10.9/km^2; the adjoining area, known, for the purpose of study, as the Ogsa,an area of 14.3 km^2 with a density of 3. 2/km^2; and Kayanja, 52 km^2. In part of the last area the density was 17. 8/km^2, in contrast to the overall figure of 9. 9/km^2. A full description of these areas has been given elsewhere (Spinage 1969, 1970).

METHODS

To determine the spatial distribution of Waterbuck within the areas a series of consecutive visits was made and the positions of animals recorded. Males were either captured and marked, or recognised from natural characters, as was a proportion of females. Arbitrary boundaries were then drawn around the male positions after each series of observations. On eleven occasions the positions of these boundaries were confirmed by observation of behaviour between neighbouring males. These incidents were not frequent enough for delineating boundaries from them, but they confirmed the positions derived from plotting.

The entire male population of the peninsula was age-determined by means of juvenile characters and tooth impressions, as well as two-thirds of the female population and a number of animals in other areas.

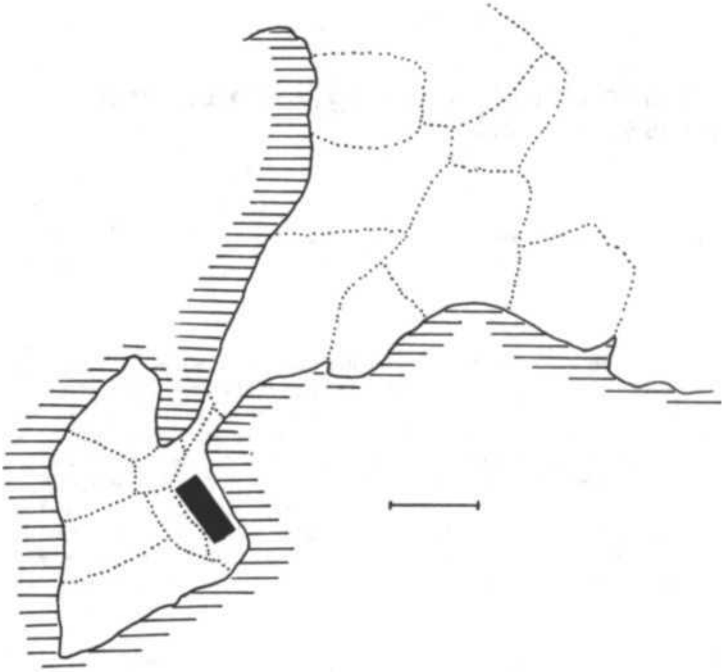

Fig. 1. Approximate outlines of Waterbuck territories in the peninsula and Ogsa areas of the Queen Elizabeth National Park, Uganda, 1965, showing differences in size. Scale = 1 km.

RESULTS

The Male

Males were normally attached to the dam for 8 to 9 months, after which they usually joined the bachelor herd. This comprised animals up to about 6 years of age. The mean herd size was 5. 3, although groups of two were most common. Herd size did not bear a significant relation to density ($p = >>0.1$), although herds of 35 and more were met with in high density areas. Analysis suggested a tendency to form herds of certain size.

Bachelor herds were not relegated to unfavourable areas but were allowed to share the territories of several adults males, relatively unhindered. Probably due to strife within the herd, certain animals, or groups of animals, of 2 to 3 years or more, may emigrate and wander to other areas. At about 6 years of age males would try to leave the bachelor herd and establish themselves in a territory, often becoming completely territorial by the age of 7 (Fig 2). Age determination of immobilised animals revealed that batchelor herds were comprised of only young animals, and that those thought to be adults were young males approaching maturity, whose horns were as long as those of the territorial adults. Territories were maintained throughout the year and defended against occupation by other adult males (Fig. 3), death from fighting occasionally taking place. The Waterbuck here breeds throughout the year, and although there are peaks of births there is no season of rut.

At about 10 years of age territorial owners were often ousted by younger males and driven to inhabit small, unfavourable areas. They did not however return to the bachelor herd, indeed their presence within it would not have been tolerated by the owners of the territories which the bachelor herd shared.

A relationship existed between territory size and the age of the owner, the largest territories being held by animals of 8 and 9 years. This seemed attributable to the fact

Fig. 2. A seven-year-old male Uganda Defassa Waterbuck

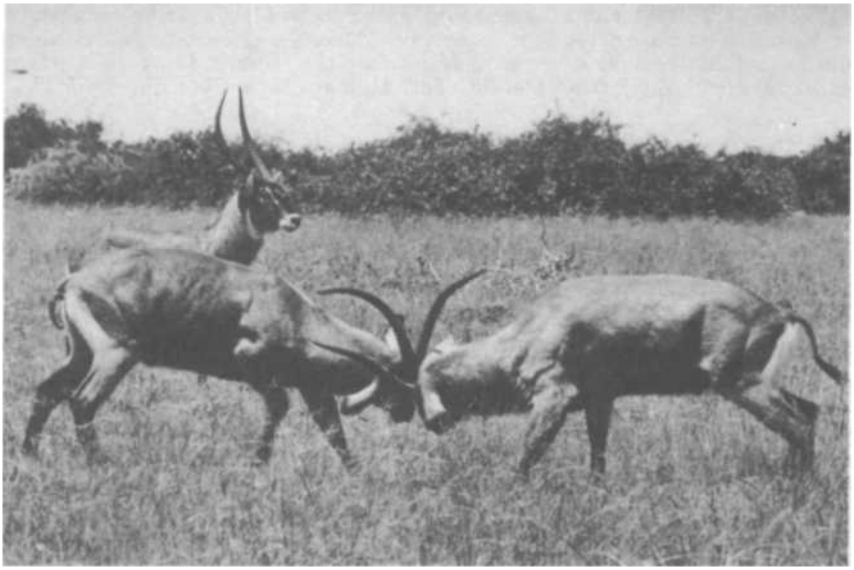

Fig. 3. Territorial males lighting, with a bachelor male looking on.

that a young male had first to establish himself amongst existing territories, and therefore commenced with a small area. Ways in which this was seen to be achieved have been described elsewhere (Spinage 1969). Conversely the older animals, as we have seen, were forced into smaller areas after they had passed their prime. But a middle-aged male seemed satisfied with an area of certain size, and I saw no evidence of attempts to extend property. Thus in two cases on the peninsula, when territories became vacant through the death of their owners, neighbouring males did not attempt to add these territories to their own. They might use them increasingly when they found no owner to challenge them, but once a new owner installed himself, then the neighbours retreated to their old boundaries. As a result the shape and size of territories did not alter much, and they could be said to be 'inherited' in that a new owner took over what the former owner possessed. But if several juxtaposed males were removed together, then new owners would probably establish quite different boundaries.

The mean territory size for a 9 year old male on the peninsula was 81 ha, and in the Ogsa 202 ha, the largest territories being 141 and 222 ha respectively. But there was one male per 24. 3 ha on the peninsula, and one per 56. 9 ha in the Ogsa. This suggested that size of the territory was dependent upon the pressure of competition and that there was no universal optimum territory size.

Despite the marked differences in occupation densities of these two areas, their vegetation appeared to be virtually identical. The advantage of the peninsula appeared to be that all territories were adjacent to water. In the Ogsa however, although one old male held a territory near the water until his death, another was isolated in the centre, a most unfavourable position from the Waterbuck point of view: to obtain his daily drink he had to pass through the territories of others. I found that he was permitted to do this, relatively unhindered, as long as he maintained a sub-dominant attitude to the owners of the territories through which he passed. At Kayanja this situation was even more in evidence.

At Kayanja there was water on one side only, with an apparently neutral zone adjacent to the water, where only mild agonistic displays might take place; the real defended territories lying inland. Thus as many as 8 adult males could be seen within a few metres of each other at a waterhole that was in the neutral zone, so, whereas on the peninsula access to water seemed to be the key factor in territorial possession, the system was clearly flexible. At Kayanja the habitable area was large compared with the water frontage, and any male who tried to defend a waterside territory against incursions by others, would find himself subjected to continual pressure. Studies elsewhere (Taylor *et al.*, 1969) have shown the Waterbuck to be completely water dependent; it must drink about once a day. Thus under conditions such as those seen at Kayanja it seems that the male defends a place in which to live, and shares the essential commodity, water, thereby reducing the pressure of competition.

The female

In contrast to the males the females inhabited a home range, which covered several male territories. The average size of the peninsula female home range was 605 ha (in the Ogsa it was 695) with a mean density of one female per 23. 5 ha in the peninsula and Ogsa areas combined, females using both regions. These home ranges appeared to be 'owned' by groups of females, in the above case a group of about 26. But the females moved within the range essentially as individuals, in groups of 3 to 6, with a mean group size of five. Analysis showed that there was no tendency to form groups of certain size, and no firm attachments between members of a group were identified.

After weaning, at about 6 to 8 months, young females remained with the dam groups, but at about 18 months constant agonistic behaviour directed towards them by the adults, tended to drive a number away. The agonistic behaviour looked innocuous enough, nothing more than a harmless butt in the flank, but its effect was presumably cumulative.

The young females so ousted possibly formed spinster groups which underwent a period of emigration and wandering akin to that seen in the male. Observations suggested that individuals settled where their first parturition took place, at about 3 years of age. After parturition, the spot, for some females at least, appeared to represent a key point in the home range, to which they repeatedly returned to give birth. One female was seen to give birth in the same place three times.

The affinities of the females thus seemed to be for the area rather than for particular males, whose territories they wandered through at will, spending anything from a few minutes to several weeks in them.

As there was no competition for water amongst the females the high density on the peninsula, one female per 19.8 ha, compared with the Ogsa, one per 63 ha, must have been attributable to other causes. The only apparent favourable difference between the two areas was the raised nature of the peninsula, cooled by breezes off the lake. This was attested by the facts that the highest densities occurred in what were probably the coolest parts of the area, and the animals did not seek shade during the hottest part of the day, contrary to their behaviour in other areas. This explanation could not account for the high numbers at Kayanja, where the only overt factor might be an absence of interspecific competition. There were few competing ungulates, namely buffalo, here, whereas buffalo densities were high in both the peninsula and Ogsa areas.

These differences in occupation densities suggested that the main factors influencing Waterbuck distribution and density were, in order of importance, water, topography and food.

Sex ratio

The examination of a significant number of foetuses (n = 60) showed the sex ratio at birth to be unity, whereas field counts revealed that the park mean for animals above 9 months of age (at which they could be easily sexed) was 1:1.6 males to females. Ratios ranged from 1 : 0. 5 in poor areas, where the males were senile ones and the females temporary visitors, to 1 :4.3 in areas where males were scarce, possibly because such areas were not conducive to maintaining territories. The peninsula overall sex ratio was 1 : 1.8, in the Ogsa 1 : 1.5, and at Kayanja 1 : 3.7.

On the peninsula the ratio amongst approximately one-year olds was almost unity, 1:0.8, in the Ogsa it was 1:0.3, and at Kayanja 1:1.5. By the time these populations have become adult the ratios have apparently changed to 1 : 4.1 on the peninsula, 1 : 2. 5 in the Ogsa, and 1 : 12. 6 at Kayanja. With increasing density of population the number of males has decreased relative to the number of females, which they may even have outnumbered when young. These changes are no doubt the result of the territorial behaviour pattern, but there is more than one way in which they could be brought about.

DISCUSSION

Factors such as water, topography and food resource may account for density and distribution patterns, whilst territorial behaviour may determine the structure of the societies within those densities and distributions. But does territorial behaviour itself serve to limit the numbers within a specified area? If we were considering birds it might be easier to separate the role that territory could play, for birds usually share territories as a pair. In the Waterbuck however we have one social system for the male, that of territoriality, and another for the female, that of an undefended home range. These two contrasting systems make the separation of cause and effect more difficult.

A study of Waterbuck survival, as in almost any other species, shows that there are so many chance factors which could kill the animal before it attains senescence, that it is hardly surprising to find that the numbers do not increase exponentially. Counts suggest that the numbers of Waterbuck do not oscillate widely, despite local fluctuations in population size. The consequences of the species' pattern of social behaviour may play a part in this, but is that part of any greater significance than the cumulative effect of other chance mortality factors ?

Let us consider food supply. Does the spatial distribution, imposed by the males' territorial behaviour, use the food supply more effectively? That is, are the males limiting the size of the population by hoarding food; or by rationing food and allowing the population to exist at a level at which it could not otherwise, by ensuring fair shares for all? In the first case the males would be denying to others food which was surplus to their own needs; in the second case they would be aiding its full utilisation.

The answer to both questions is negative, as the territorial males allow the bulk of the non-territorial sector, the bachelor herd and the females, to use the food resource without hindrance. Effective denial of food could be to only a very minor part of the population.

With increasing population density there was a decrease in the number of males relative to the number of females. The peninsula observations showed that this could be attributable to the fact that territories can only be compressed within certain limits. If the male sector continues to increase beyond these limits, and emigration cannot take place, then males must be eliminated from the population. All other things being equal, had the males survived at the same rate as the females, the density of Waterbuck at Kayanja would have been 66/km^2 instead of 17. 8/km^2, on the peninsula 20. 5 instead of 10. 9, and in the Ogsa 4. 6 instead of 3. 2. In the total park population we might have had 1800 more Waterbuck than the estimated 3000.

This sexual imbalance seems unlikely to have any effect upon reproductive efficiency as there are always enough males to accommodate the females; and there is not a surplus of breeding males. Those which are excluded from breeding are the young and the old, which will take, or have taken, their turn in the territorial system.

A function suggested for bird territorial behaviour is that it allows copulation to take place undisturbed. Observation shows that this is not necessarily so in the Waterbuck; although spatial distribution does curb sexual strife, and the fewer males that there are in proportion to the females, the less the competition for mating.

Reduced numbers of males and more effective breeding are possibilities, but now let us consider some changes which have taken place in the peninsula population during the last few years. At the end of 1956, Petrides and Swank (personal communication) recorded an average of 4 territorial males and 16 adult females on the peninsula. This was a sex ratio of 1 :4,and a density of 4.6 animals/km^2. In 1959, the hippopotamus population was removed (Bere 1959) and about a year later the numbers of Waterbuck began to increase exponentially to a mean of 53 animals. In 1964, saturation was apparently reached and the numbers declined to a mean of 48 for the three years 1964 to 1967. The sex ratio was then 1:1.8 and the density 10. 8/km^2.

In the adjacent Ogsa in 1956, there was a mean number of 44 Waterbuck; comprised of 5. 3 territorial males, 9. 7 bachelor males, 28. 4 adult females, and 0. 7 young females. This was a sex ratio of 1:1.7 and a density of 3. 1/km^2. Ten years later this was almost unchanged, the differences being sufficiently slight as to be attributable to sampling error. In 1965, the mean number was still 44, including 8.7 territorial males and 7.8 bachelor males, giving a sex ratio of 1:1.5.

The number of males on the peninsula increased four-fold during the 10 years, but the number of females only increased 1. 75 times. These changes, in the increasing population, during the 10 years suggest the antithesis of the hypothesis that territoriality may provide a means of suppressing the numbers of males. The territorially organised sector of the population had increased at the expense of the other.

If we regard the peninsula and Ogsa as one, thus taking into account possible emigration between them, then the number of males increased by 1. 5 times, whilst the females decreased by approximately one seventh. But on the whole it looks as if the Ogsa maintained its *status quo* throughout the 10 years, and changes were confined to the peninsula.

An increase of males at the expense of females could, in itself, provide a brake to population increase, as the males do not contribute as much to increase in numbers as do females. The absolute increase on the peninsula has been greater, and one could suggest that it has taken less numbers of females to reach saturation point (which the decline in numbers suggests was reached in 1964), so that further increase was restricted to the males. In the Ogsa saturation level was already attained, so the complement of males and females remains stationary.

In territorial studies we have been rather carried away by the part of the male, which is more spectacular, and seems to be more active, than that of the female. But it is clearly the female which must supply the clue to a limiting factor to population increase, if there is such a factor, for she is biologically more valuable. The question immediately arises that if territorial behaviour limits the numbers of males, and the same system does not pertain in the female, why do the numbers of females not increase exponentially-unless they possess some independent curbing mechanism?

If we postulate that the chance mortality factors operating against the male are not in themselves sufficient to regulate the population numbers, then likewise they cannot be sufficient to regulate the numbers of females. Observations suggested however that the females displayed their own regulatory mechanism, resulting from the agonistic behaviour shown by adult to young females.

Whether the process determining which young females were driven out was random, or whether the adults appraised the density within their home range and acted accordingly, was not established. Permissible density may be related to some environmental factor, such as availability of food. It is conceivable that an adult female, finding difficulty in selecting desired grasses because she is surrounded by too many competitors, would soon become aggressive towards the younger, more easily dominated, members of the group. This might explain why a higher density existed at Kayanja than in the Ogsa.

Driving away the young females would be limiting to population size if it could be shown that their chances of survival decreased as a result. The latter seems likely, for they would lack organised patterns of avoidance of hazards. Thus the adult females, by regulating the numbers within their home ranges, could lessen the chances of survival of superfluous numbers, by exposing them to the increased risk of an unfamiliar environment.

It is recorded that in 1931, there was only one adult male Waterbuck on the peninsula (Worthington & Worthington 1933). This solitary male, and the gradual increase in males thereafter, could suggest that the male is responsible for the dispersal of the species. There is a good chance that wherever there are territorial males then there is also that essential Waterbuck requirement, water.

A female needs only find a territorial male to know that water is probably at hand. But the territorial system, with its competition for the best areas, suggests that the colonisers are more likely to be in fringe areas, to which they have been driven by competition, and thus are not likely to find the best environments for successful survival.

It is more logical to assume that the females play the active role in dispersal, as they must seek out the best conditions for the rearing and survival of the young. This would imply that, at Kayanja, they have reacted to some favourable environmental factor; perhaps nothing more than an increased rainfall providing a better food supply. The females moved in amongst the territorial males, as opposed to the idea that the population was a unit which developed a wide sex imbalance within itself, as the result of male strife consequent upon increase in population numbers. This did not happen on the peninsula.

Thus a favourable area attracts the females. Eventually the population builds up to a level at which its density means that the area is no better than other areas. But before this level of occupation is reached, increasing agonistic behaviour of adult to young females, has meant that the latter have already begun leaving the unit for other pastures. Thus, as the males remain behind, not only the original complement but also those produced by the females to fill all available territorial niches, then the sex ratio begins to adjust itself.

The function of territoriality in the male could thus be seen as that of keeping the male sector of the population in one place, so that the population unit as a whole does not move from one area to another. This would ensure maximum dispersal of the species, a dispersal in which the role of the male is essentially a static one.

The changes in the sex ratio which took place on the peninsula suggest this as a more plausible explanation of sex imbalance than that of intra-specific fighting reducing the male sector. This confers no obvious advantages other than that of enlarging the biologically most important sector of the population. As such, it would serve not to regulate the population numbers but to ensure a continual increase, and the evidence does not support this.

Dispersal, the possible function of territoriality in the Waterbuck, was advanced by Wynne-Edwards (1962) as the function for territoriality as a phenomenon. He considered the critical resource to be food, as far as population density was concerned. It was highly advantageous to the species' survival, and thus strongly favoured by selection, for a species to control its own population density, and to keep it as near as possible to the optimum level for the habitat which was occupied. Food cannot be the proximate factor in this, only the ultimate, and a proximate factor, limiting the numbers of a species within the resources of its food supply, is provided by territorial behaviour.

Among birds, Wynne-Edwards considered, minimum territory size is inversely related to productivity of the habitat and to food supply; but the contest is for the possession of territory and not for the food itself. This provides a completely density-dependent mechanism which allows the habitat to fill, amid mounting rivalry, to a maximum density. This spreads the population, without clumping it in groups, and provides the 'simplest and most direct kind of limiting convention that it is possible to have' (Wynne-Edwards 1962).

There are many similarities in the waterbuck's behaviour with this concept of dispersion, except that the territorial behaviour, confined to the male, is seen only as a link with the behaviour of the female; the latter is what really determines population density within a given area.

Perhaps a more plausible function of territoriality is offered by the Neo-Darwinian view that it maintains a prime breeding stock. Territoriality ensures that breeding is denied to the young, and therefore untried, and to the old and to the weak. This could lead to selection for vigour. Furthermore it lessens the chances of in-breeding, a son with its mother, or a brother with its sisters. Weak strains that might result from inbreeding are thus eliminated, although inbreeding is not necessarily deleterious. But granted such a sexual function for territoriality, this would maximise fertility rather than act as any limiting factor to population increase.

We should not assume that the reason for territoriality in one species must be the reason for it in another. Different species have different ecological requirements, and their social behaviour will be moulded accordingly. Wynne-Edwards' conclusions, which really related to birds, have been the subject of considerable criticism (Lack 1966), much of which seems to stem from trying to impose a single solution to the concept of territoriality. Territoriality is simply a way of life which probably confers the most benefits upon a given species in a given set of circumstances, although these benefits may be obscure in light of our present inadequate knowledge. The benefits are obscure because what we have before us is a basic system of organisation being used in many different ways, under many different sets of circumstances, by many different species. When comparing one species with another we should expect to find different benefits, rather than the same ones.

The Waterbuck of the Kafue National Park of Zambia (*Kobus defassa crawshayi* Sclater) displays a similar mode of territorial behaviour to that described for the Uganda Waterbuck, in that the male maintains a territory throughout the year. But it differs in that the territorial owners apparently exclude the bachelor herd from their territories during the breeding season, which at this latitude is restricted (Hanks *et al.*, 1969). Thus a question of latitude has apparently resulted in differences of territorial behaviour, and possibly different functions that could be ascribed to it.

The ultimate question appears to be not whether territorial behaviour does, or does not, have an effect upon the numbers of a population; but whether, if it does, that effect is of greater significance, directly or indirectly, than the many other diverse mortality factors which militate against the animal's survival. In the Uganda Waterbuck territorial behaviour cannot be the ultimate behavioural factor in any population regulatory mechanism, should such a mechanism exist, as this must rest with the female, who is not territorial.

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Paper No. 34

Four Types of Territoriality Observed in a Herd of Black-Tailed Deer

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ABSTRACT

Social order and spatial regulation were exhibited by black-tailed deer (*Odocoileus hemionus columbianus*) on the Cedar Creek deer study area in northwestern Oregon between November 1963 and May 1965. Social order was maintained within the herd by the existence of dominance hierarchies in each closed group. The dominant deer of each In-group exhibited agonistic behaviour that served to control the actions of the subordinate deer within their groups. Expressions of spatial regulation by clans of deer were observed on three occasions. The first display of group spacing involved 14 deer (10 versus 4) and lasted only 11 minutes on May 3. The second display of group spacing involved 5 deer (4 versus 1) and lasted for 45 minutes on May 15. The third display of group spacing involved 3 deer (2 versus 1) and lasted for 52 minutes on November 1. On all three occasions the resident deer drove off the intruding deer. Constant individual spatial regulation by defence of an area was practised by only one animal. An adult female defended a portion of her home range against all intruders from November 1963 until September 1964. Only the alpha buck practised spatial regulation during the rut. The fourth principal type of spatial regulation was practised by does with fawns during the postfawning period. I conclude that the primary value of individual and clan spatial regulation to the deer was that it provided control of land areas that were well vegetated with winter forage and improved the chances of survival for at least some members of the local population during winters of exceptional environmental stress. Spatial regulation by clans of deer also provided a form of psychological security for subordinate animals and at the same time reinforced the dominance of the higher ranking deer. This situation thereby enhanced the social bonds of all members of the group. The primary advantage to the dominant male was that he was allowed to do most of the breeding with minimal stress from competition. He also encountered fewer dangers from possible predators and challengers, as he remained on his home range. Spatial regulation by dams during the postfawning period lessened the chances of predators being attracted to the bed sites of fawns. Active fawns would have equal opportunity to flee with the other deer from predators. Black-tailed deer, both as individuals and in groups, have the ability to recognize specific landmarks.

INTRODUCTION

I observed the social organization of a herd of black-tailed deer on the Cedar Creek deer study area in the Coast Range Mountains of northwestern Oregon between November 1963 and May 1965. My original objectives were to record the distribution patterns of black-tailed deer in relation to measured environmental factors and to relate the observed activities to previously and currently available forage, to plant communities, and to climatic conditions (Miller, 1968b, 1970b).

Historically big game management in North America has been an attempt by biologists to equate optimum animal numbers to the carrying capacity of the range. More recently efforts have been made to increase the quality of the range and thereby increase the animal numbers. This has been particularly true in the case of North American cervids which are frequently exposed to varying degrees of stress during the winter period when mobility is often restricted and food availability is reduced. There is no doubt that the capacity of the range to produce feed is a principal factor limiting the numbers of animals that can occupy a unit of land.

There are, however, other factors which affect the carrying capacity of the range, one of which is the behaviour patterns of the species in relation to the densities of their own kind. The intra-specific intolerance of individuals appears to limit occupancy. The practise of spatial and temporal regulation is apparently important as density controls either at all times of the year or at different seasons of the year.

THE STUDY AREA

The study enclosure was approximately 29 km inland from Tillamook, on the Cedar Creek watershed in that portion of Tillamook County known as the Tillamook Burn (45°36'N,123°36'W). The elevation within the enclosed area ranges from 245 m to about 650 m, measured from mean sea level. The area is approximately 138 hectares by horizontal plane measurement. Because of the rough terrain the actual surface area is nearly 2. 6 sq km. The area is comprised of three distinct land units (Fig. 1): east drainage, flats, and west drainage (Miller, 1970b). It contains the typical seral plant growth that follows fires or clear-cut logging in the Coast Range Mountains of northwestern Oregon (Crouch 1968). Detailed descriptions of the study area are given by Bailey and Poulton (1968), Crouch (1968), Miller (1968b, 1970b), Bailey and Hines (1971).

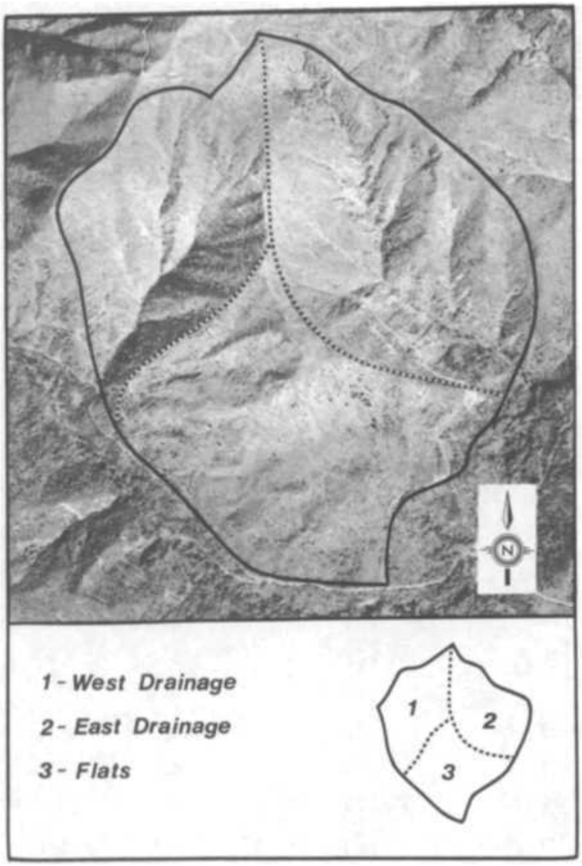

Fig. 1. Aerial photograph of the Cedar Creek study enclosure showing the three major land units within the enclosure

ANIMALS AND METHODS

From July through November 1963, thirty-four black-tailed deer were captured in areas around Cedar Creek (Miller, 1968a). Each was released in the enclosure on its day of capture. The herd numbered 30 animals by January, 1964, when periodic observations were begun. At that time the sex and age composition of the herd was 10 adult does, 5 adult bucks, 4 female yearlings, 3 male yearlings, 4 female fawns, and 4 male fawns. The density, 11. 6 deer per sq. km was thought to be comparable to that of the region.

All deer except fawns were marked with collars and ear streamers of the type used by Harper and Lightfoot (1966, Figs. 1A, 2A). Fawns of the year wore ear streamers only. The colour code of the streamers and collars and painted symbols on the collars permitted positive identification of individual deer.

The deer were observed from three huts placed outside the enclosure on surrounding prominences. Daily, nearly equal time was spent observing from each hut, but often under very different weather conditions. The hours of the day spent at a hut were rotated. For example, from 6 : 00-10 : 00 a.m. at one hut on Monday, at the second hut on Tuesday, and at the third hut on Wednesday. The entire elevational range within the enclosure could be observed from each hut. Observational equipment consisted of 10 × 50 field glasses and a 15X-60X Balscope Zoom spotting scope. Sightings of deer were placed on a gridded map derived from an aerial photograph. Each square on the map represented 0. 5 horizontal hectares. All time intervals were determined with the sweep-second hand of a wristwatch and were rounded to the nearest minute.

My deductions are based on 6, 746 sightings of known individual deer during 1,411 hours of observation throughout 1964 (Table 1), supplemented by many sporadic observations of the deer from July to December 1963 and from January to May 1965.

TABLE 1. Monthly herd sizes, number of deer sightings, hours of observations, and average number of deer sightings per hour during 1964, Cedar Creek Study area, Oregon.

Month of Year 1964	Size of Herd	Number of Deer Sightings per Month*	Total Hours of Observation	Average Number of Deer Sightings per Hour
Jan.	30	147	62	2.4
Feb.	30	260	80	3.3
Mar.	30	419	112	3.7
Apr.	29	716	100	7.2
May	26	1,025	236	4.2
June	32	507	146	3.5
July	33	701	139	5.0
Aug.	33	546	141	3.9
Sept.	31	623	142	4.4
Oct.	30	337	74	4. 5
Nov.	29	904	123	4.9
Dec.	29	505	56	9.0

* 56 sightings were deleted throughout 1964 because the observer possibly influenced the movements of the deer.

RESULTS AND DISCUSSION

Soon after introduction the deer established home ranges and formed social groups within which there were foster families. It is unlikely that there was any direct blood relationship between the individual deer as they were all captured at distances of one to several kilometers from each other (Miller, 1968a). The animals soon established dominance regimes which I recognized from displays and agonistic actions. I was soon able to assign social ranks to all members of each group. The deer established home ranges and there appeared to be no relationship between the time of introduction and the locations of home ranges occupied by individual deer (Miller, 1970b).

SOCIAL ORDER

The Annual Cycle of Closed-Groups

Fawning—(May-June)

All of the groups except the buck group had disbanded. The buck group stayed in close company throughout the summer. Pregnant and maternal does would not tolerate close association with members of their previous winter groups. Non-breeding immature deer remained together as remnants of the winter groups. Newborn fawns remained bedded between nursing periods while the maternal does foraged or rested. Spatial overlap of home ranges occurred. Temporal isolation was maintained, however, by the somewhat synchronized movements of deer, resulting in virtually no simultaneous use of common ground.

Postfawning—(June- July-August)

Maternal does began accepting back those deer from their previous winter groups which were closest to them in social rank, but remained antagonistic toward other members of lesser rank, particularly yearlings. Some non-breeding deer remained in the company of other non-breeders but their association was rather loose and the groups constantly broke up, while the individuals wandered, and regrouped throughout the postfawning period. Fawns remained bedded or travelled with their dams between nursing periods.

Pre -rutting—(September- October)

The bucks were still in close association, though, by mid-September individual bucks were beginning to wander, becoming intolerant of each other. This was especially true of the 2-year-olds (Miller, 1970b). Maternal does showed little antagonism toward other members of their previous winter groups. Most deer (especially the maternal does) did not remain in tight groups, but came together for feeding periods and often moved off to bed on separate sites. By early October group bonds were becoming stronger and by late October all groups were loosely formed.

Rut—(November-December)

By November the bucks had disbanded and were antagonistic toward each other and occasionally engaged in head pushing contests and antler fighting. Two-year-old males were involved in most of the antler fighting. Yearling males took part in most of the head pushing events. All males withdrew from the threat displays of the two dominant males. Aggressive behaviour of male *Odocoileus* is discussed in detail by Cowan and Geist (1961), Thomas *et al.* (1965), and Geist (1966). The females and juveniles were in loose groups which were constantly disrupted by sexually aroused bucks. The bucks drove the does that were in heat from the clans and in doing so scattered the other members—especially the yearlings and young of the year, which the bucks often pursued and kicked. The estrous does rejoined their clans after being serviced or having evaded the pursuing bucks. By mid-December the prime bucks had lost interest in the does and had retired to higher ground where they spent their time foraging and resting. The younger bucks, however, pursued does throughout December.

Winter Period— (January- February)

All deer with the exception of a yearling male and two mature does were members of social groups whose members foraged and rested in close association. Some fixed sites on the most productive areas of winter forage were defended from other deer by clans of deer and individual deer. The use of various sites, forage, and plant communities on the area was recorded by Crouch (1966 and 1968), Bailey and Poulton (1968), Miller (1968b and 1970b), and Bailey and Hines (1971).

One of the lone females dominated an area and tolerated no other deer on it. The other lone female spent most of her time on one small area but tolerated other deer and often joined a group for several hours or days, then left and remained alone for long periods. She was accepted by three different groups during the winter period. The one lone yearling male remained solitary most of the time. Whenever he ventured into a group of deer he was driven off. Sometimes he remained with or near the different groups for several hours but he was always turned away eventually.

Two male yearlings and one female yearling wintered on an area that was not frequently visited by other deer. The remaining deer wintered on ranges that overlapped, but intergroup contact was minimal. Non-group members seldom trespassed on defended sites, and when they did, retreated upon approach of the resident deer.

Spring Period— (March-April)

The deer were in closed social groups as observed during the winter period. Reduction in the forage supply and availability resulted in several groups feeding on common sites but they maintained their independent group structures. When in a large feeding group members of the discrete social groups would be consistently closer to other members of their groups than to non-members. During resting periods members of a group always bedded closest to other members of their group. By mid-April pregnant does were beginning to display added aggressive actions toward the younger deer. These antagonistic actions were quite sporadic in intensity and frequency. Does were observed to drive off short yearlings in the morning only to be observed a few hours later resting or feeding next to the same yearlings without showing any signs of hostility.

Prefawning Period— (May)

During May the deer became very restless and began moving about in definite travel patterns (Miller, 1970b). The pregnant does were strongly antagonistic toward all young members and by late May were hostile toward most other deer. By late May the winter and spring groups had disbanded and only the buck group remained together. The increased movement by pregnant does caused a prefawning spatial shift which resulted in the more even distribution of pregnant animals (Miller, 1970b). All other deer returned to the areas that they had occupied in the early spring.

Group Cohesion

The cohesion of the groups could also be subdivided on the basis of companion animals as noted for mule deer by Geist (1966). For example, during the winter of 1963-64, males A,B,and C were companions as were D and E and F and G, but J remained alone. With the loss of A and C in the spring of 1964, B became the dominant animal of the group and showed no strong affinity for any of the other individuals. D and E remained companions as did F and G. With the subsequent loss of E, B and D became companion animals in the summer of 1964 and F and G remained co-dominants. Similar relationships between companion animals were observed in all of the female In-groups. The possible role of mutual grooming as an act to reinforce social bonds of In-group members is discussed elsewhere (Miller, 1971b).

Home Range

Maternal does reduced the sizes of their home ranges during the postfawning period (Miller, 1970b), at which time the only adult barren does on the area had the largest home range. By August, the maternal does and does who had lost their fawns extended their home ranges, so that the annual home ranges of all the adult females that had produced fawns in 1964 exceeded that of the barren doe (Miller, 1970b). Adult males maintained their home ranges except during the rutting period. The 2-year-old males wandered the most of all deer (Miller, 1970b). Monthly and annual home ranges were related to age and sex, and varied with changes in the reproductive cycle and forage availability (Miller, 1970b).

Aggression and Dominance

In reviewing aggression among male black-tailed deer, the winter, spring, and summer can be considered as one period. The autumn, however, must be divided into three distinct periods: pre-rut, rut, and post-rut. The level of intra-group aggression remained constant from after the post-rut period when the antlers were cast to the beginning of the pre-rut. Aggression among female black-tailed deer was on the upsurge during late winter and spring. Their agonistic acts oscillated considerably during the pre-fawning period, increased rapidly as individuals approached term, and peaked during the postfawning period. Aggression among females was low during the autumn and throughout the rut, on into early winter.

The following two events were vivid examples of male interaction during the rut. On October 10, J made threat displays toward D. J locked antlers with F and threw F completely over his (J's) head and downgrade for about 5 m,then turned on D,who was bedded about 10 m away. D rose from his bed and both D and J approached each other in a stiff-legged manner with antlers presented, but after they touched noses, J turned and left the area and D bedded down again. B retired from the pursuit of females during the first week of December. He moved to high ground and took up a routine of short alternating intervals of foraging and resting. On December 5, at 7 : 30 a.m., D was observed pursuing a 2-year-old female along the eastern edge of the flats. During the following 8 hours the doe moved back and forth and out of the east drainage, back up the main ridge to the head of the drainage, down into the bottom and up the east side of the east drainage to within 10 m of where B was bedded. B rose and moved nearer to her, but then turned to foraging. D came over the ridge at 3 : 46 pm and upon seeing B next to the doe presented his antlers and moved directly at B,who surprisingly turned away and bedded down without any apparent concern for D's presence. D then herded the doe off down the drainage.

The event was the only occurrence of D ever showing any aggressiveness toward B, who had always maintained absolute dominance over D. By mid-December, when D was also no longer sexually aroused, he was again subordinate to B. D remained second in rank within the buck group during the winter of 1964-65.

Dominance hierarchies were influenced by the loss of animals from groups and changes in individual levels of aggression of males during the autumn rutting period and of females during the fawning and postfawning periods. Some females producing fawns for the first time also caused changes in dominance hierarchies by their more aggressive acts as maternal animals (Miller, 1971a). When a doe's fawn died her antagonistic behaviour toward other female deer often changed. Such fawnless does often became subordinate to does that they had dominated during the postfawning period.

The hierarchies could be stratified at three levels: absolute dominance, partial dominance, and co-dominance. Acts of aggression or displays of dominance by animals that were absolutely dominant were never challenged by the recipient. Such acts by animals that were only partially dominant were, however, sometimes challenged, but usually accepted without resistance. Co-dominant animals very seldom showed any signs of aggression toward each other.

Agonistic acts termed the crouch, occasionally with circling and nose licking, the rut-snort, and stiff-legged walk as described by Cowan and Geist (1961), the rush, antler threat, strike, flailing, stamping, and erection of the tail as described by Thomas *et al.* (1965) were observed. The deer under study also displayed the head-high threat, the rush-attack, and the present threat as described by Geist (1966).

For the purpose of my work I described seven basic agonistic acts.

1. Move—the 'move' was used as a display of dominance. In aggressive situations the dominant animal usually caused a subordinate animal to move so that it could feed upon the site occupied by the subordinate. The subordinates generally reacted by jumping aside and moving off a few meters. If the subordinate hesitated, the dominant animal followed with a foreleg kick, which the subordinates usually managed to avoid. When the 'move' was used in a nonaggressive situation the dominant animal seemingly gained nothing from moving the subordinate other than possibly reinforcing its position in the group. If the subordinate animal was

moved from its bed the dominant deer might or might not lie down in the bed. If it did, it stayed in the bed for only a few seconds or minutes before getting up and changing sites.

2. Chase—the 'chase' varied from a half-hearted run of several meters to a hard run of hundreds of meters over several minutes of pursuit. The 'chase' often resulted from a subordinate animal not responding fast enough to threat displays or an aggressive 'move' by a dominant deer.
3. Kick—foreleg kicks by dominant deer most often followed if subordinate deer were not quickly responsive to the earlier aggressive acts of dominant animals. Most foreleg kicks did not find their marks.
4. Bite—definite biting was only observed on five occasions. Biting has not been described for any New World deer so far. On four occasions the bite was delivered to the back of the neck in horse-like fashion. On one occasion the subordinate deer was bitten on the middle of the back.
5. Nudge—the 'nudge' was used on both bedded and standing animals. The blow was delivered by the dominant animal directing its hooves backwards and swinging its foreleg forward in a pendulous manner striking the subordinate lightly on the rump or side. The subordinate animal was never struck with the apices of the hooves in the manner of an aggressive downward foreleg kick.
6. Rake—The 'rake' was executed by the dominant deer extending its foreleg forward at about a 45° angle and raking its foot along the side, back or rump of the subordinate.
7. Stance—the 'stance' is similar to the first part of the 'rake' in that the dominant animal extends its foreleg at about 45° and rests its foot on the subordinate's rump, back, side, and infrequently its head. The 'rake' and 'stance' were used as displays of dominance on bedded subordinates only.

Other Behaviour

Play by black-tailed deer was observed on 42 occasions. Their patterns were categorized as: (1) contagious, (2) exploratory, (3) care-soliciting, (4) sexual, and (5) agonistic. The dominance hierarchy seemed to breakdown completely during play. A stereotype behaviour pattern in response to the death of their fawns was displayed by four dams (Miller, 1971a). Behaviour associated with parturition was recorded (Miller, 1965). Aberrant behaviour was expressed by the first ranking (alpha) buck toward a newborn female fawn (Miller, 1970a).

SPATIAL REGULATION

Spatial Regulation by Clans of Deer

I observed expressions of spatial regulation on three occasions by 10, 5, and 2 black-tailed deer, respectively. The first display of spacing involved 14 deer (10 versus 4) and lasted only 11 minutes on May 3, but proved to be the most outstanding event. The second display of group defense involved 5 deer (4 versus 1) and lasted for 45 minutes on May 15. The third display involved 3 deer (2 versus 1) and lasted for 52 minutes on November 1, 1964 (Fig. 2). On all occasions the resident deer drove off the intruding deer. The total deer sightings for the 14 deer involved in the first display of spatial regulation by clans of deer were 3, 228; for the five deer in the second event, 1, 050; and for the three deer on the third occasion, 556.

On May 3, ten deer (three mature does, two rising 2-year-old does, four velvet-antlered adult bucks and one rising 2-year-old male) were being observed in the east drainage system. Three bucks and one doe were bedded. The rest were foraging. All were within 50 m of each other. The group was resident in the east drainage system, and had never been seen anywhere else.

At 10 : 50 a.m., a different group of deer (two mature females and two rising female 2-year-olds), whose normal range was in the area designated as the flats (Fig. 1) and who had never before been observed on the east side of the east drainage system,

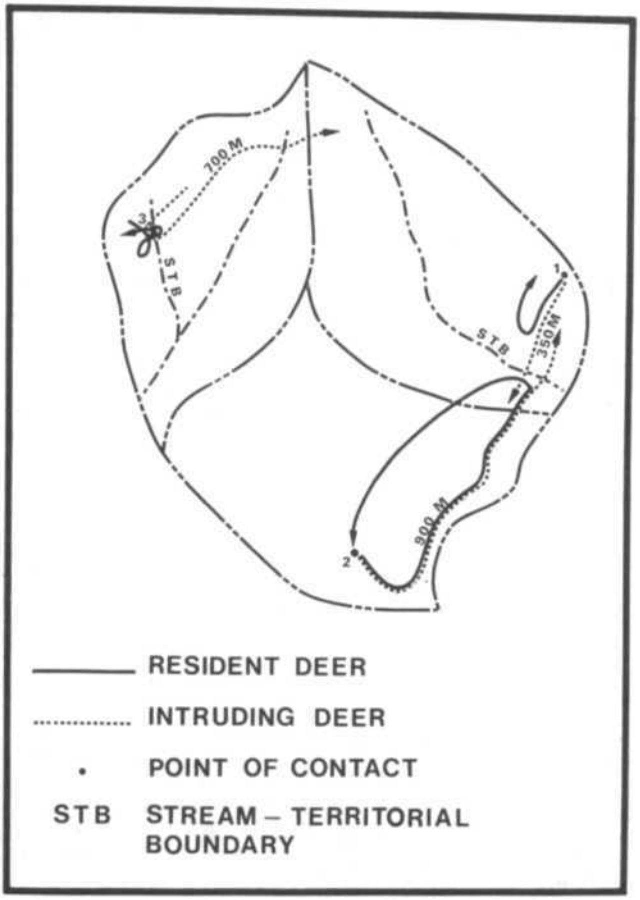

Fig. 2. Schema of movements by deer during three conflicts in which resident groups exhibited group territoriality

(1) May 3; (2) May 15; (3) November 1, 1964

was seen moving at a fast walk up the fence line about 300 m below the 10 animals under observation. The lead doe stopped frequently to stick her nose through the wire, seemingly interested in getting through the fence. Their hesitant actions indicated that they were not familiar with the area they were entering.

When the four intruders reached the elevation of the ten resident deer it appeared, at first, that the two groups were going to ignore each other. In an apparently co-ordinated movement resident deer suddenly surrounded the intruders. All animals moved about, smelling and looking at each other. As the resident deer crowded closer, touching noses with the intruders and laying their ears backwards, the intruders grouped tightly and faced the resident deer, seemingly sensing the coming conflict.

The first aggressive act came from the 'lead' doe of the intruder group. She struck out with her forefeet at a mature doe, striking her several times on the side and rump. Immediately, a mature resident buck charged with his head down at the intruding doe's rear, but she turned before he made contact and struck him in the neck with her left front foot hard enough to make him stagger and retreat. A second resident buck charged with his head down at the lead doe, but he too retreated after receiving several blows to his right flank. Instantly, all the resident does, 2-year-olds, and a third buck were fighting. This buck was defeated by one of the intruder 2-year-old females. The fourth resident buck did not attack nor was he struck by any of the intruders. All three mature bucks were defeated after initial contact. None used their front feet, but charged head down as though they still possessed their hard antlers. The intruders directed all their blows against the resident deer and vice versa.

Initially, the lead doe and one 2-year-old doe of the intruders were the most aggressive. Later, however, a 2-year-old male of the resident group became very aggressive, defeated the lead doe and once left the ground completely to land on the back of an intruder. Two resident mature does, after being kicked several times, rose on their hind legs and struck the intruders with their front feet.

After the 11-minute engagement, the intruders began to retreat downgrade. The resident deer moved to the opposite ridge of the drainage and followed at a distance of about 100 m until the intruder group had crossed the creek in the bottom of the main drainage. Observable agonistic behaviour then ceased, indicating that the stream, approximately 1 m to 1. 3 m in width and only several centimeters deep along most of its course, was the boundary of the defended area. The 10 resident deer then moved up the ridge about 150 m, stopped, and resumed their previous routine. Five lay down and five began foraging. The four intruders did not feed until 10 m west of the creek.

On May 15, at 9 : 00 a.m., a parturient doe from an east drainage group was seen moving at an alternating trot and brisk walk. She was travelling along an old logging road that cuts the face of the south end of the main ridge between the east drainage and the flats. She left the road, turned southwest, and descended onto the flats. Her location was well beyond the western boundary of her home range, but she was still moving at a fast pace.

By 9:15 a.m. she was well within the home range of a group of four deer that were resident to the east end of the flats, but she continued wandering about the area. At 9 : 25 a.m. she turned east and entered a stand of red alders (*Alnus rubra*), a site that I knew was a well-used resting area of the resident deer.

Suddenly, at 10 : 10 a.m., two deer, the intruder doe and the second-ranking doe of the resident group broke from the alders. The intruder doe ran about 50 m across a grassy opening, then stopped and faced the oncoming doe. An exchange of foreleg kicks occurred and the resident doe retreated into the alder stand. The intruder doe followed her in but quickly reappeared at a full run. This time the dominant doe of the resident group broke from the cover, followed by the other three does of her group. The intruder doe ran east with the resident deer in pursuit until she reached a logging road that led around the mountain to the east drainage.

At the road the intruder doe hesitated and both the dominant and second-ranking does charged her, kicking her several times on the left side and rump. She then began to trot along the road with the four resident does repeatedly charging at her. Whenever she slowed down one or more of the resident deer would rush in and kick at her. The dominant doe was the most aggressive as they herded the trespasser back over the main ridge and down the west side of the east drainage. On several occasions when the intruder doe attempted to run uphill, the resident deer forced her back onto the road.

At 10 : 50 a.m. the intruder doe reached the main creek in the bottom of the east drainage, crossed, and stopped some 10 m to the east. The four resident deer came to the western bank of the creek and stood looking at her. The intruder doe turned, faced the four deer, and laid back her ears. The act seemingly caused the dominant doe of the resident group to jump across the creek, but as soon as she landed on the other side, she sprang back to the west bank. Her action was enough, however, to make the intruder doe start running upgrade. After several meters she slowed to a walk, then turned and looked back at the resident deer, before continuing up the ridge. She then began foraging and moving slowly in the direction of her group, which was about 200 m upgrade from her.

The four resident deer started back over the main ridge along a higher route at 10 : 55 a.m. They then descended onto the flats and foraged as they moved slowly back to their bed sites in the alders, where they bedded at 11 : 31 a.m.

On November 1, at 7 : 10 a.m., two resident does were observed bedded in the lower southwest corner of the west drainage about 20 m from the western edge of a small lateral creek. At 7 : 35 a.m. a doe whose home range included the upper portion of the eastern side of the west drainage and a part of the east drainage was sighted moving from the eastern side of the creek directly towards the two bedded does. She crossed the creek without hesitation, and the two resident deer rose from their beds. The two does charged at the oncoming intruder, who veered from one animal but received a kick in the right rump from the second doe as she jumped back across the creek.

The intruder doe immediately turned and charged back across the creek at the two does, who met her head on. Many foreleg kicks were delivered, but relatively few actual strikes were made. Each time the intruder doe would flee across the creek and the two resident deer would stop their chase at the western bank. The routine of charge and retreat was repeated three times in 6 minutes.

The intruder doe then turned to foraging east of the creek and the resident deer began moving back to their bed sites. At 7 : 50 a.m. she attempted to pass through the territory by moving rapidly upgrade, but the dominant deer of the two resident does cut her off and chased her back across the creek.

The non-resident doe moved about for several minutes and the two resident deer turned to foraging. Then, at 8 : 08 a.m., the would-be trespasser again attempted to get by the two does by running downgrade and cutting across the creek. But she was cut off by the subordinate resident doe and chased back across the creek. The resident doe was apparently so aroused by the chase that she followed the intruder some 20 m beyond the eastern side of the creek. The intruder stopped suddenly, turned, and charged the resident doe. Several foreleg kicks were exchanged and the resident deer retreated to the western side of the creek with the intruder in close pursuit.

The intruder doe then moved upgrade along the creek and bedded in a well-used bed about 2 m east of the creek. The subordinate resident doe was only about 4 m to the west of the bedded intruder but showed no signs of antagonism even though the bed site was the birthplace of the resident doe's fawn (Miller, 1965).

The two resident deer resumed foraging. At 8 : 23 a.m. the intruder doe was up and foraged for 2 minutes. She then made one last attempt to trespass, but both does moved in her direction. She charged at the subordinate resident doe, but the dominant doe cut her off and chased her back across the creek. Both resident deer crossed the creek, but the intruder doe continued moving slowly up the west drainage and crossed over to the east side and out of sight. The two resident deer returned once more to their beds.

The dominant doe (No. 7) of the two resident deer involved in the incident of November 1, 1964, had been a subordinate companion animal of the intruder doe (No. 2) prior to July 1964. Both deer had moved from the east drainage to the west drainage during the prefawning spatial shift. As parturition approached, No. 2 became very aggressive toward No. 7. No. 7 was forced to occupy the upper west side of the west drainage, while No. 2 remained for the most part on the east side of the west drainage and the northwest corner of the flats. No. 2 produced two fawns and No. 7 had one fawn. The subordinate doe (No. 1) of the November 1, 1964, resident group had one fawn. Nos. 1 and 2 lost their fawns as described in Miller (1970b). No. 7 then became a co-owner of No. l's area in September 1964 (Miller, 1970b). At that time the home ranges of all three does overlapped considerably. I think that the past domination of No. 7 by No. 2 and the degree of overlap of the three does' home ranges probably explains No. 2's aggressiveness in the conflict on November 1, 1964.

The home ranges of all of the intruder and resident deer involved in the three group conflicts either overlapped or bordered on each other. The relationship of home ranges of clan members to areas defended by clans is illustrated in Fig. 3.

On 17 occasions in March, 8 in April, and 3 in May individual clan members were observed to turn away would-be intruders on the areas defended by their respective clans. When clan members detected non-clan deer on or about to enter the area defended by their clan they took a fixed stance and stared at the intruders. The display was comparable to the head-high threat as described by Geist (1966). This action usually caused the intruder to retreat, but if the intruder came closer, the resident

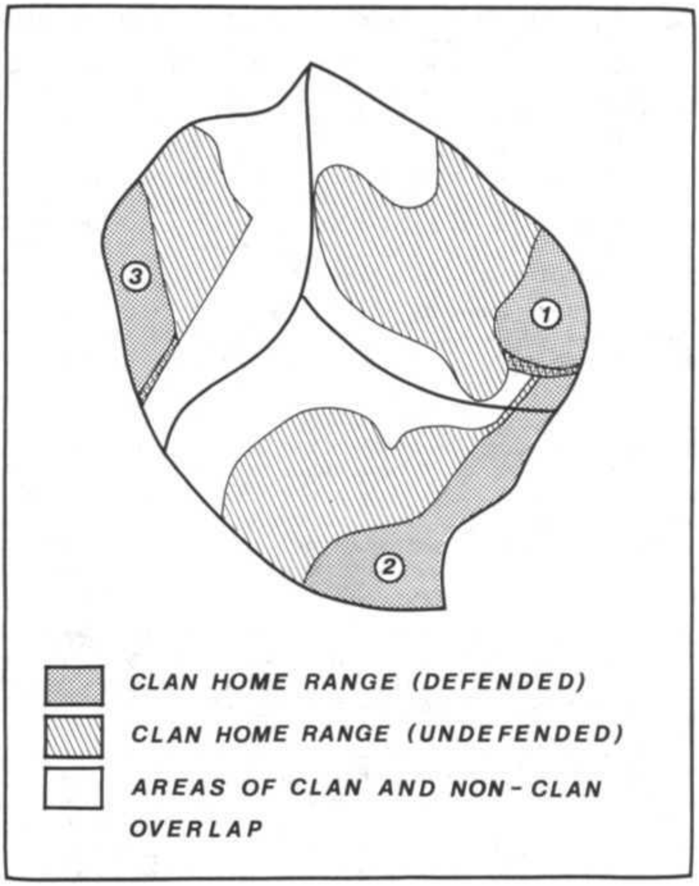

Fig. 3. Schema of relationship between home ranges of clan members and the area defended by the clan (1) and (2) January-May 1964; (3) August-December 1964

deer always charged and this caused the trespasser to withdraw from the area. The actions of the resident deer were probably reinforced in most cases by other clan deer being nearby.

On other occasions from January to May, non-clan deer that were about to trespass on defended areas were seemingly diverted by the mere detection of nearby alerted resident deer. On some occasions several resident deer would stand staring at an oncoming non-clan deer. The approaching deer, upon detecting the resident deer, would stop well before entering the defended area and make abrupt changes in its direction and often its pace of travel.

Spatial Regulation By Individual Deer

Only one of the 10 does 3 years of age or older was observed to defend a specific area of land throughout the year. She was captured on November 21, 1963, about 0.3 km west of the study area. After introduction she made a circuit of the area and established her home range in the west drainage. It is possible that some of the hillsides that could be seen to the west of her new range were familiar to her and might have been part of her original home range. Of all the deer, this doe was captured closest to the study area and was the only animal captured from west of the study area.

The area defended by the doe was 9. 5 ha: 16. 5 per cent of her annual home range (57. 5 ha) and 78. 5 per cent of her average monthly home range (12. 1 ha). The mean annual home range of all adult does was 69. 6 ha with a standard error of plus or minus 5.6 ha.

The doe was observed to have aggressive contacts with other deer on 16 different occasions. The deer that she attacked on any one occasion ranged from 1 to 5 individuals: 1 deer, 5 times; 2 deer, 6 times; 3 deer, 3 times; and 5 deer, 2 times. When she charged more than two deer at a time, she would first scatter them, then run each one individually from the area defended by her. She undoubtedly had the psychological advantage of being on her own ground as even the groups of five intruders retreated when charged. When an intruder was hesitant in retreating it received a series of foreleg kicks from the resident doe, and no deer was observed to fight back.

Deer sometimes retreated from the area upon sighting the resident doe before they crossed the small creeks that marked the eastern and northern edges of her defended area. If the resident doe was bedded on her defended area and she detected deer approaching her, she would stand and face the oncoming deer. Her display most often caused the would-be intruders to stop and watch her for several minutes, then change their course or retreat along their backtrails.

When the resident doe was bedded or feeding on other sections of her home range she allowed other deer to pass without noticeable concern for their presence. She was, however, never sociable to any other deer and her threat displays, similar to 'the head-high threat' as described by Geist (1966), were always sufficient to discourage close direct approach by other deer. This doe, after the death of her fawn, became subordinate to a young aggressive maternal female through a series of overt interactions in September 1964 (Miller, 1971a). Her subordination to the younger doe resulted in co-ownership of the defended area.

Post-fawning Defence of Fawns by Dams

I previously applied a generalized concept of territoriality to the aggressive behaviour exhibited by maternal deer while defending their bedded young (Miller, 1971a). Existing definitions of territoriality allows this consideration. If, however, one is to accept only the more stringent prerequisites of territoriality as applied to African ungulates (Buechner, 1961; Leuthold, 1966; and Spinage, 1969), one must reject the possible existence of mobile or semi-mobile territories.

I have observed that a doe establishes an overall home range for raising its fawns, but defended areas are determined by the fawns movements. Thus, there is a shift of defended areas within the home range. For about 6 to 8 weeks after fawning, does seldom tolerated other deer within about 15 m of their bedded fawns and often charged deer at distances of 30 m or more. When her fawns were absent, the doe no longer defended their bed sites (Miller, 1971a).

During postfawning the does with fawns made 141 close contacts with other deer, of which 112 contacts (79%) were aggressive and 29 (21%) non-aggressive. During the pre-rut, dams made 410 close contacts with other deer of which only 68 contacts (17%) were aggressive. The resultant reduction in aggressive actions by dams during post-fawning *vs.* pre-rut was 1 in every 1. 2 contacts to 1 in every 6.0 contacts (Chi-square 185, 1 d.f., $P < 0.001$).

When the fawn is active, the dam will often tolerate a deer that she had previously driven off and may allow it to approach to within about 5 m of her active fawn. Often her fawn runs out and frolics about the intruders without the dam responding to the close association. While the fawn is active the dam is more tolerant of certain deer than others. Animals who were close companions from her previous winter groups might even sniff the fawn without her reacting. Low ranking subordinates, however, are often charged at the first sign of the close approach.

There appears to be a distinct difference between the aggressive actions of a doe when her fawn is bedded and her agonistic acts toward other deer when the fawn is active. When a fawn is bedded it usually cannot be seen by the dam and most often its exact location is not known. The dam must associate a price of ground with the presence of her fawn and will readily attack all intruders, including former companion animals.

In 43 contacts when fawns were bedded dams threatened or attacked in all cases, whereas in 98 contacts when fawns were active the dams threatened or attacked in only 69 cases (70%—Chi-square 14. 3, 1 d.f., P < 0.001). On the basis of this difference in behaviour and, especially, because of the dam's indiscriminate rejection of all deer from within the defended areas around her bedded fawn, I had believed that maternal black-tailed does practise semi-mobile territoriality during the postfawning period.

If, however, territoriality is only the defence of a single geographically fixed unit of land with clearly defined boundaries, the exclusion of all deer from the immediate areas around bedded fawns must be considered only as an intensified form of maternal protection.

On the basis of the above qualification of territoriality one must assume that 'moving territories' do not exist. Therefore, I now must conclude that my observations and also observations by Dasmann and Taber (1956), Altmann (1958) and Espmark (1969), were not of territorial behaviour by maternal females during the postpartum period, but other forms of spatial isolation associated with the defence of their young.

Rutting Behaviour of the Alpha Male

Only the first ranking (alpha) buck (B) maintained exclusive use of a large unit of land during the rutting period: the east drainage. He was the most vigorous in pre-rutting activities and the first breeding male to retire from rutting activities. The other males remained sexually aroused for 1 to 3 weeks beyond B's withdrawal from the rut.

By the first week of September the bucks were shredding the velvet from their antlers by vigorously thrashing red huckleberry (*Vaccinium parvifolium*) and thimbleberry (*Rubus parviflorus*) and rubbing red alders and vine maples (*Acer circinatum*). B was most violent in his attacks on vegetation. On several occasions he seemingly fought mock battles with stands of red huckleberry, sometimes 'beating' several bushes in succession. If other bucks were present during one of B's thrashing displays, they would just stand off and watch, but never attempted to join in.

As the pre-rut progressed B and D became antagonistic toward F and G, and J whenever he attempted to join the group. J returned to the flats and F and G left the east drainage together and wandered about elsewhere within the study area. By the onset of the rut B became antagonistic toward D and drove him from the drainage.

During the rut B controlled the entire east drainage and did not tolerate any of the other bucks on his ground. He was often sighted moving back and forth along the main ridge that separated the east drainage from the west drainage and the flats. Other bucks offered no opposition when B crossed the ridge and cut does away from them.

Aggressive pre-rut and rutting contacts between B and other breeding bucks were as follows: 11 in September, 6 in October, 15 in November, and 5 in December. Of the 37 contacts, antlers were used on 7 occasions in September, 3 in October, and none in November and December. Antler contact was of low intensity and involved only antler touching and to a lesser degree head pushing with D. The other bucks were turned away by threat displays.

From my observations during the rut it is reasonable to assume that B probably bred 9 of the 13 adult does. B retired from the pursuit of females during the first week of December. He moved to high ground and took up a routine of short alternating intervals of foraging and resting.

TERRITORIALITY

References to the complex phenomena termed 'territoriality' started with a statement by Willugby in 1622 (Carpenter 1958 : 224). But it was not until by Heape (1931) and Burt (1943) that the concept of territoriality as it applies to mammals was examined. Carpenter (1958 : 224-250) in his review of the concepts and problems of territorial phenomena cites 146 references that relate to the problem. He (Carpenter 1958 : 228-229) has aptly summarized the problems of attempting to define territoriality:

> 'The organismic mechanisms, the drives and incentives or motives, and the sensory-response and learning processes are all different aspects of the behavioural systems of territoriality. These are expressed with reference to loci in space, and to the topography of habitat areas, as well as to other organisms living in the areas. Behavioural systems change over periods of time. Those which constitute territoriality in animals are so complex, and involve so many adaptive and even nonadjustive mechanisms, that they defy adequate description by condensed definitions. Fully systematic and analytical descriptions are required.

Carpenter (1958 : 242-243) also listed 32 inferences on functions of territoriality.

I have previously concluded that the spatial regulation observed in this study in fact comprised four types of territoriality. Dr. F.R.Walther (pers. comm.) has argued that the value of the concept of territoriality is lost if one applies the generalized definitions which I have used in the past. I am willing to accept his line of reasoning and apply a more stringent definition. That is, territoriality is the defence of a geographically fixed unit of land with distinct boundaries. I do contend, however, that if one uses the following definitions of territoriality that my original conclusions are valid.

Noble (1939 : 267) stated that 'territory is any defended area'. Burt (1943) favoured Noble's (1939) definition because it could be modified to fit any special case. Etkin (1964 : 21-22) defined territoriality 'as any behaviour on the part of an animal which tends to confine the movements of the animal to a particular locality.' Etkin's definition is even more all encompassing.

Eibl-Eibesfeldt (1970:309) has proposed 'that any space-associated intolerance be called territoriality, where a "territory owner" is that animal before which another conspecific must retreat at a given time.' Even though the Eibl-Eibesfeldt definition falls short of the desired or necessary complexity for a definition of territoriality, it takes into account both the spatial and temporal aspects and encompasses all four types of spacing regulation observed in this study.

CONCLUSIONS

The process of socialization forces some poorer deer to utilize marginal forage sites. Thus the poorest stock should be the first to succumb to severe environmental stress. The process of group cohesion, however, allows some subordinate deer to have nearly equal chances of survival as members of strong discrete social groups. This maintains the variable expression of genotypic plasticity that benefits the species over a long period of time. Survival of the subordinate animals with the instinctive drive to follow and of dominant animals with the drive to lead ensures the continual cohesion of the groups.

I think that the primary value of spatial regulation to the clans of deer under consideration was that it provided control of land areas that were well vegetated with winter forage and improved the chances of survival for at least some members of the local population during winters of exceptional environmental stress. It also provided a form of psychological security for subordinate animals and at the same time reinforced the dominance of the higher ranking deer. This situation thereby enhanced the social bonds of all members of the group.

I believe that the primary advantage of spatial regulation by the individual doe was also that it increased her available winter food supply. The area defended by the doe was nearly the only portion of the west drainage in which vine maple and huckleberry-salal (*Vaccinium-Gaultheria*) plant communities predominated and were found together. The remaining portion of her home range was comprised primarily of the thimbleberry (*Rubus*) plant community which has a low winter forage value (Miller, 1970b; Bailey and Hines, 1971).

As witnessed in this study the ability of ungulates, both as individuals and in groups, to recognize specific landmarks has been observed by many investigators, as noted by Klopfer (1969 : 86) and Eibl-Eisbesfeldt (1970 : 309). The boundaries of the defended areas on the study area were easily recognizable but were not physical barriers to the deer, with the exception of the fence line. The boundaries included small streams, stream beds, logging roads, sections of the fence, and in one case the slope of a flat-topped knoll of ground. Subordinate males that ventured into the east drainage during the rut were probably aware of having crossed boundaries, but at the time were driven by their sexual urge. Upon encountering a dominant male, a subordinate male made a hasty retreat as far as the territorial boundary but once there showed no further signs of alertness toward the dominant male.

I believe that my observations of certain behavioural patterns expressed by black-tailed deer on the Cedar Creek study area represent the complex behavioural system of social order and spatial regulation practised by black-tailed deer. My observations suggest that black-tailed deer can and do practise spatial regulation under various conditions and at different seasons of the year.

I think that the primary advantage derived through spacing by the dominant male from his behaviour during the rut was that he was allowed to do most of the breeding with minimal stress from competition. He also encountered fewer dangers from predators and challengers, as he remained on his home range and did not have to roam on unfamiliar ground and compete with other males.

The control of a relatively large unit of land by superior dominant males during the rutting period could have the following effects on the species: (1) selective breeding; (2) restricted rate of gene flow; (3) reduced sexual fighting and killing of superior stock; (4) increased breeding by superior stock; and (5) reduced physical stress.

The exclusion of all deer from near the bed sites of fawns by their dams during the period of postfawning lessens the chances of predators being attracted to the bed sites of fawns. Deer movements around bedded fawns could attract predators. The flight of the deer in response to approaching predators might startle bedded fawns and cause them to rise unwarily and be taken by surprise.

In contrast active fawns would have equal opportunity to flee with the other deer from predators. Both individuals and groups of deer can benefit from spatial regulation by some animals, even though the expression of intolerance may vary greatly among individual deer.

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Paper No. 35

The Social Organization of the Roan Antelope *Hippotragus equinus* and its Influence on the Special Distribution of Herds in the Kruger National Park

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ABSTRACT

The dominance relationships amongst males and the members of nursery herds is described, with an appraisal of their influence on the social organization of the species. The characteristic distribution pattern of roan herds is ascribed to the intolerance of herd bulls toward one another and the dominance hierarchy amongst the females. Exclusive activity zones in favoured habitat place a restriction on population size and imply that the expansion of range could only be achieved by special management procedures.

INTRODUCTION

Geographically the roan antelope occupies a wide range of distribution in Africa. Though human settlement, hunting and poaching activities have caused serious inroads in many of the natural populations, the species still occurs over extensive areas south of the Sahara desert. Despite this wide distribution it is only in a few local areas that the roan populations constitute a significant proportion of the wild animal communities. In most areas herds consist, on the average, of six to 12 individuals (cf. Blower, 1961) and comprise, in terms of numbers and biomass a relatively unimportant position. This holds true for the Kruger National Park where a total population of some 250 to 300 animals has caused considerable concern for their chances of survival. It was therefore decided to do a comprehensive bio-ecological study of the roan antelope in the Kruger Park. To provide realistic study opportunities and simultaneously build up a small population from which groups could be released periodically to augment the natural population, it was decided to erect a gameproof enclosure and release a nucleus herd of roan into it. This ideal was achieved when the enclosure was completed during 1967 and a group of ten roan was released into the camp during July of the same year.

METHODS

Observations were made on the herd in the enclosure as well as on free roaming herds. A four-wheel-drive Land Rover vehicle proved most satisfactory for this purpose as it did not cause any undue disturbance among the animals being observed and could also be used to follow herds through rugged country. Direct observations were usually made with a pair of 10 × 50 binoculars and a 40 × 60 spotting scope. Photographic equipment consisted of an Asahi Pentax camera with 55 mm, 200 mm and 500 mm lenses.

STUDY AREA and ASSOCIATED SPECIES

Most of the data discussed in this paper was collected from observations on the roan herd in the enclosure and also from free roaming herds in the vicinity of the camp. This area comprises the northernmost reaches of the Lebombo flats and lies between the Shingwedzi River in the south and the termination of the flats in the Punda Milia-Klopperfontein area in the north. Topographically this area represents a flat, slightly undulating stretch of country with the topsoil consisting mainly of a heavy black soil derived from basalt. The major woody component of the vegetation is the tree and shrub form of the Mopane, *Colophospermum mopane* and hence the designation of this vegetation type as 'mopani scrub and tree savanna' (Pienaar, 1963). Other important tree and shrub species include *Combretum imberbe,Sclerocarya caffra, Lonchocarpus capassa, Dalbergia melanoxylon* and *Grewia* spp. The grass stratum is mainly comprised of *Themeda triandra, Panicum coloratum, Schmidtia pappaphoroides, Cenchrus ciliaris, Heteropogon contortus, Digitaria* spp., and *Aristida* spp.

Associated large mammal species, occurring together with the roan include elephant *Loxodonta africana,* buffalo *Syncerus caffer,* blue wildebeest *Connochaetes taurinus,* eland *Taurotragus oryx,* sable antelope *Hippotragus niger,* tsessebe *Damaliscus lunatus,* reedbuck *Redunca arundinum,* and zebra *Equus burchelli.* Larger carnivores include lion *Panthera leo,* leopard *Panthera pardus,* cheetah *Acinonyx jubatus* and hyaena *Crocuta crocuta.*

RESULTS and DISCUSSION

This paper will endeavour to illustrate that the social behaviour of roan has exerted an important influence in stabilizing its population in the Kruger Park and also plays a role in the spatial distribution of the population. From this point of view the social organization of the species may be divided into the following categories:

(i) position among bulls;

(ii) interrelationships of the cows; and

(iii) the spatial distribution of the herds.

(i) Position among bulls

One of the characteristic features of the roan herd is that it is accompanied by one mature bull only. By implication this would infer that at some stage the immature males must leave the nursery herd either on their own accord or be forcibly driven out by the herd bull.

Of 12 calves born under controlled conditions six were males and six females. It would therefore appear that male calves are born at a ratio of 1 : 1 to female calves and remain with the nusery herd for the first 30 to 36 months. During this period the young males are tolerated in the nursery herds and their position, in relation to the older animals, is no different from that of the heifers of similar age.

Once the young male reaches the age of two years the dominance/submissive ritual between the herd bull and young male becomes more pronounced and frequent. In this display the herd bull approaches the young male to within a few metres and, with head held erect and the ears held slightly away from the body and pointing backwards, assumes the dominance posture. The young male reacts by lowering his head, pulling his tail in tightly between his legs and twitching the ears which are usually held straight up. In this posture the young male slowly approaches the dominant bull face on. On approaching the herd bull the young male usually lowers his head even further with his nose close to the ground. In this manner the youngster slowly ambles past the bull from front to rear at a distance of approximately one to two metres. On passing, the young male may also shake his head but does not lift it from the head-low position. As the young male passes, the bull points his nearest ear towards him and may also turn his head and thrust his horns at him. In this display the dominance of the herd bull is constantly asserted over the subordinate male in the normal dominance/submissive relationship between the two.

With the commencement of the eviction process at the age of approximately two and a half years the distance at which the young male is tolerated from the herd bull gradually increases. Once the individual distance between the two has reached approximately 15 metres the eviction process is in full operation. At this stage chasing of the young male by the herd bull commences and takes the form of zig-zag running through and along the perimeter of the herd. Chasing is initiated when the herd bull approaches the young male with nose pointing forward and ears extended laterally. The

Fig. 1. The bull on the left displays the Dominance Display towards the bull on the right, which has assumed the Submissive Posture

Fig. 2. The Dominance/submissive display in the reverse-parallel stance.

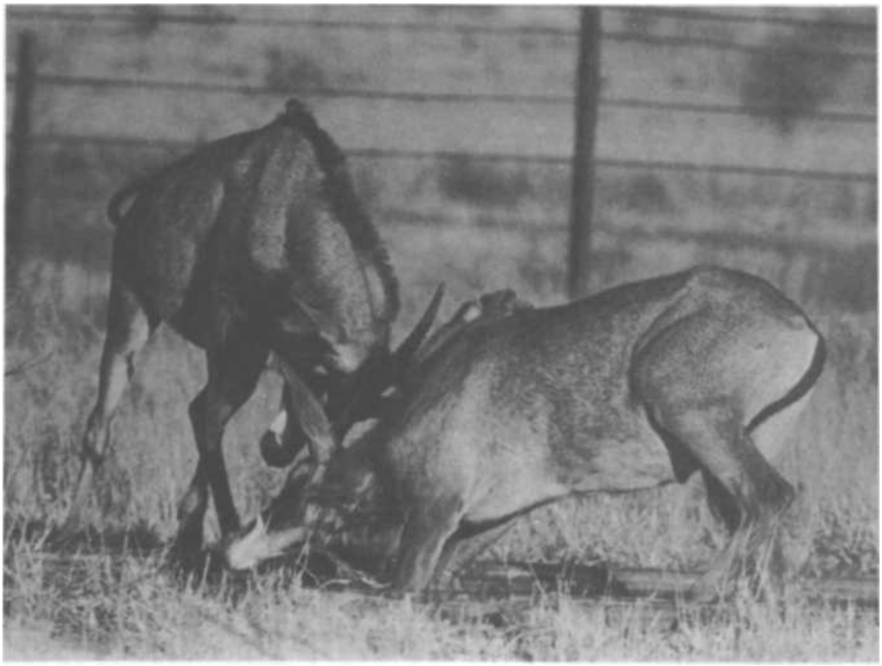

Fig. 3. Actual fighting consists of clashing the horns together followed by a fierce pushing duel.

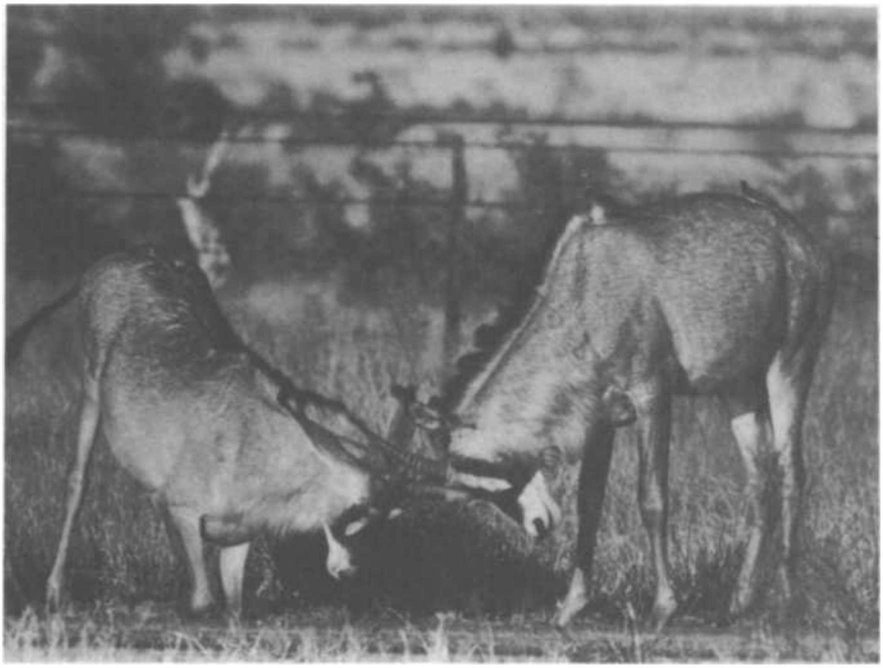

Fig. 4. Two immature males clash their horns together in a low-intensity fight. Low-intensity fights primarily serve the purpose of establishing the dominance hierarchy amongst members of a herd.

subordinate male invariably reacts by lowering his head, turning and fleeing. Chasing may be quite brief at first, with a few short bursts, but as the tolerance of the herd bull towards the young male diminishes chasing increases. The harassment of the young male also increases in frequency, and chasing is only terminated when the pursued withdraws to the perimeter of the herd. Eventually the young male has to withdraw about 200 metres from the herd to escape the persecutions of the herd bull. It is noteworthy that during the eviction process there is no bodily contact between two males. Once the young male has actually withdrawn from the herd he is constantly attacked if he attempts to rejoin it again. After some time all contact between the young male and the herd is severed and the youngster breaks away to join other evicted young males. The onset of the eviction process is gradual and prolonged and two or three months may elapse before total isolation of the young male is achieved.

Following its eviction from the nursery herd the young male enters the 'interphase' period during which it joins company with other ousted males. In the Kruger Park these bachelor groups vary between two and five males though larger groups have been observed in areas with a higher roan antelope density (e.g. Quiçama National Park in Angola).

During the interphase period there is constant skirmishing and fighting amongst the bachelors and a definite—apparently age determined—social ranking order exists among the members of such a group. At the age of five to six years a male becomes more intolerant toward the other males with a gradual increase in the individual distance until he eventually drives them away. A young male therefore spends three to four years in a bachelor group before attaining the ultimate in dominance, i.e. total intolerance towards other males older than three years. Males which have emerged from the bachelor groups are fully suited to become herd bulls. Figs. 1, 2, 3 and 4 illustrate three incidents in the process.

(ii) Interrelationships between the members of a herd

The roan antelope nursery herd consists of a herd bull, a varying number of adult cows and their offspring. The dominance/submissive relationships play an important role amongst the members of the herd with the bull being dominant over all the cows. Once a bull has acquired a harem he asserts his dominance over all the members of the herd. In fully mature bulls mere displaying in the dominance posture is sufficient to subordinate the cows. This is achieved in identical fashion to that described for the bull and young male in the previous section. The dominance of the bull over the cows plays an important role in the mating ritual which is initiated by the bull displaying the dominance posture to the cow. The dominance/submissive relationship between the bull and cow is maintained throughout courting and mating phases and is therefore considered essential for successful copulation.

Amongst the cows the dominance/submissive relationships are equally well developed and give rise to a clearly defined dominance hierarchy. This provides for a social ranking order with an alpha cow as the most dominant and the rest following in order of declining dominance. The alpha cow also fulfils the role of leader of the herd (cf. Backhaus, 1959). The influence of the leader-cow may easily be recognized as paramount in all forms of activity which may have a bearing on the herd as a whole, i.e. in determining movements from one area to another, location of grazing grounds and guidance to and from watering points. It is therefore amply clear that the determination of the daily routine of activity, especially movements, is dependent on the guidance of the leader-cow and in this way she is also responsible for the plotting of both the 'home range' of the herd over a short period of time and also the herd's 'activity zone' over a more extended period, covering the different seasons of the year.

Maintenance of the hierarchy is achieved both by the dominance display as well as by actual fighting. Duelling between partners is frequent among the lower rank-and file members of the herd and usually takes the form of play—or low intensity fighting. More serious fighting may also develop from the play fighting while high intensity fighting is restricted to the most dominant animals in the hierarchy.

The dominance display in females is performed much less frequently in determining dominance/submissive relationships than in the case of the bull. However, the posture assumed by a dominant cow is the same as that described for the bull; in fact, the entire dominance/submissive ritual is the same as that described for the males.

Low intensity fighting occurs most frequently among the immatures and low-ranking individuals of a herd (Fig. 4). This type of fighting usually commences when two individuals approach one another and start rubbing their foreheads together. Also the nasal, sides of the face and eye regions are rubbed together. Eventually their heads are drawn in slightly to tilt the horns forward after which the animals make horn to horn contact. Slight pushing between the two may also occur. Once pushing starts, one or both animals fall to their knees. From the kneeling down position the same rather gentle rubbing or pushing may continue as in the upright position. However, the duelling may also develop into a more serious bout with heavy pushing until one or the other withdraws. During the pushing the tails are switched from side to side or held tightly between the legs while the ears are twitched about continuously. Though the termination of such a fight is merely the withdrawal of one of the contestants, the victor can invariably be predetermined by merely knowing the social rank of the two animals. In animals which are well matched the pushing duel may become quite severe though the dominant one sooner or later pushes his or her adversary 'off the mark.'

Amongst high-ranking cows fights are less frequent but usually of a much higher intensity. If a cow cannot assert her dominance over another by means of displaying, direct aggression results. One some occasions a cow may charge directly at another from a distance of ten to twenty metres. If the attacked animal is inferior to the aggressor it will soon surrender by jumping away and thereby end the aggression. If it is of higher social standing it will respond to the charge by falling onto its knees and clashing horns with the other cow. A short and sometimes vicious pushing duel ensues until the subordinate animal ends the fight by jumping up.
Of the dominance hierarchy Scott (1958) writes that 'this kind of social organization is relatively stable and permanent... (which)... is presumably due to the drastic and long-lasting emotional responses connected with fighting and avoidance...' In the herd of roan studied in the enclosure no positional changes took place over a period of three years. This is regarded as sufficient proof of the stability of the ranking order of the individuals in a herd. It may therefore be concluded that the social hierarchy in roan is established by dominance—whether through sex or age—and maintained by continued aggression. Aggression here primarily serves the purpose of endorsing the dominance of the senior animal on its subordinates and not the reverse in which a subordinate challenges a senior in the hope of gaining higher social status.

One of the important features emerging from the hierarchical system is that it leads to herd stability. Herd stability implies, on the one hand, that the members of the herd are governed by a strict social organization resulting in a bond between the individuals of the herd. On the other hand, herd stability may—and in many species in fact does—lead to closed social units which do not readily assimulate other individuals of the same species. In this respect King (1954) remarked that with regard to dogs '... the more rigid the social hierarchy, the more exclusive the group.' This also clearly implies that conspecifics seeking assimilation in 'foreign' groups elicit aggression from such group members and are therefore inhibited from leaving their own group to join another. This has lead Collias (1944) to conclude that 'strangers among the vertebrates appear almost invariably to be attacked when they try to enter small groups organized on a hierarchial basis.' In the case of the roan antelop the hierarchical system results in both stable and exclusive social units. Not only does this system regulate the social organization of the species but it also exerts an important ecological influence on the spatial distribution of the herds.

(ill) The spatial distribution of roan antelope herds

The spatial distribution of roan herds is of such a characteristic nature that anyone familiar with the species can verify that it is possible to allocate a certain area to each herd. Superficially this is correct and the mosaic pattern obtained by their distribution is primarily due to the stability of herds and their habitat preferences. The habit of a roan herd to remain in a particular area for a prolonged period of time is a phenomenon that has been observed throughout their range of distribution. In

East Africa the herd around Banagi hill in the Serengeti presents a classical case and has been observed in its usual haunts for the last 30 years or more (Moore, 1938; Turner, pers. comm.; Walther, 1968a). In the Kruger National Park individual herds have also become known to the field staff due to their preference for a particular locality, e.g. a herd in the area of the Malopanyana windmill has been known in this area for at least the last six to eight years or more. In their study of the habits and ecology of roan and sable antelopes Wilson and Child (1964) found that a particular herd (it could easily be recognised due to a tailless individual) inhabited an area of approximately 30 sq. miles (77 sq. kilometres) for the total period of ten months that it was kept under observation.

From the study by Wilson *et. al.* (1964) in Zambia and observations of free-ranging herds in the Kruger Park, it appears that the average area covered by the activity of a herd in the course of a year is of the order of 25-40 sq. miles (64-104 sq. kilometres). Obviously this area is much too large to be effectively protected by one bull from intrusion by neighbouring rivals and the whole area can certainly not qualify as a single 'territorium' at any one time. In a discussion of the factors affecting spatial distribution in roan atelope, and especially in the light of any ecological consequences this system may have for the species, it is also important to consider the annual movements and home range as background to facilitate a better understanding of both the activity and intolerance zones. Taking into consideration the entire 80 odd sq. kilometres utilized at some stage or another in the course of a year (a year in this sense rather implying the different seasons of the year and their effect on the behaviour of the animals than mere calendar months) the various herds' spatial activities may conveniently be divided into: (a) Activity zone; (b) Home range; and (c) Intolerance zone.

(*a*) *Activity zone*

The heading given here is a translation, intended to convey the essential meaning of Walther's (1967) German title of 'Aktionsraum.' This category is intended to include all those areas which are utilized or occupied by an animal at some stage of its annual or life cycle and is best defined by Walther (1967) as: 'das gesamte Gebiet, das ein Individuum oder eine ständige organisierte Gruppe (Rudel, Herde) während der Zeit ihres Lebens bzw. Bestehens uberhaupt betritt. Hierin sind sowohl verschiedene Saison—Territorien un Aufenhaltsgebiete wie auch die Wanderwege zwischen diesen eingeschlossen.'

Climatologically the Kruger Park has two distinct seasons: a hot summer season corresponding with the wet or rainy period which extends from October to March or April, and a dry winter season from May to September. The winter season, and especially the latter half from the end of June to October, imposes the greatest stress upon the herbivorous fauna of the Park as most of the natural waterholes dry up during this period and the bulk of the animals are compelled to resort to artificial watering points to quench their thirst.

As with most other species, roan too have developed a clearly rhythmic pattern of activity in accordance with the conditions prevailing during each season. With the first substantial summer rains the animals disperse from the perennial waterholes and seek more favourable grazing and living conditions (i.e. less competition and predator pressure) further afield. As the veld pans dry up progressively toward the end of the dry season, the animals are once again compelled to return to the various permanent pools. The degree to which the animals disperse during the favourable summer months varies considerably from species to species, e.g. in the southern half of the Kruger Park the first rains stimulate the great concentrations of blue wildebeest and zebra to migrate to their summer grazing grounds up to 100 kilometres or more from their winter haunts; a large percentage of the eland population of the Park can be regarded merely as temporary residents due to the fact that they disperse to areas beyond the limits of the Park during the summer months. The manner and degree to which the various species respond to the different seasons of the year not only determines the activity zones of the species but clearly represents one of the important ecological facets influencing the management of wild animal communities. Not all species, however, move such considerable distances away from their winter ranges and undoubtedly the territorial tsessebe and impala as well as Waterbuck remain within a very limited area throughout the year. Roan antelope fall between these extremes as has been indicated by Wilson *et. al.* (1964) and by observations made during the course of the present study.

Though the activity zone of roan antelope is by no means synonymous to a territory it is nevertheless quite significant that only rarely have two adjoining herds been found to overlap into one another's activity zone and this phenomenon therefore primarily determines the characteristic mosaic pattern in the distribution of roan herds. It has already been indicated that this 'aktionsraum' is not patrolled and protected daily against intrusion from adjoining territorial males and does not therefore comply, in the strictest sense, with the definition of a territory. The explanation for the sole occupation of the activity zone by a single herd may be due to the following reasons: the activity zone consists of a definite summer and winter range; competition would therefore be for either one of the two but not for both areas at the same time. As the herd moves through its range the adults, but in particular the bull, mark the area by thrashing their heads in shrubs, defecation, interdigital gland secretions, etc. and thereby indicate their presence in a particular area. It is believed that in this way each herd's activity zone is scent-and visually-marked and that this has an inhibitory influence on intruding herds. In this respect the function of the interdigital glands may play an important role (Fig. 5). Whereas shrub-beating with the horns, defecation and other marking methods are largely, but not exclusively, confined to the activities of the herd bull, both sexes, adult and immature animals have functional interdigital glands which must constantly be leaving a scent where the animals are active.

Fig. 5. Cross sections through the front (left) and hind (right) foot of a roan antelope, illustrating the well-developed interdigital glands.

Marking doubtlessly plays an important role in advertising the presence of a herd in a particular area and is believed—at least in part—to facilitate in barring neighbouring herds from the different activity zones. Detection of the presence of a herd in an area does not necessarily deter an intruding herd from entering the occupied area. However, it does have an inhibitory influence on the intruders and, in a direct confrontation between the two herds, the intruders suffer a definite disadvantage in the conflict. The absolute intolerance of adult males to one another and the closed social units of the nursery groups are considered to be the basic factors resulting in group avoidance and therefore also the establishment of exclusive activity zones.

(*b*) *Home range*

To avoid any confusion in the interpretation of the terms 'home-range' and 'intolerance zone' and the context in which they are used here, it is only appropriate to give a short definition of what is considered to be a 'home-range'. Basically the term refers to what Dice (1952) has defined as 'the area over which an individual animal habitually travels while engaged in his usual daily activities.' Walther's (1967) definition is somewhat more circumscriptive: 'Ein Gebiet, in dem sich ein Tier oder häufiger eine Gruppe von Tieren über einen längeren Zeitraum hinweg unherstreifend aufhält. Die Streifzüge schliessen sich (wahrscheinlich) in Tagersrhythmus zu einem "Kreis". Eine gewisse Gliederung des Gebiete in Weideplätze, Tränken, Salzlecken, Ruhestätten, Wechsel, bzw. ist gegeben. Ausserdem kann das Aufenhaltsgebiet (Home range) markiert werden. Verteidigt wird es jedoch im allgemeinen nicht.'

Roan are water-dependent animals and under normal conditions drink at least once a day during the dry winter months. With the rather restricted water resources in the Park during winter it is not surprising that the water holes form the focal point of their daily activities.

Normally, roan drink between 1000 and 1100 hours when, under Lowveld conditions, it is already starting to get fairly hot—the dry winter season. After drinking the animals slowly move away from the water, grazing intermittently until they are roughly 400-800 metres from the water where they lie up in the shade of a tree or shrub or in open grassland during the hottest hours of the day. When the herd again becomes active and resumes grazing during the late afternoon it does not return to the water but gradually meanders further away from it, while grazing. During this period before sunset the herd may move up to two or more kilometres away from the waterhole. Observations were generally discontinued after dusk due to fairly thick stands of shrubs which made tracking of the animals extremely difficult. Therefore, little is as yet known of the nocturnal activities of the roan. However, animals which had been observed in an area until dusk could be located in the same locality at sunrise the next morning. During the early morning active grazing once more commences and the herd leisurely works its way back to the same waterhole. This pattern may be followed for a shorter or longer period, after which, for no apparent reason, the herd may move off to another waterhole only to return to the original one after a few days. However, there is always one particularly favoured watering point where each herd usually drinks. The reason the herd moves away from the waterhole to graze during the afternoon and morning may be of a two-fold nature, i.e. for the benefit of obtaining more favourable grazing conditions and possibly also to escape the intense competition of the other herbivores concentrated around the waterholes. From time to time the herd may also change its direction of approach and departure from the waterhole.

The total area covered by the home range of a herd would, on the average, comprise approximately two to four square kilometres. This figure is attained by assuming that a herd may move 2-4 kilometres from its watering point and spread out an average of 500 metres along the line of its daily course.

The fact that roan adhere to one home-range for a period and then change to another naturally facilitates leaving the "mark" of the herd evenly distributed over the activity zone of the herd to the exclusion of other herds.

(c) *Intolerance zone*

Roan bulls defend an area around their herds from intrusion by neighbouring bulls. This phenomenon closely approaches the position found in many territorial species where the males defend a well defined area as their exclusive 'property'. However, some differences exist between the true territory and the intolerance zone, which justify a distinction between the two. In the context in which it is used here, the intolerance zone may be defined as an area actively defended by an adult roan male against intrusion from other adult males, with a radius of approximately 300 m to 500 m around the herd. This intolerance zone is maintained wherever the bull may find himself within his activity zone. From the manner in which young males are evicted from the nursery herds and driven from the intolerance zone of the herd bull, the distance at which other adult males will not be tolerated may be considered as an extended individual distance applying to adult males.

Though many of the characteristics of a true territorial species may be reflected in the intolerance zone of the roan antelope, the lack of fixed boundaries in the latter must be seen as the major difference. In the case of a true territory, any (observed) trespassing of the boundary by an intruder releases the owner's aggression; thus the latter's intolerance is clearly linked to the occupied area regardless of his position in it. In this respect true territoriality has already been described for, among others, the following species: Uganda kob (Buechner, 1961, 1963; Leuthold, 1966), Grant's and Thomson's gazelles (Walther, 1964, 1965, 1968b; Estes, 1967), Waterbuck (Kiley-Worthington, 1965), wildebeest (Estes, 1968), tsessebe (Joubert, 1971), etc.

The existence of an intolerance zone, and the consequent absence of a territory, was clearly illustrated in the roan enclosure during the course of 1970. The lone bull that had been totally subordinate to the herd bull gradually started penetrating the herd bulls' intolerance zone. Initially the lone bull could not face up to the vicious attacks of the herd bull and retreated to 300 or 400 metres from the herd where he was free of persecution. However, the lone bull persistently tested the superiority of the older male and eventually, after two or three months of continual skirmishes, succeeded in ousting the old bull from the herd. During the entire process there was not the least indication of territorial defence in either of the two males. Subsequent to the eviction of the old bull, the herd and its new bull retained its customary activity zone in the enclosure while the evicted male withdrew to a few hundred metres from the herd. As before, neither of the two adult bulls showed any inclination to defend a definite area or fixed boundaries respectively.

Once the intolerance towards other males is fully developed in a bull and he has successfully established himself with a nursery herd in an activity zone, he maintains this intolerance zone throughout the year. If there is an intruder in the vicinity of a herd, the bull will leave the herd and face the rival though he may still be some 300 to 500 metres away from the herd. If the intruder happens to approach closer than this distance the herd bull immediately shows aggression towards his rival. This entails the usual routine of challenge (threatening), chasing and/or pushing horns. In the chasing that follows, the dominant herd bull pursues his adversary until the latter is again about 500 metres from the herd before turning back to his herd. In the course of the eviction of young bulls from the nursery herds, as already pointed out, the individual distance between the herd bull and the rejected youngster becomes progressively larger; initially the younger male is harassed until he moves away 150-300 metres from the herd where the herd bull leaves him in peace. Once evicted from the herd he may also elicit aggression from the herd bull at a distance of 300 metres.

If, then, the area protected by the herd bull comprises a zone with a radius of 300 metres around his herd the actual size of his intolerance zone will be roughly .56 sq. kilometres. This, of course, is only a rough estimate as the absence of definite, fixed boundaries makes a more accurate calculation impossible.

Blower (1961) mentions that 'the territory of any given [roan] herd is usually fairly well defined, and is restricted to an area of a few square miles.' There may possibly be some confusion as to the interpretation of the term 'territory' in this case, and in all probability Blower is here referring to what has been termed the activity zone in the present report. Nevertheless this once again emphasises the remarkable consistency with which one herd occupies a particular area.

ACTIVITY ZONES (INTOLERANCE ZONES AND HOME RANGES) IN RELATION TO HABITAT AND ITS POSSIBLE ECOLOGICAL SIGNIFICANCE ON THE ROAN POPULATION OF THE KRUGER PARK.

The successful establishment of an activity zone in an area depends entirely upon the nature of the habitat; and although the habitat preferences of roan do not, strictly speaking, fall within the scope of this paper, a brief discussion of their habitat requirements will suffice to illustrate the importance of the interrelationships between activity zones and habitat availability, and its possible ecological influence on the species.

Roan antelope have been observed in three different vegetation types viz.

(a) The Quiçama National Park, Angola

This area represents one of the peaks in the density of the species throughout its range of distribution. The particular vegetation type especially favoured by roan is an open grassland savanna, dominated by *Eragrostis superba,* with sparsely distributed clumps of trees and shrubs. The ecotone between the grassland and the adjoining woodland is an open tree savanna with tall grass. In the open grassland there are numerous grass-covered depressions which serve as catchment pools for run-off rain water and provide the game animals with drinking water and green grass shoots during the dry months.

(b) Bicuar National Park, Angola

This Park is situated in the southern end of Angola and provides a totally different habitat to that of Quiçama, i.e. the main vegetation type is light to heavy woodland and thickets which are drained by broad, shallow drainage lines, variously referred to as 'dambos' in Rhodesia and Zambia and 'mulolas' in Angola. These dambos may be up to 400 or 800 metres wide, are grass covered and thereby represent an ideal grassland savanna, fringed on either side by open tree savanna which gradually merges into thick woodland. It is these dambos which are frequented by roan—the adjoining woodland providing important shelter from the sun, Carnivora, etc.

(c) Kruger National Park, South Africa

The area which supports by far the greatest proportion of the roan population is collectively referred to as mopane (*Colophospermum mopane*) veld. The area is characterised by the shrub form of the mopane tree which occurs in stands of various density throughout the range. Interspersed among the shrubs is a good coverage of grasses. Somewhat in the fashion of the dambos described above the mopane veld is also drained by large, shallow, grass-covered drainage lines. By far the greater majority of roan herds known to have established activity zones in the Kruger Park are intimately associated with these open grass 'plains'.

From very brief notes above it clearly emerges that optimum roan habitat has to comply with the following requirements:

(i) open grass plains;

(ii) easily accessible cover in the form of trees or shrubs; and

(iii) open surface water.

The delicate balance between habitat selection and the social system of exclusive 'activity zones' per herd operates as a natural regulatory system on the roan population of the Kruger Park. The available roan habitat in the Park lies along the rather restricted open drainage lines in the mopane veld, with a further restriction caused by the lack of sufficient surface water during the dry winter months. Roan antelope have been strictly protected in the northern mopane veld for at least the last half century since the proclamation of the area in the original Shingwedzi Reserve, which was later incorporated in the present Kruger National Park. Though meagre, the earliest reports indicate a low population density of roan in the area. As time progressed more accurate surveys confirmed the first reports of low numbers which have, with slight fluctuations, remained at a consistently low level through the years. The proclamation of the Shingwedzi Reserve followed a period of intensive hunting in which most species, including roan antelope, had suffered severely. In 1911, the Warden noted in his annual report: '(roan) being a buck partial to rather open bush country, it is one of the first to be exterminated by hunters.' To illustrate the history of the roan population in the erstwhile Shingwedzi Reserve and later Kruger Park the following extracts from the Warden's reports are of interest: (before 1926 the present Kruger National Park consisted of the Sabie Reserve—southern area—and the Shingwedzi Reserve—northern half).

1903: roan considered to be exterminated in both reserves though there were still 'a good many' in the adjoining Portuguese Territory.

1905: animals (generally) increasing.

1911: 'this formerly rare species is now increasing well and numerous small troops are to be seen...'

1912: 'increasing largely in the parts of the Reserve favoured by them'

Estimates: Sabie Reserve: 300
Shingwedzi Reserve: 150

(For the present consideration, only the animals of the Shingwedzi Reserve are of importance as the later decline in the Sabie Reserve population was due primarily to the results of changes in the boundaries of the Reserve in 1923).

1918: Estimate of the Game Reserves Commission: Shingwedzi Reserve: 500.

1925: 'exists in considerable numbers north of the Olifants to the Limpopo river.' The warden further reports that 'I have reason to believe that my calculations (1912) were then considerably under the mark, and since that time the total has increased at least fourfold...'

1929: 'Roan have always been scarce...'
A slight decrease in numbers was observed during a severe three-year drought prior to 1929.

1944: 'the position of roan antelope north of the Olifants river continues to be favourable...'

1946: 'numerous in the northern sections.'

1948: 'the roan position seems to have deteriorated...'

1949: Quite significant in the 1949 report is the following remark: 'I do not think these animals are nearly numerous enough considering the favourable grazing and other conditions in the Park' and further: 'in the Northern areas they seem to be just holding their own.'

1954: Biologist's estimate of roan numbers in the Park: Northern district: 440
(Total for K.N.P. 477)

1955: Population in Northern district estimated at *400 to 500.*

During 1959 and 1960 two anthrax epizootics raged through the roan habitat in the northern area of the Park and a total of 47 roan carcasses could be accounted for (Pienaar, 1960, 1961), with an unknown number never found. The decimation caused by the anthrax outbreak, together with one of the most severe droughts ever suffered in the area, caused a decline in the roan population and in 1963 the total number in the Northern district was estimated at 200-220 (Pienaar, 1963). In 1969 the total population for the northern districts was estimated at 250-300. However, at least 35 animals succumbed to anthrax during 1970 and at present (1971) the population numbers approximately 230 animals.

The short survey of the history of the roan antelope given above is sufficient to indicate at least two important features of the population:

(i) despite the critically small population at the beginning of the century their numbers rapidly increased until they reached their asymptote at approximately 400 animals between 1912 and 1918. Influx from the adjoining Portuguese Territory may also have contributed to this total;

(ii) since reaching the 400-500 level the population has remained remarkably stable for at least the last half century. The many seemingly contradictory remarks in the Annual Reports (increasing, decreasing, static, etc.) appear to accentuate, and confirm, the normal fluctuations in numbers of a population that has reached its maximum. The only serious decline in the population since 1912 (i.e. a period of 57 years!) was caused by the anthrax epidemics mentioned above. The apparent inability of the population to regain its prior 1959 level may confidently be ascribed to the severe 10-year drought which commenced in 1960 and was partially relieved only at the end of 1968. The relative stability of roan populations has also been observed in other areas of its distribution range and Guggisberg (1966) writes that 'in many areas it occurs in small, widely separated herds, which even under strict protection, do not show much increase in course of the years.'

A few facts on the population dynamics of the species will further serve to shed some light on the conclusions to be drawn from the preceding discussion. At three years of age a roan cow may drop her first calf; two to three weeks after parturition she enters her first *postpartum oestrus* cycle and after a gestation period of 275 days she may have another calf at heel. Essentially, this means that every 10-10½ months a roan cow can give birth to a calf, and if it is accepted that the reproductively active life of a cow is of the order of 10 to 12 years, it becomes apparent that the reproductive potential of the roan antelope is quite considerable, measured by any standards for animals of similar size! In a period of two years seven adult roan cows gave birth to 15 calves in the experimental camp at Nwashitsumbe. Needless to say, if the full reproductive potential of roan were to be realized, the Kruger Park would certainly not still be concerned about their low numbers.

The phenomena pointed out above, i.e. an animal species with a high reproductive potential yet with an apparent maximum population density of a comparatively low level, indicate an intricate, natural regulating mechanism operating on roan antelope. This mechanism, it is believed, operates along the following lines:

(a) The major features determining suitable roan habitat have already been outlined and, using these prerequisites as a standard, it is found that the Kruger Park in fact contains only very restricted areas suitable for occupation by roan. In this sense the Kruger Park must be considered as marginal country for this species and this is borne out by reliable authorities (see Wardens' Reports), who have indicated that the former stronghold of the species in the Lowveld was along the foothills of the Drakensberg mountain range. (The old Sabie Game Reserve, the southern half of the present K.N.P., was estimated to have twice as many roan as the Shingwedzi Reserve in 1912. With the formation of the Kruger National Park in 1926, a large portion of the Drakensberg foothills was reclaimed as European farming and Bantu trustland with the exclusion of the most favourable roan habitat. Today the once prospering roan population of that area is represented by a small group of 25-35 animals, only just holding their own!);

(b) The second factor is the social organisation of roan antelope, by which each herd inhabits a certain area (activity zone). In discussing the various functions of territoriality Etkin (1964) remarks that '... territoriality still seems to play a role in regulating animal economics... in acting as a population-regulating mechanism. Since territories are not indefinitely compressible it is clear that, as the population increases, the range of the species is extended by the new individuals claiming territories peripheral to the group. In general, this entails less favourable areas.' Though not territorial in the true sense of the word, the non-overlapping activity zones of roan herds fulfil the same function in this species as defended territories in some other species.

It is proposed, therefore, that the 'carrying capacity' of each habitat-type for roan is determined primarily by (i) physiognomy and quality of the vegetation and (ii) social spacing; and that once the maximum density has been reached the surplus animals are compelled to seek new activity zones elsewhere, while basically the population level in the favoured habitat remains at a relatively constant level (cf. Errington, 1956). This point of view allows for an explanation of the thin scattering of roan herds along the western half of the Kruger Park which appear to be far less stabilized, both numerically and locality-wise, than their counterparts in the preferred habitat. From this argument it may be concluded that the best way to ensure population growth would be the artificial manipulation of the habitat in accordance with the social and ecological requirements of the species.

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Paper No. 36

The Social Organization of the East African Buffalo (*Syncerus caffer* Sparrman)

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ABSTRACT

The social organization of the East African buffalo (*Syncerus caffer*) is described. All females and juveniles live in herds numbering up to 2,000 animals. Some 15% of the males live in small bachelor groups away from the breeding herds. These bachelor groups utilize the same preferred habitat and food as the breeding herds. Some breeding males leave the herd during the dry season but return for the rut. Old males remain permanently in bachelor groups. Within the herd post-weaning family ties are retained until the third year of life. Thereafter immature males form their own subgroups within the herd, and adult males form a rank hierarchy; the most dominant males obtained most matings. Hence the rank hierarchy could have evolved through natural selection.

The splitting up of herds and movements of bachelors are considered to be adaptations to seasonal changes in habitat. Evidence from lion kills suggested that herding evolved as an anti-predator behaviour, and tape-recording experiments suggested that group protective behaviour had evolved for the same function. Home range and herd spacing is described and it is suggested that this is an adaptation to the more efficient utilization of localized food supplies.

INTRODUCTION

The African Buffalo (*Syncerus caffer* Sparrman) is one of the most widely distributed ungulates in Africa south of the Sahara (Sidney, 1965). It is a member of the sub-family bovinae and is related to the Asian water buffalo (*Bubalus bubalis*), cattle (*Bos indicus, B. taurus*) and American bison (*Bison bison*). Although considered as only one species (Ansell, 1968), *Syncerus caffer* shows considerable geographic variation. Those in east, central and south Africa, are large black animals weighing more than 500 kg, with the males showing massive compressed horn cores, the bosses. The west African form is almost half the size, red-brown in colour and the males do not possess pronounced bosses. These differences suggest that there are also associated differences in behaviour, but at the present time almost nothing is known of the west African forms and this paper is concerned mainly with the east African race; the various aspects of the social organization are discussed with respect to their evolutionary function.

Buffalo live characteristically in well defined herds or groups near water. They are catholic in habitat choice, occurring in montane and lowland forest, moist and dry woodlands, savannah and steppe but not Subdesert. Most of the observations were carried out in the Serengeti National Park, Tanzania, an area of 10, 000 km^2 of open *Acacia* woodland and plains with a mean rainfall of about 800 mm. Rain falls in two periods, November-December and March-June, and there is a pronounced dry season between July and October.

Large herds were counted from aerial photographs. Because the animals lived in such densely packed herds, it was difficult to observe the behaviour of individuals within the herd, at ground level. Hence observations were also made on a herd of about 400 animals that lived in Ngurdoto Crater, Tanzania. From the lip of the crater it was possible to obtain an aerial view of the whole herd using a telescope at distances ranging from 100 to 400 metres. Vocalizations carried up well from the floor of the crater. At these distances the ages of young and the sex of adults could be discerned easily from the shape of the horns and the size of the animal.

HERD STRUCTURE AND FAMILY RELATIONSHIPS

All females and juveniles less than two years old lived in herds numbering more than fifty animals in the Serengeti area. These were the breeding herds and their sizes were extremely variable. Any one herd remained more or less constant in size but different herds varied between 50 and 2,000 animals. When the frequency distribution of herd sizes (there were about 150 herds) was plotted there was a steady decline in frequency from small to large herds, and the mean was about 350 animals. The mean herd size was found to be much smaller in drier areas or forested regions of Africa (Sidney, 1965), sometimes being of the order of only 20 animals; and in the montane forest region of Mt. Meru, Tanzania, the mean size was 50 animals.

Some of the adult males were found in small bachelor groups rarely larger than 20 animals, and usually they consisted of 3 to 4 animals. Very old males were often solitary. Censuses showed that the bachelor males comprised about 15% of the adult male population, the rest remaining with the breeding herds.

The structure and family relationships within the breeding herd at Ngurdoto Crater were analysed by recording the position of all animals with respect to each other when they lay down to ruminate. Although the absolute distances between animals was inaccurate, the age or sex of the nearest neighbour could be discerned. For every individual, its nearest neighbour older than two years was scored according to age or sex.

All calves (less than 1 yr.) and yearlings (1-2 yrs.) remained close to their mothers. Since weaning occurred at about one year of age, this association of yearlings with their mothers was a post-weaning bond. For the other classes of animals the expected number of nearest neighbour scores for each class was calculated from the known percentage of that class in the population. Thus, for example, females comprised 47% of the animals two years old and over, and so 47% of the nearest neighbours of, say, two year old males should have been females. The difference between the observed and expected scores was examined using the Chi-square test, and the degree of significance is shown in Table 1.

TABLE 1. THE DEGREE OF DIFFERENCE BETWEEN THE OBSERVED AND EXPECTED NUMBERS OF OBSERVATIONS OF EACH CLASS (A) HAVING NEAREST NEIGHBOURS OF (B).

x = $P < 0.05$, xx = $P < 0.02$, xxx = $P < 0.01$, xxxx = $P < 0.001$
+ and – = greater and less than expected. Spaces are non-significant differences.

		(A)				
		2 yr. F.	2 yr. M.	3-4 yr. M.	M.	F.
	0. 5 yr.					
	1-5 yr.					
	2 yr. F.				– xx	
(B)	2 yr. M.					
	3-4 yr. M.			+ xxxx		– xxxx
	M	– xxxx	– x	– xxx	+ xxx	– xxxx
	F	+ xxxx	+ xx	– xxxx		+ xxxx

Two year old females had significantly more adult females, and significantly fewer adult males as nearest neighbours than expected, ($P.< 0.001$). The adult females with which they associated were probably their mothers.

Two-year old males also had adult females as nearest neighbours more often than expected ($P < 0.02$) but less so than 2-year old females, indicating that in this class there was a tendency to break away from the mother. Grubb and Jewell (1966) found the same phenomenon with yearling male Soay sheep. However the 2-year old male buffalo avoided adult males as well ($P < 0.05$).

Subadult males (3-4 yrs.) had significantly more nearest neighbours of their own class than expected ($P < 0.001$); this was a most noticeable aggregation. On the other hand they had adult males as nearest neighbours significantly less than expected, indicating that subadult males avoided adult males and this may be the case with adult females as neighbours also, since significantly fewer than expected subadult males remained with adult females.

Thus all 18 month males remain with their mothers; this tendency is still apparent in 2 year old males, but less so than in 2 year old females, and between 3 and 4 years old they break away from the mother and associate with their own class.

In contrast to subadult males, the proportion of adult males with adult females as nearest neighbours was close to the expected. Adult males remained together significantly more than expected ($P < 0.01$) but the proportion with subadult males as nearest neighbours was no more than expected. Hence the all-male grouping persisted into the adult ages but many were also associating with females.

Adult females had subadult males and also adult males as nearest neighbours significantly less than expected, and remained closer together more than expected ($P<0.001$). This could be due to both the grouping of males and to the continuation of family ties of females older than two years. This family grouping could possibly last throughout life, as Grubb and Jewell (1966) have suggested for Soay sheep.

To summarise, it appears that family ties last for at least the first three years of life, and with females this may continue longer. Males begin to break away in the third year of life, and in the fourth and fifth years form sub-groups of their own. Older males are found to associate once more with adult females, but retain the all-male grouping.

AGONISTIC BEHAVIOUR

Males

Both adult and young males showed a number of postures which were often directed laterally at other males. These postures are shown for a young male in Fig. 1.

The *submissive posture* consisted of a sloping back and lowered head which was held horizontal. A subordinate male would often approach a dominant male in this posture and place its muzzle under either the neck, belly, or between the hind legs of the dominant. Immediately afterwards the subordinate would turn away making a loud *bellowing* noise. It is possible that this posture was derived from suckling behaviour. This submissive posture has also been noted in cattle (Schloeth, 1961).

Another form of appeasement behaviour occurred when an animal had been attacked. The attacked animal would run a few paces, stop abruptly, and stand with body oriented away but with head turned slightly towards the aggressor. The head was held high, nose in the air, and back sloping. This appeared to be an exaggerated form of the normal alarm position and seemed to indicate an *intention to flee.* Aggressors did not usually continue the pursuit under these circumstances.

The *threat* stance normally consisted of holding the head up but with nose pointed down. The withers were exaggerated by hunching the shoulders. Usually it was directed laterally at an opponent, but dominant animals would occasionally stand facing subordinates. Sometimes the dominant animal would show *'head tossing'.* If the opponent showed similar threat behaviour there followed a period of *circling* in slow motion with much head tossing. From time to time one would break off and vigorously toss

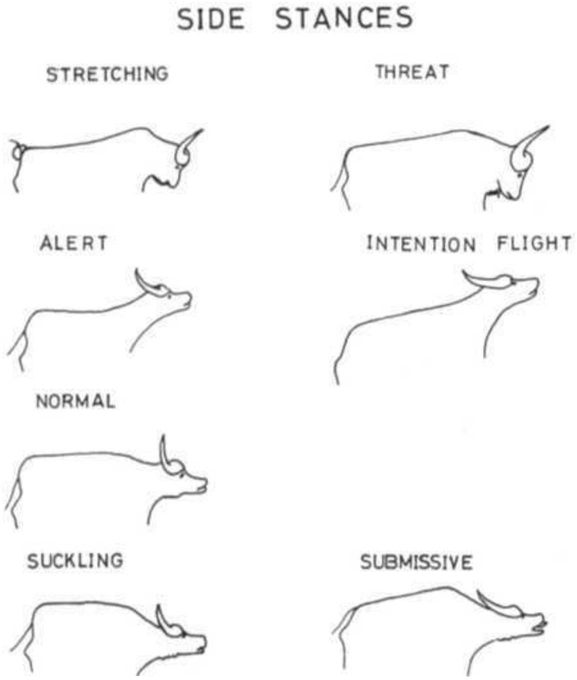

Fig. 1. Postures of a male buffalo: those in the right hand column were often directed laterally at other males.

his head from side to side in the foliage of nearby bushes. Circling often reversed direction and when it did so, the animals always turned outwards.

This circling ended by one animal facing and charging the other. The second animal would either turn and flee immediately or charge also. In the latter case the two animals would collide head on, the impact being met on the bosses. The outcome of the contest was decided in that instant, for one animal always turned and fled without further fighting. The victor would continue in pursuit for about fifty metres. This form of *fighting* was always between dominant males and happened only during the rut. Rutting took place over a period of four months towards the end of the rainy season.

Immature males of all ages were often seen to 'spar'. This was frequently preceded by the two animals rubbing themselves against each other and then interlocking horns. They would twist their horns from side to side for several minutes and usually the outcome of the contests was not clear. Unlike fighting, sparring occurred frequently, and the position in the linear rank hierarchy in adult males found by Grimsdell (1969) may well be determined initially by this behaviour.

Schloeth (1961) and Frazer (1968) have described an aggressive display in feral and domestic cattle. In the feral cattle, the animal paws the ground with the forefoot, rubs the face in the exposed earth and also thrusts the horns at the ground. Frazer (1968) mentions that in domestic cattle, earth is also tossed over the withers. Schloeth (1961) suggests that these behaviour patterns are derived from wallowing behaviour. Pawing is also described in the American bison (McHugh, 1958) and European bison (Jaczewski, 1958), but it has been recorded only once in the African buffalo and is not an important feature of display. On the other hand, the face and horns are rubbed into exposed earth on banks or side of wallows, and the earth is often tossed into the air. In mud wallows, dominant males have been seen to *roll* onto their backs and cover themselves with mud between bouts of *earth tossing;* this was always seen immediately before or after interactions with other males. Subadult males and females have never been seen to cover themselves with mud. Dominant males of cattle and bison have been heard to bellow, but this has not been recorded for buffalo. Chasing has been observed several times. On one occasion an adult bull ran at another from a distance of fifty metres and then chased it for another 300 metres out of the herd. This bull was kept out of the herd for the rest of the day. On other occasions the exclusion from the herd took place at walking pace.

Females

Adult females showed submissive behaviour and threat stances similar to those of the males. Attacks were confined to a sweep with the horns at nearby animals. Circling and redirected attack behaviour were never seen, but on a few occasions sparring was seen between 2-year-old females and yearlings.

The rank hierarchy

In a herd of about 100 known animals Grimsdell (1969) was able to demonstrate a linear rank hierarchy in adult bull buffalo. This was also demonstrated for feral cattle of both sexes by Schloeth (1961) and American bison males (McHugh, 1958), and from the description of Jaczewski (1958) it was also present in the European bison. Grimsdell was not able to find a linear order for female buffalo but this has been described by many authors for small dairy herds (e.g. Schein and Fohrman, 1955; and Brantas, 1968).

During this study, the aggressor and aggressed were recorded where possible in interactions. An 'attack' was recorded if these roles could be determined from any interaction whether by threat or fighting. A total of 358 interactions were recorded and in only 2. 5% of these were animals less than three years old the aggressor. Subadult males confined their 'attacks' to other subadult or two year old males.

TABLE 2

Agressed	Aggressor			
	Adult Females		Adult Males	
	Obs.	Exp.	Obs.	Exp.
1. 5 yrs.	36	24	3	15
2 yr. F.	41	12	0	7
2 yr. M.	7	12	5	7
Sub. M.	8	24	37	15
Adult Male	0	48	77	30
Adult Female	109	83	0	52

'Attacks' by adult females against other classes are shown in Table 2. The expected number of 'attacks' on each class was calculated from the proportion of each class in the population. Clearly females tended not to 'attack' males. Even 2-year-old males received only as many as would be expected on a random basis whereas 2-year-old females received significantly more ($P < 0.05$). Subadult males received significantly less ($P < 0.05$) and adult males were never observed to be 'attacked'. Juveniles between one and two years old were 'attacked' more often than expected ($P < 0.05$). When these observations were broken down into those with calves and those without, it was found that single females 'attacked' other single females more often and females with calves less often than expected from their proportion in the adult female population ($P < 0.01$). Females with calves, however, did not differentiate in their 'attacks' between these two categories.

It was observed that yearlings received most of the 'attacks' from their own mothers, and this was probably so with 2-year-old females. Therefore it would appear that the family bonding in yearlings and 2-year-old females is maintained, at least in part, by the 'following behaviour' of the juveniles. In spite of the 'attacks', family cohesion must have been advantageous to the juveniles. Altman (1963) has suggested that post-weaning bonds, which have also been observed in other ungulates, function by affording guidance in choice of feeding places, shelter and decisions regarding safety and flight.

'Attacks' by adult males were directed at other males only (Table 2). Age was important, for two-year-old males received no more attacks than expected, whilst subadult males received significantly more ($P < 0.05$). This, together with the observation that there was very little aggression between subadult males, could be the reasons for the formation of subgroups at this age, as described above; greater tranquillity would be achieved. McHugh (1958) observed that bison formed subgroups that were peripheral, and the subgroups of young male buffalo in the Serengeti were often seen to be on the outside of the herd.

Adult males 'attacked' each other more often than expected ($P < 0.05$). Grimsdell (1969) found that there was less overt aggression between animals close in rank, as was also found by Schloeth for cattle, where only low ranking members were chased. Thus it would appear than in buffalo it was the lower ranked adult members which were chased out of the herd.

From the above evidence it would appear that the rank hierarchy in males consisted of a number of dominant males that were linearly ranked, and other adults that were expelled from the herd. Subadult males were tolerated as subordinate male groups. In females some form of ranking existed as was shown by single females not 'attacking' females with calves. The ranking could have been based upon age class as a group; it seemed unlikely that a linear ranking of individuals could have existed in the large herds with several hundred females. If family clans exist, each one could have had a rank hierarchy of its own.

Grimsdell (1969) observed that the more dominant males obtained most of the copulations. Frazer (1968) found in the Chillingham feral cattle, that the dominant bull obtained most matings, as did the two dominant bulls in the Camargue feral cattle (Schloeth, 1961). Thus in all these species the dominants would leave more progeny, and hence such a social organization could have developed through natural selection; and as a result of this dominance hierarchy subadult male groups within the herd and bachelor male groups separated from the herd would develop. Thus, as Tinbergen (1965) has pointed out, it is unnecessary to suggest that this rank hierarchy has evolved through group selection (Wynne-Edwards, 1962, 1965).

BACHELOR MALES

The ages of bachelor males ranged from the occasional subadult to the very old, but there were two distinct categories—those younger or older than approximately ten years.

The old males

Most males over 10 years old had left the herd permanently, apart from occasional returns. These old males have been described by Verhayen (1954) as territorial, but he used the term more in the sense of 'residence'. To clarify the point, no bachelor males were observed to defend a territory. They were however extremely sedentary-one group of males did not move more than half a kilometre from one locality during three years. By comparison over the same period of study the distance between the ends of the range of a herd animal was found to be as much as 50 km in the Serengeti (see later), and a herd may travel as far as 30 km in one day.

Provided that the habitat of these old males was suitable, it was clearly an advantage to become more restricted in range in terms of conservation of energy and time for grazing and rumination.

An association analysis of herd animals with different habitat types showed that riverine vegetation including both forest and grassland were the preferred areas. A similar analysis for bachelors showed that these vegetation types were also preferred; they were not being driven out of preferred habitats. Similarly an analysis of rumen contents showed that grass leaf was the preferred component of the diet. During the dry time of year when conditions were found to be difficult for the animals (Sinclair, 1970) there was no difference in the proportion of grass leaf in the rumen of adult females, herd males or bachelor males.

Therefore it would appear that the habitat and food of bachelor males was not essentially poorer than that for herd animals, and hence these males must have gained in terms of energy and protein relative to the herd animals. However there was a significant disadvantage for bachelors through predation as will be mentioned later. It must be emphasized that since these males were old and rarely returned to the herd, they were in the post-reproductive phase and hence any advantages gained from their

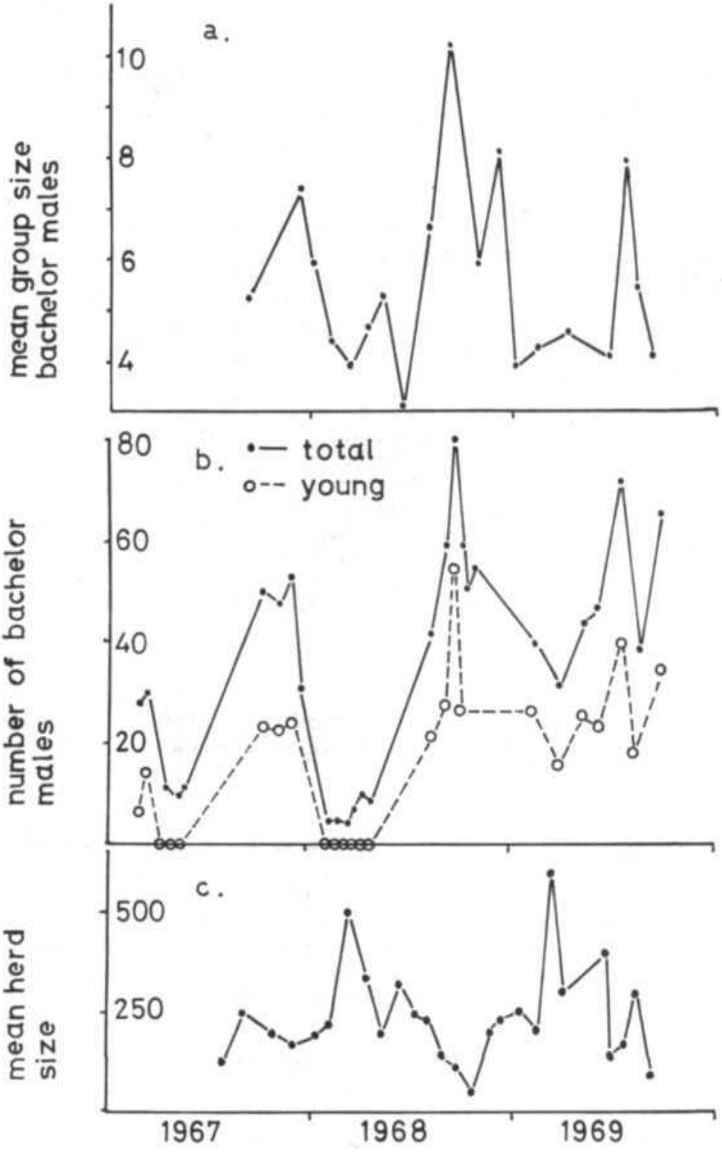

Fig. 2. The bachelor group size (a) and the number of bachelors (b) increase in the dry season, whilst the mean breeding herd size (c) decreases.

behaviour would not be selected for. Conclusive evidence that they were in the post-reproductive phase was obtained by Grimsdell (1969), who recorded a marked increase in interstitial cell tissue and a decrease in cell function in the testes of these males. Therefore these advantages were merely incidental; they lived out of the herd probably because they had been driven out by younger and stronger males (older animals lost weight), and had been prevented from returning until they had become too decrepit to keep up with the herd. The advantages and disadvantages of the behaviour of these post-reproductive old males were probably merely the incidental result of the natural selection for reproductive success during their prime age.

The younger males

These males were the young adult (5-7 yrs.) and middle aged adult (8-10 yrs.) categories. From the monthly censuses of study areas, the mean group size of bachelor males for each month over two years was calculated (Fig. 2a). It is clear that for each dry season the mean group size doubled. This was due to an increase in the number of younger males that became bachelor males. They lived in groups of as many as ten or even twenty animals. These young males, already occurring in groups on the periphery of the herd, broke away during the dry season as natural units. This movement was confirmed by ground counts in another study of 4 km^2 along a permanent river (Fig. 2b). The fluctuations in total number of bachelor males paralleled the increase in mean group size in the dry season. The number of younger males in these censuses (Fig. 2b) largely accounted for the fluctuations whilst the number of old males remained much more constant. During the wet season the younger males returned to the herd leaving only the old males in the bachelor groups.

HERDING BEHAVIOUR

Quite apart from the behaviour of individuals within the group, the herd itself behaves as a unit.

Protective behaviour

A noticeable feature of herding ungulates such as wildebeest (*Connochaetes taurinus*) and topi (*Damaliscus korrigum*), is the ability of the newborn calves to run fast enough to keep up with the herd. The newborn buffalo, however, takes several weeks before it can keep up with the running herd; females with newborn calves were often seen to drop behind when a herd took flight. If being in a herd has survival value against predators, then one might expect that in buffalo some compensatory behaviour would have developed to counteract the poor running ability of the calves. That predation could act as a selection pressure to maintain herding behaviour, was indicated by an analysis of kills by lions; significantly more old male buffalo that lived out of the herd were killed by lions ($P < 0.05$) than would have been expected from the age distribution of the male population. Several reports (e.g. Grimsdell, 1969; Mitchell *et al.* ,1965) have described members of a buffalo herd showing protective behaviour by actively defending other members from predators.

This behaviour was tested experimentally by tape recording a calf distress call and then playing it back to a herd. During the tests I was downwind and out of sight. In the first test the herd was approximately 200 metres away. Shortly after the start of the recording the whole herd of 300-400 animals approached the sound whilst making a deep croaking noise very similar to that produced by a mother when calling to its own calf. The recording was being played initially from within a bush, but later up a tree, and the herd moved right through the bush and stopped under the tree. An old solitary bull also arrived making the same croaking call. When the recording was stopped, there was a pause of about 30 seconds during which the croaking stopped and then the herd panicked and took flight for about 100 metres. They stopped, turned and waited. The recording was replayed at this point and the herd once more approached and stopped under the tree. The process was repeated for a third time also.

It was only possible to carry out six tests on separate occasions. On the same piece of tape was a recording of a human talking, and this was used as a control sound, to test whether they were merely approaching any sound. In all six experimental trials the same approach and croaking call was displayed but in none of the control trials was there any response. Although the number of tests were not sufficient to show statistical significance, the data indicated that the buffalo were showing protective behaviour.

Observations from other bovidae have been reported. McHugh (1958) observed that when a bison calf was trapped the herd surrounded it, and Tener (1954) described the group protection behaviour against dogs and wolves, shown by muskoxen (*Ovibos moschatus*). I suggest that it has developed as an anti-predator behaviour, possibly through 'kin selection' (Maynard-Smith, 1964) if family clans formed. Wiens (1966) has pointed out that kin selection is functionally no different from individual selection which operates through differential reproduction in the long run (Mayr, 1963 p. 183). The individuals selected are those whose parents showed the most adaptive behaviour.

The splitting of herds

During the dry season, herds tended to split up. The main herd size for the whole Serengeti in September 1968 was significantly lower ($P < 0.05$) than for the previous May during the rains. The mean herd size from monthly censuses in study areas (Fig. 2c) shows that the lowest and highest points in each year occurred in the dry and wet season respectively.

Pienaar (1969) has also observed this phenomenon and has suggested that the larger the herd the further and more often it has to travel in order to find fresh grazing in the dry season. He suggested that this movement could be detrimental to weakened calves and therefore it would be advantageous for herds to break up. In the Serengeti this argument can be extended, for in the dry season the localized patches of suitable habitat are not large enough in any event to accommodate the very big herds.

In a sample of some 17,000 buffalo in herds ranging from 50 to 1, 500, the percentage of calves in each herd was calculated from photographs taken at one time of year during an aerial census, and this percentage was plotted against herd size (Sinclair, 1969). The percentage remained constant for herds of over 300 animals, and below this there was a decline with decreasing herd size but the calculated regression line was only significantly different from zero at $P < 0.1$. These results could have been affected by differing proportions of males with decreasing herd size. So in a smaller sample the number of calves per 100 females was calculated, but no difference was found from the above result.

Therefore, although there might have been a slight disadvantage with respect to predation in the smaller herds, there was no disadvantage for calves in the larger herds. So the advantage in the splitting of herds, in terms of the food utilization as suggested by Pienaar (loc. cit.), must have lain with all the individuals, including adults as well as calves.

HOME RANGE

In order to study the movements of a particular herd it was necessary to be able to identify the herd by a few known individuals. Since the herds travelled considerable distances and sometimes during the wet season they were inaccessible from the ground, the marked individuals had to be conspicuous from aircraft. This was achieved by attaching brightly coloured collars to females (males tore the collars off within 24 hours).

Capture of animals was carried out by immobilization using 4 mgm Etorphine hydrochloride (M. 99) and 30 mgrm Acetylpromazine. A 6-inch-wide collar made of very bright white, yellow or red PVC in different combinations was attached, and a single animal with one of these collars in a very large herd could be spotted with ease from the air. The collars remained on the animals for up to 9 months and new individuals were marked before the old collars disintegrated. Observations of the herds which contained the marked animals were plotted on large-scale vegetation maps. It was extremely improbable that the few marked animals remained within an area whilst unmarked animals changed areas, and so it was considered that the marked animals were valid identifiers of a given herd.

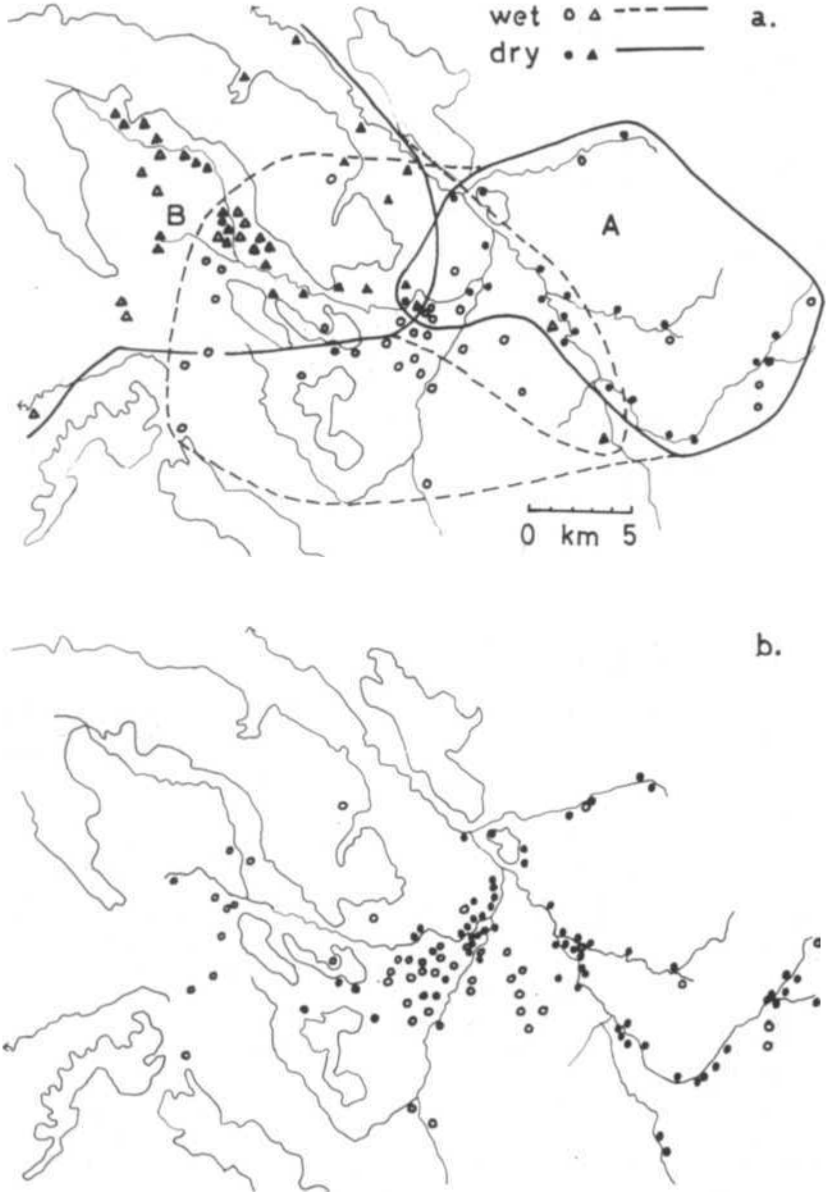

Fig. 3. Home range: (a) sightings of collared animals from the buffalo herds A (circles) and B (triangles); (b) all sightings of the herds over a period of 3 years.

One herd was identified by these methods for a period of 20 months and an adjacent herd for a period of 12 months. Figure 3a shows the sightings of the two herds in the wet and dry seasons. The dry season lines include 95% of the observations. These lines are not biological entities but are drawn in for ease of description. It can be seen that the movements of the two herds cover areas which overlapped considerably in the wet season but very much less in the dry period. For each herd there was a concentration of observations in particular areas, and there were also areas that were used exclusively by one herd. The latter could be described as 'monopolized zones' (Jewell, 1966), similar to those of Soay sheep.

The dry season records were clearly confined to the rivers, and a more accurate description, than the above, of the range in this season would be to subdivide it into feeding areas of riverine grassland and non-feeding areas where animals were usually in transit.

On most occasions the herds were photographed to estimate their size and it was found that the herds remained very constant in size. Therefore it was possible to identify herd A from records obtained in 1966 and 1967 and plot all observations for this herd over three years in Fig. 3b. The seasonal ranges were not essentially different from those described from the fewer observations of marked individuals. The wet and dry season observations were also separated into their different years, but no obvious changes in range were found.

The term 'home range' has been used in the sense of Jewell (1966), who defined it as 'the area over which an animal normally travels in pursuit of its routine activities'. Over the period of study, herd A remained more or less within a defined area, and this area was not delimited by the inability of the animals to move greater distances, nor unsuitable habitat; herd A could have moved along two rivers that were utilized by herd B but it did so only very occasionally (Fig. 3a). This restriction was most pronounced in the dry season. Similarly herd B could have utilized the dry season range of herd A, but did so infrequently.

The wet season range of herd A included all habitats, and this is consistent with the finding that most habitats are suitable grazing areas during this time of year. Hence the animals must have been familiar with the whole area. During the dry season they utilized only a part of the annual home range: this was the part that contained green pasture and flowing springs. Thus they were either avoiding unsuitable habitat at this season or preferring riverine vegetation. If no learning was involved in these movements then the herd was as likely to move completely away as they were to stay, and conversely other herds should have moved into the area to stay. This did not happen. Moreover the range in three consecutive dry seasons remained exactly the same. Therefore the evidence indicated that the animals had learned the locality of suitable food and water which was available when the rest of the annual home range had become unsatisfactory.

This learning could be facilitated by the same individuals remaining in the same herd. Grimsdell (1969) observed two herds that had intermingled for a few hours and then had separated with the same individuals as before. Thus individuals appeared to differentiate between their own herd and others. The pronounced following response and family ties previously described could maintain this herd cohesion, especially if these should remain throughout life. Hunter and Davies (1963) demonstrated in domestic sheep that lambs raised with the mother adopted the home range of the mother, whereas those reared separately adopted new ranges; the proximate factors determining the range were not so much the prevailing quality of the habitat as the learning of the range of the mother.

Therefore, the evidence from home range behaviour—the restriction in range, the confinement to particular habitats which were not used for protection from predators in the dry season—indicated that it involved the learning of important features of limited resources, as has been suggested by Altman (1963).

The spacing out of herds

During censuses of the population in the 1968 wet season, the position of all herds was accurately mapped. For a part of the area the distances of nearest neighbouring herds of greater than 350 animals, and of herds of any size, was measured. The restriction to the larger herds was made because some of the smaller herds were thought to be merely splinter groups from larger herds. The frequency distribution of nearest neighbours at different distances was then compared with the expected distribution if all herds were scattered at random in the same area (Fig. 4). The expected frequency of nearest neighbours was calculated from the formula of Cullen given in Patterson (1965), and the two distributions were compared using the Kolmogorov-Smirnov test (Seigel, 1956).

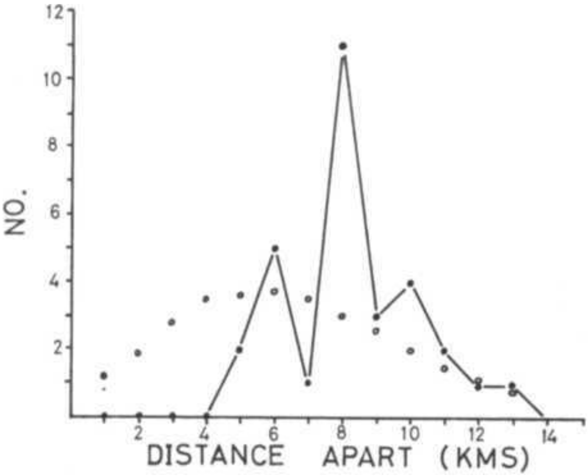

Fig. 4. The frequency distribution of nearest neighbouring herds of over 350 animals. The unjoined circles show the expected distribution.

The spacing of herds of greater than 350 animals was significantly different ($P < 0.05$) from the random distribution; the herds were uniformly spaced out about 8 km apart which indicated that the home range was having a spacing out effect. When all herds were considered, the differences in the observed and expected distributions were not significant and this supported the suggestion that the small groups had temporarily split from the herd. The observed spacing of larger herds was not due to the mere distribution of habitat, for at this time of year the herds were found to be utilizing all grassland types (Sinclair, 1970). Therefore this observed spacing of large herds could have resulted from home range behaviour although the mechanism for this is not as yet clear.

Within the home range there are thin strips or small pockets of suitable buffalo habitat in the dry season. If herds moved at random in this season the food supply would not be utilized efficiently; some areas would be utilized, by chance, by too many herds (to the detriment of those herds) whilst other areas would be under utilized. By remaining within a certain area containing suitable habitat known to them, more herds would thrive better. It is suggested, therefore, that home range behaviour functions to maximise the efficient utilization of locally distributed food supplies.

CONCLUSION

The dominance hierarchy in buffalo males resulted in the most dominant obtaining more matings; hence this social organization could have evolved through natural selection. Subadult male groups develop within the herd whilst old males leave the herd, forming bachelor groups.

The splitting up of herds was related to the fragmentation of the preferred habitat, and the preformed male subgroups could have broken away as a natural consequence of this splitting. Thus more bachelor males were observed in the dry season. The return of these males to the herd was correlated with the start of the rut; old males did not return because they had become too decrepit and were in the post-reproductive phase with probably low sexual motivation. All these movements were adaptations to seasonal changes.

It is suggested that herding could have been evolved as an anti-predator behaviour in buffalo. Furthermore, protective behaviour was shown by the herd and could have developed to compensate for the poor running ability of these animals, and particularly the calves.

Buffalo herds possessed a home range which resulted in their becoming spaced out in a rather uniform manner. It is suggested that this was a further adaptation to the fragmentation of the preferred habitat in the dry season, resulting in a more efficient utilization of the food supply. Home range attachment could be brought about through the learning of the area by calves and immature animals that maintained a close attachment to the mother. Such post-weaning family bonding was identified in the buffalo herds, and this behaviour would be selected for because the animals would have an increased chance of surviving the dry season.

It has been suggested by Wynne-Edwards (1962, 1965) that social behaviour functions as a population regulating mechanism and that it has evolved through 'group selection'. Wiens (1966) has outlined the difficulties of such a process and Tinbergen (1965) amongst others has pointed out that there is no need to postulate 'group selection' if observed features can be explained in terms of natural selection. It is suggested that the aspects of the social organization in the buffalo that have been described here, could have developed through natural selection.

ACKNOWLEDGEMENTS

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Paper No. 37

Aspects of the Social Organization of Moose

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ABSTRACT

Associations among sex and age groups and the home range characteristics of moose were investigated in Grand Teton National Park, Wyoming, from 1963-1969. Observations of group sizes of 3351 moose showed that 58% occurred as single individuals, 26% in groups of two, and 16% in groups of three or more, demonstrating the solitary nature of the social organization. Females with calves and yearling males appeared to be the most solitary classes. Observations of tagged moose showed that groups were temporary and that there was little lasting association between particular animals. Agonistic behavior appeared to contribute to the maintenance of a solitary social organization. Observations of tagged moose showed that summer and winter home ranges for many adults were apparently well established, with animals occupying the same areas in consecutive years, and that home ranges were mostly less than 2.0 sq. miles in size. Yearling moose showed erratic and sometimes extensive movements, and apparently did not have established home ranges. The adaptive nature of the solitary social organization and the management of moose in a natural area are briefly discussed.

INTRODUCTION

The associations among sex and age groups and home range characteristics of moose (*Alces alces*) were investigated in Grand Teton National Park, Wyoming, from 1963-1969. Other study objectives were to evaluate habitat relationships and population dynamics of moose in relation to maintaining the ecosystem of a natural area in as near pristine conditions as possible.

The 800-sq.mile study area included Grand Teton Park proper plus surrounding forest lands in the northern Jackson Hole valley. Physiography, climate, and vegetation of the area have been described elsewhere (Houston, 1968). Historical records suggest that moose were not present in the Jackson Hole area during the first half of the nineteenth century, and that they may have become established around the beginning of the twentieth. Moose have subsequently colonized much of western Wyoming. Moose hunting is not permitted within Grand Teton Park, but surrounding areas are hunted on a limited permit by area basis. Calculations suggested that the moose population was composed of a resident segment of perhaps 200-250 animals that remained on the area yearlong and migratory segments, totaling perhaps 450-550, that were present only during winter and spring. Recent aerial counts tend to confirm initial calculations of 700-800 animals in winter populations (Yorgason, 1970). Records from tagged moose indicated movements of up to 50 miles between summer and winter ranges of migrants. Winter densities were commonly 20-40 moose per square mile on major range areas. The willow (*Salix* spp.) vegetation type, located on floodplains of major rivers and streams, was a major forage source, and received the greatest yearlong and seasonal use.

METHODS

Data are from field observations obtained by covering established routes through the study area with a vehicle or on foot. A total of 5610 observations of moose was obtained from 591 route coverages during the study. Moose numbers, locations (to nearest 0. 25 miles), sex and age classes, and behavior were recorded during route coverage. Home range characteristics were determined from 117 immobilized and eartagged moose (Houston, 1969). Numbered or coded symbols on both sides of small (2.5 × 2.5 in.) pendant eartags were subsequently read in the field to identify individual moose. The following criteria were used to field classify moose into sex and age categories: calves were recognized until they were approximately one year old (to May 15) by their relatively small size and by facial characteristics. Yearling males were distinguished only during late spring through fall (May 16-November 15) by their comparatively small size and by antler structure ('spike' or small palms less than about 10 in. in width). Female moose, including calves over 5 months, were distinguished from males by the presence of a tan patch of hair surrounding the genital area (Mitchell, 1970) or lack of antlers or pedicels. Field observations, coupled with examinations of the dentition of immobilized animals, showed that yearling females could not always be reliably distinguished from older females in the field.

RESULTS AND DISCUSSION

Associations among sex and age classes

Although earlier workers have commented on the solitary nature of moose (Altmann, 1956;Denniston, 1956), quantitative data are limited (Geist, 1963). I attempted to measure the different associations among sex and age classes from observations of 3351 moose occurring as 1955 single individuals, and in 574 groups. Singles were distinguished from groups by being at least 150 ft. apart, or exhibiting independent actions or movements. All moose were free-ranging and on natural foods. Calves were omitted from calculations because they showed little social interaction with moose other than their own mothers. The presence of calves, as part of the overall physiological state of motherhood did, however, generate distinctive behavioral attributes in maternal females.

TABLE 1. ASSOCIATION AMONG SEX AND AGE GROUPS OF MOOSE

	Percent Animals Within Groups							
Period	Group size	Adult males	Females	Females with calf	Adult males/ females	Adult males/ female with calf	Yrlg. males	Yrlg. males/ female or adult male
Late spring-fall (May 16-Nov. 15)	1	55	67	99[a]			79	
1407 moose in 1802 groups	2	28	30	1	62	86	16	74
	3+	17	3		38	14	5	26
Pct. total groups		35	22	24	5	2	10	2
Winter-early spring (Nov. 16-May 15)	1	52[b]	75	91				
1944 moose in 1447 groups	2	20	23	7	49	66		
	3+	28	2	2	51	34		
Pct. total groups		25	28	36	6	5		

[a] Excluding all calves

[b] Yearling males were not distinguished

The observed frequency of different moose groups (Table 1) was probably not representative of their occurrence in the population. This was due to seasonal changes in behavior which included secrecy of maternal females, the influence of the rut on movements and associations, and the difficulty of observing young calves. I combined data for late spring through fall, since there were no significant differences in group sizes, even though behavioral changes influenced the frequency of various groups. Groups containing both adult males and females were comparatively uncommon and involved 7% of the animals observed during late spring through fall periods; 11% during winter and early spring. The predictable change in associations occurred between late spring-summer and the fall (September 16-November 15) rutting period with adult male/female groups increasing from 8% to 31%. Mixed groups containing yearling males with other sex and age classes were uncommon and involved only 18% of the total number of yearling males observed.

Nearly 58% of all moose observed occurred as single individuals (group size one), 26% in groups of two, and only 16%, in groups of three or more. Females with calves were the most solitary during all periods. Yearling males and females observed without calves were also quite solitary. Adult males (all males during winter and early spring) were generally more 'gregarious' than females, with groups of two or more comprising 45-48% of the animals observed during seasonal periods. The group classes are not equivalent, since by definition some contain two or more animals. Even in these cases, however, groups containing only two moose usually constituted a majority of the observations.

In addition to the small group sizes encountered, observations of tagged moose suggested that groups (or more properly, aggregations) were usually temporary, and that moose showed preferences for specific areas, rather than attachments to groups. Tagged animals that shared summer ranges occasionally wintered on different areas, and when sharing range areas often arrived and departed at different times. I attempted to evaluate the degree of association among tagged moose by calculating coefficients of association (Knight, 1970), using: $\frac{2\,ab}{a + b}$ where a and b were the number of times animals A and B were observed, and ab is the number of times they were observed together. Coefficients were calculated for the period in which both animals were known to be in the population. A coefficient of 1. 00 indicates perfect association, or the probability that the two animals would consistently occur together. Only 31 associations involving 30 different animals were observed during the study, even though 60-80 tagged moose were in the population during the period of calculations and over 600 sightings of tagged moose were made during the study (Table 2). The mean coefficient of association among adult moose was 0.15, and none of the values exceeded 0. 50, suggesting little attraction or association between particular animals. Furthermore, 4 of 21 associations among adults occurred during the rut. Associations between tagged females and tagged 5-10 month old calves showed a value of 1. 00, and indicated a not unexpected perfect association.

Age class	No. moose	No. associations	Mean coeff. assoc.	Percent in frequency classes			
				0.00-0.25	0.26-0.50	0.51-0.99	1.00
Adults[a]	24	21	0.15	84	16	0	0
Females and calves	6	10	1.0	0	0	00	100

[a] Includes two yearlings.

Observations of group sizes and of tagged animals demonstrated the solitary nature of the social organization of moose. Females with calves and yearling males appeared to be the most solitary classes, and there appeared to be little lasting association between particular adult animals.

Agonistic behavior

Major sex and age classes involved in 178 instances of agonistic behavior are shown in Fig. 1. Aggression involved in agonistic behavior was overt (physical contact or attempted contact) or involved the 'head high' or 'head low' threat postures described by Geist (1963).

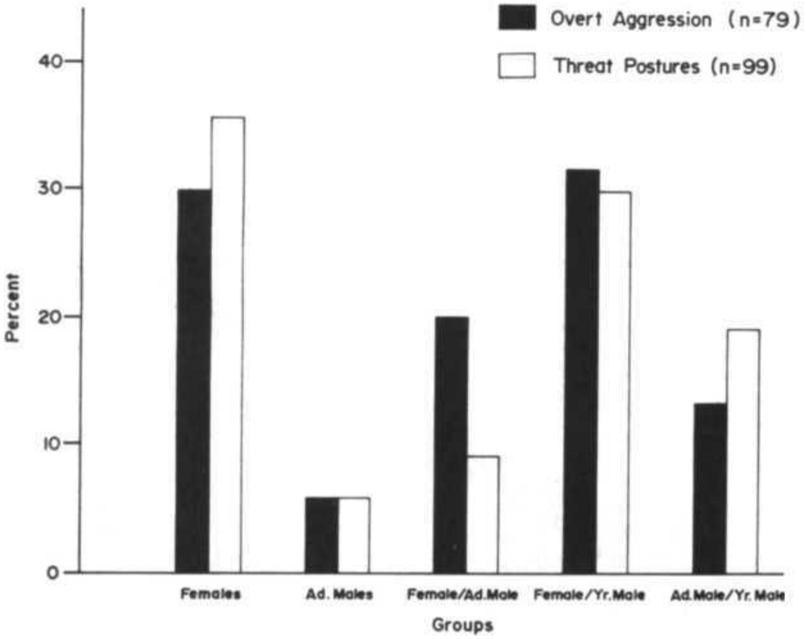

Fig. 1. Sex and age classes of moose involved in agonistic behavior.

Agonistic behavior was observed between females throughout the year and often involved those with calves. Females with calves showed aggression toward all other sex and age classes during winter. Agonistic behavior and the solitary social organization appeared to result in segregation of females with calves on winter ranges. Winter range was limited and substantial winter mortality of calves was observed during the study. It seemed possible that the better established and/or more aggressive females might be comparatively more successful than others in bringing calves through the winter.

Agonistic behavior was observed less frequently between adult males, but was particularly prominent between yearling males and adults (males and females) during late spring and summer. Additionally, yearling males demonstrated a type of avoidance behavior wherein they sometimes moved from the vicinity of an adult when becoming aware of its presence. What appeared to be avoidance behavior was observed among other sex and age classes of moose, was often subtle, and no attempt was made to quantify its occurrence.

The frequency with which yearling males (and probably females) encountered aggressive behavior probably contributed to the rate and distances of their summer wanderings (discussed below). By late summer, yearlings were nearly absent from areas having high densities of resident adults. Locations of tagged and untagged hunter-killed yearlings, and summer field observations suggested a dispersal of this class into areas having low densities of adults. Low densities were in what could be considered to be marginal habitats, or areas subjected to locally heavy hunting pressure.

Subtle forms of agonistic behavior and social interaction may have significant population consequences for many species (Davis, 1964; Stokes and Balph, 1965). Observations suggested that this probably applied to moose, with agonistic behavior contributing to maintenance of the solitary social organization and influencing the population attributes of dispersal and mortality.

Home ranges

Relocations (repeat observations) of tagged moose showed that many occupied distinct areas during summer and winter. These areas were called seasonal home ranges. Tagged moose were considered to be residents if observed on the area during summer and fall; migrants if observed only during winter and spring. The occurrence of a tagged moose within the same general area (1 mile from other relocations) for two or more consecutive years was considered to show that the animal had an established home range.

A total of 108 summer relocations of 18 resident adults (8 males, 10 females) showed that 17 of 18 returned annually to establish home ranges. Sixty winter relocations of 12 resident adults (7 males, 5 females) showed that all returned to established ranges. Three resident males observed for four years and one male and one female observed for five years always used the same seasonal range areas.

Eighty relocations of 20 migratory adults (10 males, 10 females) observed for two or more consecutive years showed that all returned to established winter ranges. Five other migrants were observed on winter ranges only during alternate years. Eight migrants were not re-observed on winter ranges after a lapse of one or two winters following tagging.

These data showed that seasonal home ranges of adult resident moose were apparently well established. Some migratory moose consistently returned to established winter home ranges. Although observational errors (animals present but not observed), tag loss, and unreported mortality influenced observations, it appears that other migratory moose wintered on the area only during severe winters. The observed annual variation in moose densities on winter ranges also suggested differences in wintering areas of migrants.

Three of four 2-year-olds did not return to winter ranges used as yearlings. One of these animals observed when 3-years-old reoccupied the same winter range used as a 2-year-old.

Three tagged 2-year-old moose did not reoccupy summer areas used as yearlings. One of these animals observed when 3-years-old reoccupied the same summer range used as a 2-year-old. Additionally, 40 summer relocations of 13 yearlings showed that distances between relocations frequently exceeded 2 miles, and movements appeared to be erratic.

These data suggested that yearlings usually did not have an established home range, and that establishment might not occur until moose were 2-years-old. It seems possible that the time involved in home range establishment could also depend upon the density of adult moose.

Relocations of tagged moose were used to calculate areas occupied on summer and winter ranges. Winter home ranges were calculated for January 15-April 1 periods. Only moose with three or more relocations, each made at least 5 days apart, were used to plot areas. Relocations made during different years were not separated.

Over 95% of the observed summer ranges of 25 adult residents (14 males, 11 females) were 2.0 sq. miles or less in area; over 70%, 1.0 sq. mile or less (Table 3).

About 95% of the observed winter ranges of 39 adult migrants and residents (19 males, 20 females) were 2.0 sq. miles or less in area;nearly 80%, 1.0 sq. miles or less. Three of four moose using winter ranges larger than 2.0 sq. miles (up to 8 sq. miles) were migrants. This further suggests that areas occupied by certain migrants varied with the rigor of the winter.

Males and females showed no significant differences in sizes of summer and winter home ranges. However, 9 of 13 relocations of four males made from September 15-October 31, during the rut, were over 2. 5 miles from the center of established summer ranges. Greatest observed movement was 12 miles. By contrast, 12 of 15

TABLE 3. SUMMER AND WINTER HOME RANGE SIZE OF MOOSE

Ages of moose	Home range type	No. moose	No. relocations	No. of moose by size of area occupied (sq. miles): 0.25-1.00	1.25-2.00	2.25+
Adults	Summer	25	132	18	6	1
	Winter	39	173	31	6	2
Yearlings	Summer	9	31		4	5
	Winter	6	21	5	1	

relocations of six adult females were 1.0 mile or less from centers of established summer ranges and greatest movement was 2 miles. The extent of female movements may be a function of the density of breeding males.

These data showed that summer and winter home range areas of many adult moose were small. Movements of males increased during the rutting period. Knowlton (1960), McMillan (1950), and de Vos (1956) reported limited summer movements for moose. Ballenberghe and Peek (1971) reported similarly small summer and winter home ranges for moose in Minnesota.

All of the summer areas occupied by nine yearling exceeded 1.25 sq. miles, over one-half of the areas exceeded 2.25 sq. miles, with three areas plotted at about 8, 10, and 24 sq. miles (Table 3). Winter areas occupied by six yearlings were all 2.0 sq. miles or less in size, and were comparable to areas occupied by adults.

Some additional considerations

Presumably the solitary social organization of moose has survival value and has been the best evolutionary strategy for the species. As such, the social organization, in combination with morphological and physiological adaptations, permits the species to occupy a wide range of habitats at varying densities, and to respond to the availability of short-lived habitats composed of seral vegetation (Geist, 1971). Over much of its range the moose occupies a niche in the boreal coniferous biomes (Peterson, 1955). Winter moose densities appear to be one or less per square mile in coniferous forests of eastern North America and the northwestern Soviet Union (Pimlott, 1961;Semyonoff, 1956). Although locally higher densities occur throughout the range of the moose, often associated with seral vegetation, it may be that the successful occupancy of extensive boreal areas at low densities has been of greatest importance in the evolution of the species. An evolutionary premium may have been set on small group sizes wherever conditions of deep snows and scattered winter forage supplies occur in boreal areas. Single moose or small groups may have been more successful in finding and utilizing forage. Conversely, large groups might have been at a selective disadvantage under such conditions, with energy expenditures exceeding income.

An hypothesis resulting from this study and presently being tested was that the moose population within Grand Teton Park was essentially 'naturally regulated'.i.e., the artificial manipulation of numbers within the park was unnecessary. Regulation appeared to result primarily from periodic winter mortality and by reductions in natality following severe winters. Data suggested that emigration of subadults, as influenced by social organization and density, contributed to the regulatory process. Regulation of the moose population has not resulted in adverse effects upon other faunal species or upon forage supplies, and is presently considered to be in harmony with the objectives of a natural area (Houston, 1968). This same hypothesis is being tested in other natural areas where 'management' involves preventing or compensating for modern man's alteration of natural ecological relations (Cole, 1971; Houston, 1971).

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Paper No. 38

Merino Sheep: Some Factors Affecting their Distribution in Very Large Paddocks

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ABSTRACT

This paper describes observations on ranging behaviour of a flock of 450 Merino sheep in a 2, 000 ha paddock in a semi-arid environment. The observations covered periods of hot weather and of cool weather, and periods of feed abundance and of feed shortage.

The sheep tended to graze in preferred areas and travelled up to ten km per day; movement away from water was limited by the fences.

Observations on the separation of the flock into small units suggest that formation of a group of sheep that behave homogeneously is governed by factors that include ambient temperature, hunger and thirst.

INTRODUCTION

Caskey (1969) in reviewing the managerial problems of graziers in semi-arid areas of Australia pointed to the paucity of knowledge on factors affecting utilization of pasture. Problems include the optima for paddock size, distance between watering points and flock size. To provide an understanding of the manner in which pastures are grazed, information is needed on the formation, maintenance and dispersal of groups, on the distance sheep walk in large paddocks, and on the frequency that sheep are found in different parts of a paddock.

This paper is a report of the movement, behaviour and group formation of sheep in a 2, 000 ha paddock in a semi-arid environment. The observations were made in hot and in cool weather and in seasons of feed abundance and shortage.

METHODS

Description of Study Area

The observations were carried out at 'Marfield', a property near Ivanhoe, 240 km east of Broken Hill, New South Wales.

Climate. The mean annual rainfall of 272 mm is extremely variable with much of the rain falling in winter and a summer component from thunderstorms. In the three years of the observations (1966-68) annual precipitation was 198, 72 and 199 mm. The winter of 1966 and summer of 1968 were periods of pasture scarcity while the summer of 1967 and winter of 1968 were periods of abundant feed.

The summers were hot with maxima reaching 46°C and rarely dropping below 30°C, while the winters were cool with maxima ranging between 10°C and 16°C.

Vegetation and Soils. The vegetation is a Casuarina-Heterodendron Association (Beadle, 1948). The density of the trees varies greatly and in some areas visibility is only ten metres, while in more than three-quarters of the paddock, sheep are visible over 800 metres. In the densely wooded areas there is negligible herbaceous flora but in open wooded areas there are perennials such as *Bassia lanicuspis* F. Muell., *Stipa* spp. and *Eragrostis* spp., as well as annuals such as *Medicago* spp., *Tetragonia tetragonioides* (Pall.) Kuntze, and *Portulaca oleracea* L. Timberless areas of varying size are also seen. They contain similar herbaceous species as the open wooded areas. The soils are red sands or sandy loams, and the country is gently undulating.

Water supply. The only permanent drinking water for sheep is collected in dams, that is, large holes dug in the ground which collect surface runoff after rain. Low lying areas do not hold water for more than two weeks after rain and the numerous small depressions hold water for shorter periods.

Sheep Management on Property

The flock consisted of Peppin Merino ewes and wethers of all ages. Except for rams, sheep were run together without separation on either age or sex. Rams were introduced into the paddocks for two ten-week periods a year, beginning in late February and late August. Sheep were handled on only four occasions annually including shearing in April and crutching in October when the rams were removed.

The stocking rate of the property was approximately one sheep per five ha but this varied from month to month depending on available feed. The owner sold sheep when he considered there was insufficient pasture to support his flocks for at least six months. Sheep were shifted out of a paddock only when the water supply was exhausted. When food was scarce the gates of all paddocks which still had water were opened.

Observation Paddock

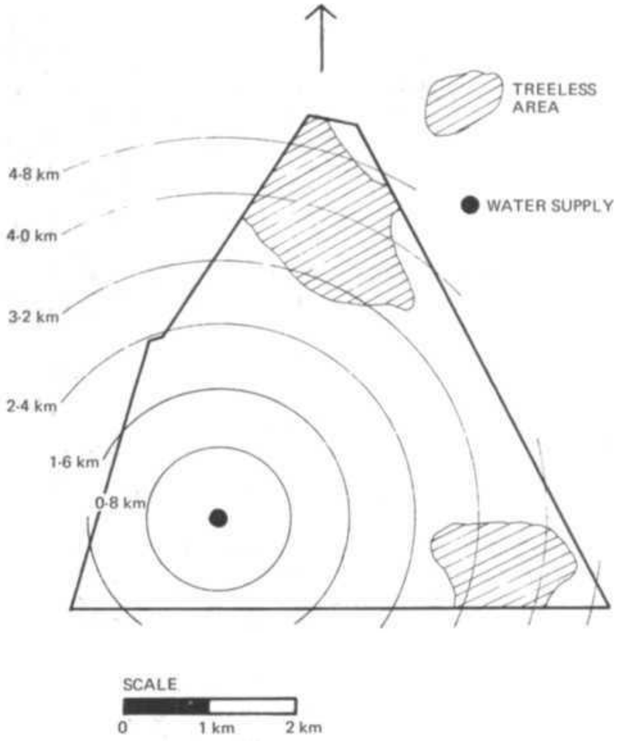

Fig. 1. Map of the paddock where the observations were made. Of particular importance is the location of the water supply and the treeless areas where the sheep were frequently seen in periods A.H. and A.C.

The major feature of the paddock (Fig. 1) is that the only water supply is in the south-west corner. During the observation periods all gates were shut so that the number of sheep in the paddock remained constant.

Identification of Sheep

The presence of three or four black sheep (Table 1) with easily identified white marks was used to aid in identification of groups and provide an estimate of distance walked. These sheep are referred to, hereafter, as key sheep. No attempt was made to mark other sheep, as attempts to identify them at each observation period would have resulted in severe disturbance to the group.

Observation Technique

The paddock was searched by an observer driven in a car along the length of one fence and then along parallel traverses spread at 550 m intervals. Key sheep within about 270 m of the car were identified and the number in the group counted. If necessary a short detour from the traverse was made to confirm the identification, but the car was never closer than 180 m. The position and number of sheep was marked on a scale map and the presence or absence of key sheep was indicated.

A group of sheep was defined as those sheep sufficiently close to one another as to be able to see at least one other sheep and as those which ran together when approached; a group defined in these terms could be scattered over 100 ha. This definition differs from that of Dudzinski, Pahl and Arnold (1969) who considered sheep to be in a group if they were less than fifteen metres from one another.

Provided the observations were made rapidly the sheep stayed within twenty to fifty metres of their original position. When sheep were in poor condition they were far less likely to run from the car than when they were on a rising plane of nutrition.

Frequency of Observations. Observations were made during four periods, hereafter referred to as periods A.H., A.C., I.H., and I.C. (Table 1). In periods A.H. and A.C. feed was in adequate supply as assessed by the condition of the sheep, while in periods I.H. and I.C. feed shortage prevailed. In periods A.H. and I.H. ambient temperatures were high while in periods A.C. and I.C. they were low. No rain fell during any of the four observation periods.

In periods I.H. and I.C. few observations were made because the flock had split into many groups comprising four sheep or less and many were not accounted for; periods I.H. and I.C. have been included in the data only to give some quantitative information about the effects of drought on group structure.

Grazing, Camping, and Watering Behaviour

The grazing and camping habits of the sheep were observed during daylight hours. If sheep camped at the same site at consecutive observations it was assumed that they camped there between these periods. The camping behaviour and the time grazing commenced in the afternoon were observed during periods A.H. and A.C. on eight of the eleven days.

A group was considered to have drunk water if some sheep were seen near the dam and if sheep tracks had cut the tyre marks made by the car around the water supply.

Distances Walked

The minimum distances that sheep moved per twenty-four hour period were estimated as the distance between the positions of key sheep at successive observations.

Quantity of Herbage Available

Food was considered adequate when sheep were in good to fat condition. When sheep were very poor and weak, almost no pasture was available and the leaves on shrubs or trees had been eaten to a height of one to one-and-a-half metres from the ground.

TABLE 1. Summary of Climatic Data, Times of Observations, and Number of Sheep in Paddock

	Period	Mean max. daily temp. (°C)	Mean min. daily temp. (°C)	Rainfall (mm) preceding 3 months	Times of observations (hr of day)	No. key sheep	Total no. sheep in paddock
Abundant feed (hot weather)	A.H. 13 February 1967 to 24 February 1967	37.6	24.3	68	0500 0800 1200 1500 1800	4	420
Abundant feed (cool weather)	A.C. 7 July 1968 to 18 July 1968	10.4	1.3	54	0600 0900 1200 1500 1700	4	300
Feed shortage (hot weather)	I.H. 16 January 1968 to 19 January 1968	35.2	23.4	18	0900 1700	3	< 200
Feed shortage (cool weather)	I.C. 25 September 1966 to 28 September 1966	20.2	10.8	16	0900 1700	4	<450

RESULTS

Group Sizes and Number of Groups

In period A.H. there were twelve out of the fifty-five observations when all sheep were together; during the other forty-three observations the sheep were split into two or more groups with a median size of fifty to one hundred sheep per observation (Fig. 2). In period A.C. the sheep were together at each of the fifty-five observations. There were only eight observations in periods I.H. and I.C. but the results clearly show that small groups of one to five frequently occurred during severe drought.

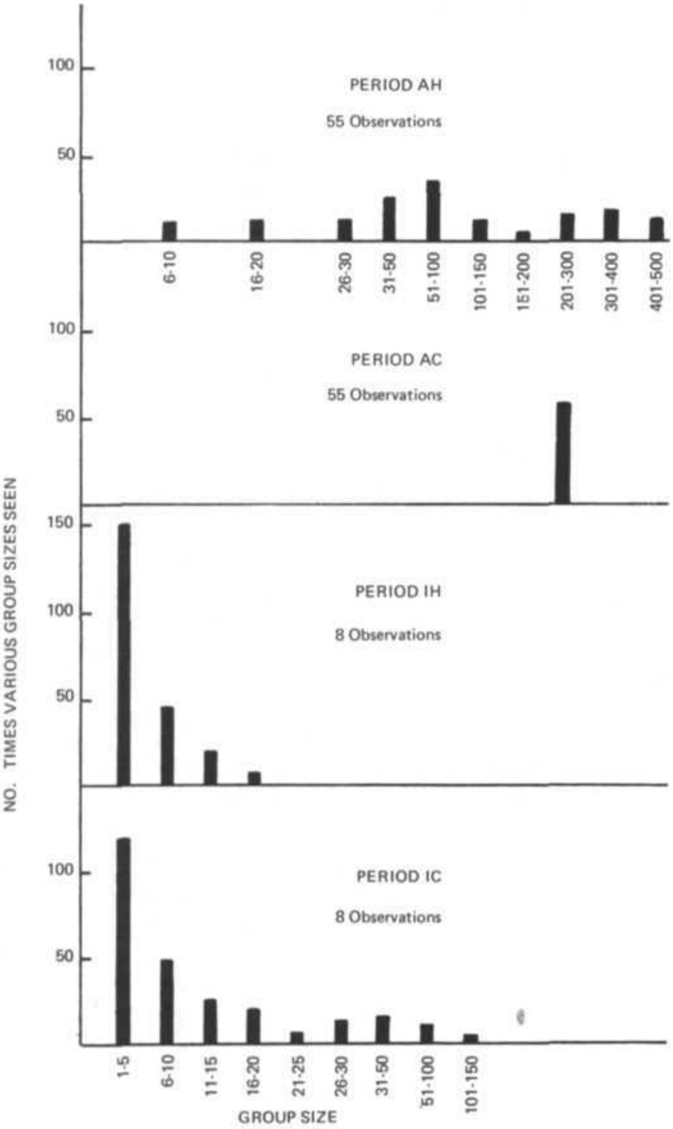

Fig. 2. Frequency histogram of groups of different sizes seen during the observations.

In period A.H. when the flock split into groups sheep *b* was with other key sheep about 90 per cent of the time while sheep *d* was seen with other key sheep about 50 per cent of the time. Sheep c was generally found in a group of greater size than any of the other key sheep (Table 2).

TABLE 2. THE VARIATION IN GROUP STRUCTURE SHOWN BY THE SIZE OF GROUP ASSOCIATED WITH KEY SHEEP DURING PERIOD A.H.

Key sheep	Nos. of observations of key sheep	Size of associated group (mean)	Size of associated group (range)
a alone	14	50	20-180
b alone	7	40	20-100
c alone	14	160	30-230
d alone	27	70	30-120
a + b together	14	140	20-120
a + c together	1	210	—
a + d together	1	100	—
b + c together	8	100	80-190
b + d together	—	—	—
c + d together	6	60	60
a + b + c together	5	320	310-350
a + c + d together	—	—	—
b + c + d together	1	220	—
a + b + c + d together	19	340	80-420

On six of the eleven days of period A.H. all sheep were camped together at 0500 h and on five of these days two or more groups were formed between 0500 h and 0800 h. The sheep remained in the same groups from 0800 h on eight of the eleven days but tended to come together after 1800 h (Table 3).

TABLE 3. INFLUENCE OF TIME OF DAY ON GROUP SIZE DURING PERIOD A.H. THE BODY OF THE TABLE SHOWS THE NUMBER OF DAYS ON WHICH A PARTICULAR NUMBER OF GROUPS WAS SEEN.

No. of groups seen during traverse	No. of days on which various Nos. of groups seen				
	0500 h	0800 h	1200 h	1500 h	1800 h
1	6	1	1	1	3
2	2	2	2	2	1
3	2	2	3	3	3
4	0	2	3	3	2
5	0	1	1	1	0
6	0	2	1	1	1
7	1	1	0	0	1

Distribution of Groups throughout the Paddock

In period A.H. there was a tendency for sheep to be camped well away from the water (Table 4). During period A.C. sheep were usually more than 3. 2 km from water. By contrast, in period I.H. most groups tended to be found between 1. 6 and 3. 2 km from water during the summer drought.

TABLE 4. FREQUENCY (PER CENT) WITH WHICH GROUPS WERE FOUND AT DIFFERENT DISTANCES FROM WATER OVER ALL OBSERVATION PERIODS

Distance (km) from water	Period A.H. (hot, abundant feed)	Period A.C. (cool, abundant feed)	Period I.H. (hot, insufficient feed)
0, < 0.8	15	2	4
0.8, < 1.6	12	4	13
1.6, < 2.4	10	11	23
2.4, < 3.2	15	16	28
3. 2, < 4.0	20	56	24
4.0, < 4.8	28	11	8

TABLE 5. FREQUENCY WITH WHICH GROUPS WERE FOUND AT VARIOUS DISTANCES FROM WATER AT DIFFERENT TIMES OF THE DAY (PERIOD A.H. ONLY)

Time (h)	Distance (km) from water					
	0, < 0. 8	0. 8, < 1.6	1.6, < 2.4	2.4, < 3.2	3. 2, < 4. 0	4. 0, < 4.8
0500	0	1	1	5	4	14
0800	14	9	9	3	7	4
1200	7	4	2	5	6	4
1500	3	4	2	8	7	8
1800	0	0	2	2	7	13

When sheep drank (period A.H.) they moved from their night camp and arrived at the water by 0800 h (Table 5). By 1800 h the sheep had returned to the area near the fence.

When the paddock supported abundant herbage (periods A.H. and A.C.) sheep were normally found grazing in one of two treeless plains which were situated more than 3. 2 km from the dam, yet there appeared to be as much pasture near the dam as in grazed areas further from water.

Watering, Grazing Behaviour and Distance Travelled

During period A.H. it appeared that the whole flock went to water on only three of the eleven days (Table 6). There was some variation in the frequency of drinking by the key sheep and this appeared to be reflected through the whole flock. The maximum daily temperature did not appear to influence the frequency that sheep went to the water supply although long periods of high temperatures such as those experienced on days eight to ten, may have resulted in more frequent drinking. During period A.C. no sheep drank water during the eleven days even though some of the ewes were lactating.

TABLE 6. THE NUMBER OF SHEEP AT THE WATER SUPPLY AND THE DAILY MAXIMUM TEMPERATURE (PERIOD A.H.)

Day	Max. temp. (°C)	Number of sheep at water supply
1	33	180
2	30	250
3	29	340
4	28	420
5	34	0
6	36	250
7	38	50
8	42	220
9	42	0
10	46	420
11	31	420

In summer sheep tended to camp from 0800 h to 1500 h and graze in the early morning and late evening (Table 7), while in the winter sheep camped at noon but sometimes were grazing by 1500 h. When temperatures were over 30°C more than half the sheep camped (Table 7). High maxima tended to prolong camping during the day but all sheep were grazing by 1800 h even though the maximum was over 40°C.

The mean minimum distances walked by sheep were approximately 5. 5 km in period A.H. and 3. 2 km in the other three periods (Table 8). Some sheep walked up to ten km a day.

TABLE 7. PERCENT OF GROUPS OBSERVED CAMPING AND GRAZING IN RELATION TO (A) TIME OF DAY, (B) TEMPERATURE

(a)					(b)		
	Period A.H.		Period A.C.			Period A.H.	
Time (h)	per cent camping	per cent grazing	per cent camping	per cent grazing	Temp. (°C) range	per cent camping	per cent grazing
0500	0	100	100	0	15, < 20	40	60
0800	40	60	0	100	20, < 25	45	55
1200	90	10	100	0	25, < 30	25	75
1500	65	35	65	35	30, < 35	70	30
1800	0	100	100	0	35, < 40	65	35
					40, < 45	75	25

TABLE 8. MINIMUM DISTANCES THAT KEY SHEEP WALKED PER DAY (KM) DURING EACH PERIOD

	Period A.H. (hot, adequate food)				Period A.C. (cool, adequate food)	Period I.H. (hot, inadequate food)			Period I.C. (cool, inadequate food)			
Sheep	a	b	c	d	a	a	b	c	a	b	c	d
Day												
1	3.0	2.5	2.5	3.0	2.5	2.5	2.5	1.0	3.0	4.0	4.0	1.5
2	6.0	1.5	1.5	7.0	3.0	7.5	3.0	5.0	1.5	4.0	3.0	5.0
3	2.5	2.5	2.5	2.5	2.5	3.0	5.0	1.0	1.5	2.5	4.0	4.0
4	7.5	10.0	7.0	7.5	7.0	3.0	1.5	1.5	2.5	1.0	3.0	6.0
5	3.0	5.5	5.5	6.0	3.0							
6	8.5	3.0	4.0	5.0	1.5							
7	4.0	6.0	3.5	7.5	4.0							
8	8.0	9.0	7.5	1.5	2.5							
9	5.0	1.5	5.0	3.0	3.0							
10	9.0	9.0	9.0	9.0	4.0							
11	7.0	7.0	3.0	3.0	6.0							
Mean/day*	6 0	5.0	4 5	5.0	3.5	4.0	3.0	2.0	2.0	3.0	3.5	4.0
	(9.5)	(8.0)	(7.0)	(8.0)	(5.5)	(6.5)	(5.0)	(3.0)	(3.0)	(5.0)	(5.5)	(6.5)

* The estimated mean distances actually walked per day are given in brackets; a correction of van Dyne and van Horn (1965) was used.

DISCUSSION

These observations suggest that Merino sheep prefer to graze in certain areas of a paddock. Although abundant feed was available close to water sheep were seen more than 2. 5 km from water in 63 per cent of the observations during period A.H. and 83 per cent during period A.C. (Table 4). In period A.H. the sheep came to water around 0800 h and although they stayed within 1. 5 km of the water supply for the next five hours they were not grazing. They were more than 2. 5 km from the water for the rest of the twenty-four hours (Table 5). These results are in contrast to those of Osborn, Wood and Paltridge (1932) and Lange (1969) who found, with *Atriplex* and *Kochia* communities, that Merino sheep rarely grazed beyond 2. 0 to 2. 5 km from the water supply.

One reason for walking shorter distances than in the present observations may be that Merinos require more drinking water when eating *Atriplex vesicaria* leaves (Wilson 1966). Their water requirements during summer may be greater than the quantity they can consume at one visit to the water supply and drinking twice daily may limit the distance they are prepared to walk from water each day.

In the Casuarina-Heterodendron Association Merino sheep appear to be limited by the fence in the distance they walked from water; the minimum distances walked were up to ten km which is much further than the distance from the water to the furthest point in the paddock, and are further still if corrected by the factor of van Dyne and van Horn (1965) (Table 8). The distances walked were in the range reported by Squires (1970) from accurate measurements. On the diets available the sheep did not drink water daily except in extremely hot weather. Thus distance walked daily can be independent of watering behaviour.

These observations are consistent with those of Brown and Lynch (pers. comm.) who found that even lactating sheep would not be stressed if deprived of water during winter. Thus ranging behaviour was not limited by proximity to water except in very hot weather. If distance walked is a major determinant of paddock size then the paddock in the present observations was too small to provide an answer to the question, 'What is the largest area that allows all the pasture to be reached with the most economical use of fencing?'

The present results suggest that the formation of a group of sheep as defined earlier is affected by environmental factors such as hunger, temperature or thirst. At a particular time, thirst, for example, will be the overriding influence on an individual's behaviour and a group will be formed of all those sheep that move to water. Thus, in period A.H. some sheep moved to water more frequently than others (Table 6); and if the maximum temperature remained over 40°C for several days all sheep drank water and coalesced into a flock. Once the group was formed (by 0800 h, Table 3) it generally remained as an entity throughout the day. These factors may explain the difference in number of groups between periods A.H. and A.C. Similarly, hunger may be an overriding influence on an individual's behaviour and a group will be formed of the sheep that move to graze. In fact, it is possible that the more factors operating the more the flock will be split and so the homogenous groups will be smaller. It is also possible that the amount of attention to other sheep and to other internal or external factors in the environment will vary diurnally, and depending on the 'state' of the animal, influence the formation of groups.

The results (Fig. 2) support the observations of Nicholls (1944) and Dudzinski, Pahl and Arnold (1969) that in periods of food scarcity sheep are scattered throughout the paddock and there is a breakdown of group structure.

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Paper No. 39

Movement Patterns and Habitat Utilization of Ungulates in Ceylon

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ABSTRACT

In order to develop accurate biomass estimates for the ungulate populations resident in two of Ceylon's National Parks, special attention was devoted to the seasonal movements of the dominant species. The two study areas differed with respect to climate, vegetation and the distribution of water; hence differences in movement patterns of the two study populations could often be related to the specific patterns of resource distribution. Seasonal shifts in grazing by elephants and buffalo could give fluctuating biomasses for small sample areas ranging from 750 to 2, 900 kg/km^2. Average biomass estimates for the study areas in Ceylon are in reasonable agreement with comparable studies in India and Java, but far lower than biomass estimates for the savanna habitats of East Africa. On the average two to three ungulate species contribute at least 70% of the total mammalian biomass in the forested habitats of Ceylon, India and Java. Although the species diversity of ungulates in African savannas may be two to three times as great as in Asia, three to five species in four African study areas account for 75 to 84% of the mammalian biomass. Ungulate species which contribute to high biomass levels are also characterized by great potential mobility and the capacity to form cohesive social groupings. Such social groupings may facilitate the development of traditions in the use of resources.

INTRODUCTION

Measurements of the density and biomass of ungulates have been used extensively to compare estimates of carrying capacity for different habitats (see for example Bourliere, 1963a, b; Sharkey, 1970; Stewart and Zaphiro, 1963). These data have been used to demonstrate such points as the differences between various habitat or community types (e.g., Stewart and Zaphiro, 1963) and the differences in productivity between wild and domesticated herbivores (e.g., Sharkey, 1970; Dasmann, 1964). Talbot (1964), while stressing the need for such comparisons, emphasized that any determination of biomass depends on (a) the numbers of animals, (b) accurate estimates of weights, (c) the unit of time, (d) the unit of area, and (e) seasonal factors such as births, growth and mortality.

As part of our study of the ecological conditions in Ceylon's National Park System, we required accurate estimates of the biomass of herbivores using the National Parks. Since the major concern of our study was to obtain an overall estimate of the status of the ungulate populations (in particular of the elephant) in the parks, the following information was required:

(1) Population sizes and population dynamics of each species.

(2) Relationships between species (competition, predation, etc.).

(3) Usage of different habitat types within each park.

(4) Adequacy of the resources available within each park for the support of each species.

In considering the latter two problems, it was necessary to study not only the density and biomass of the various ungulate species in these areas but also the movement patterns. In this paper we will consider both of these problems, especially the relationship between movement patterns and the concentration of biomass.

THE STUDY AREAS

Ceylon's three National Parks (see Fig. 1) all lie within the 'Dry Zone'—the area of Ceylon which receives < 2000 mm annual rainfall.

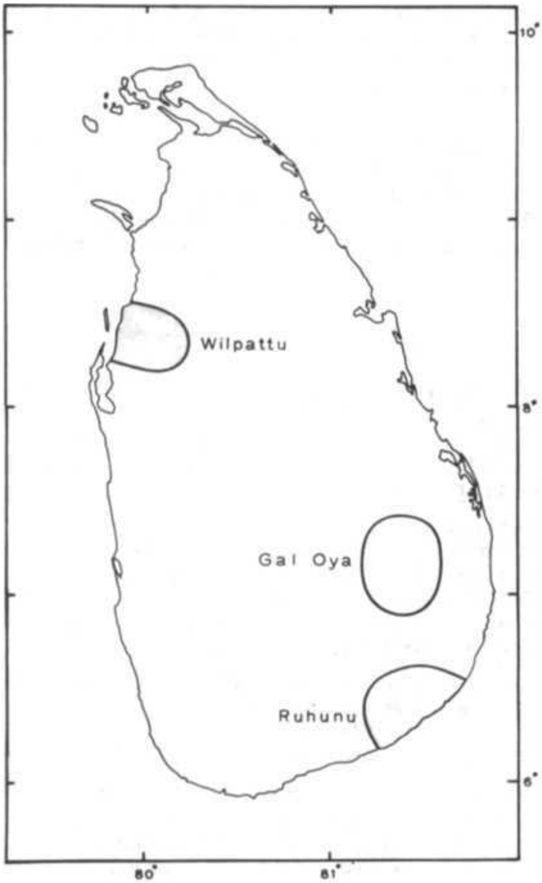

Fig. 1. Ceylon, showing the position of the three National Parks, which constituted the study areas.

Wilpattu National Park, situated on the northwest coast, is in an area with a climatic gradient, being drier to the north and west. The park is bounded to the north and south by rivers but no major river flows through the park. The western portion of the park has a limestone base and is characterized by vertical drainage. Within this portion of the park are many villus,or depressions in the limestone, which contain water. Some are seasonally dry, others contain water year round. The eastern portion of the park which has a base of gneissic rocks is characterized by horizontal drainage by seasonal streams and a lack of villus. Apart from the villus, the banks of which are covered with grass and other herbaceous plants, the remainder of the park (ca. 90%) is forest or forest-scrub (Eisenberg and Lockhart, in press).

Gal Oya National Park surrounds a large (36 km^2) reservoir, the Senanayaka Samudra. This reservoir, constructed in 1948-50, lies at the confluence of a large river (the Gal Oya) with three major tributaries. These streams plus their numerous smaller tributaries give this area a water distribution pattern quite different from Wilpattu. The major vegetation types in this area are forest (48%) and savanna woodland (33%), the latter being concentrated in the western half of the park. Grassland, occurring on the banks of the reservoir, covers 10% of the total area on an average, depending on the water level (for a more detailed description, see McKay, in press).

Ruhunu National Park, on the southeast coast, shows a greater similarity to Wilpattu than to Gal Oya. Two rivers pass through the park but have few tributaries within the park itself. Especially in the southwestern sector of the park, there are numerous water holes, some natural, others man-made; along the coast there are several lagoons of varying salinity. The vegetation of this area is scrub intermixed with grassland along the coast gradually being replaced by forest further inland (Mueller-Dombois, in preparation).

Work in Wilpattu was conducted by Eisenberg and M. C. Lockhart from July 1968 to April 1969 and continued by Lockhart until October 1969. McKay worked in the Gal Oya area from October 1967 to October 1969 and in Ruhunu National Park from June to October 1967. F. Kurt worked in Ruhunu National Park from June 1967 to March 1969. For details of methods the reader is referred to Eisenberg and Lockhart (in press), Eisenberg, Santiapillai and Lockhart (1970), and McKay (in press).

THE MAMMALIAN FAUNA

The mammalian fauna of Ceylon is derived from that of South India. A few endemic species (one primate, one viverrid, several rodents, and insectivores) occur, but all of the larger mammals are closely related to mainland forms, being at most subspecifically different (Eisenberg and McKay, 1970). Within the areas of the National Parks, the following species are important.

Elephant (*Elephas maximus*) occur throughout the dry zone. Total elephant populations around the National Parks are estimated to be: Wilpattu—120 (Eisenberg and Lockhart, in press); Gal Oya—300 and Ruhunu—150 (McKay, in press). The elephant feeds on both browse and grass showing a higher usage of the latter during the rainy season. Females accompanied by juveniles of both sexes travel as herds or as subgroupings of herds; adult males are primarily solitary (McKay, in press).

Water buffalo (*Bubalus bubalis)* occur in all three parks. Not all individuals within any park are wild. There are many recent escapees from domestication, and in Gal Oya one or more herds released there for grazing by their owners. The buffalo is primarily a grazer, although wild buffalo at least will take some browse.

Three species of deer—Sambar (*Cervus unicolor*), Chital (*Axis axis*) and Muntjak (*Muntiacus muntjak*)—occur in all three parks. The sambar and muntjak are primarily browsers; the chital feeds on both grass and browse, showing a preference for grass. One tragulid, the mouse deer (*Tragulus meminna*) occurs in this area also. This small forest dweller is primarily a browser/frugivore.

Wild boar (*Sus scrofa*) occur in all three parks. Although the boar do graze, especially in the wet season, they feed primarily upon tubers and roots dug from the ground.- They also act as scavengers.

Two non-ungulates, the porcupine (*Hystrix indica*) and the hare (*Lepus nigricollis*) are also important terrestrial herbivores. The porcupine is abundant only in drier areas but the hare is common throughout the dry zone wherever there is open vegetation.

Not only do the feeding levels of these species overlap extensively; the same overlap is also shown in the species taken. Elephants use all of the browse plants eaten by the other species as well as the grasses. The elephant will, however, eat coarse grasses such as *Imperata* and *Cymbopogon* which are not used by buffalo or chital.

MOVEMENT PATTERNS

1. The Elephant

In Wilpattu the herds of elephants show a pattern of movements which is dependent upon the seasonal rains. During the rainy season, which normally lasts from October to January (a second smaller rain peak occurs in March-April), the elephants are concentrated in the West Sanctuary. This area, which lies along the coast, has several large villus which, when wet, support a lush growth of grass (Eisenberg and Lockhart, in press). These large areas of grass are evidently attractive to the elephants as they form a concentrated supply of food with water readily available. During this time of year the elephants tend to remain in the West Sanctuary and movements are generally from one villu to another.

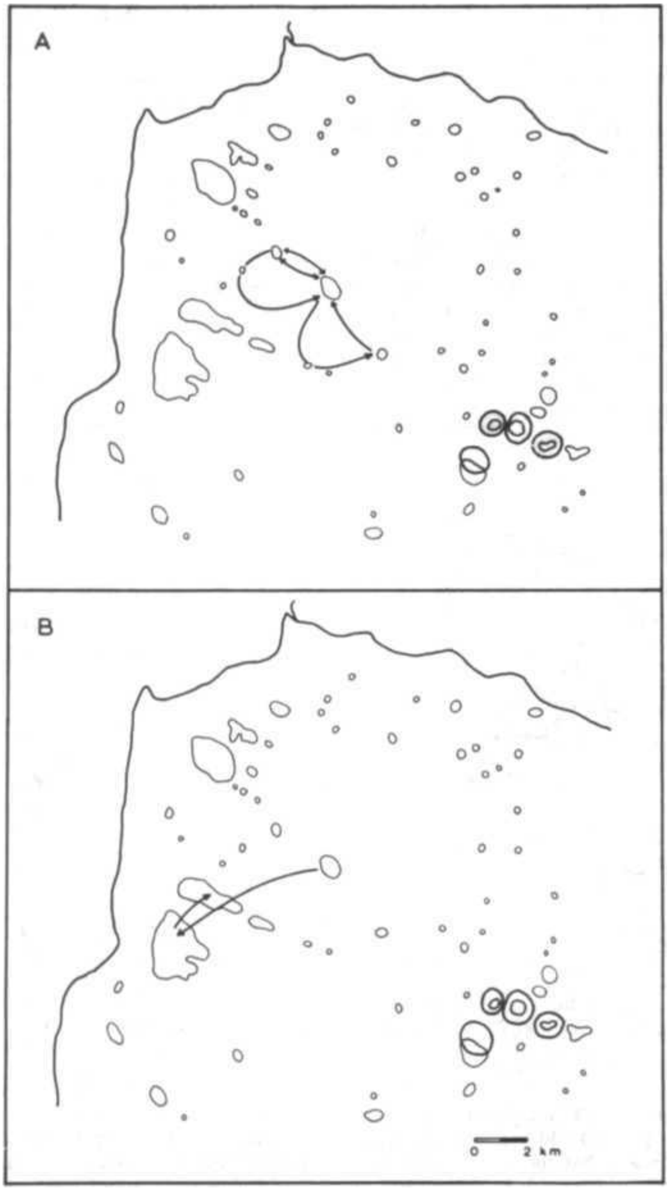

Fig. 2. Movements of a herd of elephants in Wilpattu, August 1969:

A Movements during August 1-15 during drought;
B Movements during August 15-31 immediately after onset of rains.

Following the rains these large villus begin to dry and the available surface water decreases. As the dry season progresses, the elephants leave the West Sanctuary and move either towards the rivers which lie to the north and south or to the villu region in the center of the park. This results in two types of movement pattern which are maintained throughout the dry season. Throughout this period the elephants forage during the day in the forest and scrub areas coming to water in the evening to drink and bathe. Those herds which spend the dry season around the rivers tend to remain in the vicinity of those rivers for foraging and their movements, from day to day, are generally parallel to the rivers.

The herds which remain in the central region of the park, however, show a different pattern. They forage in the forest areas around the villus, often remaining in the vicinity of one villu for several days. Their movements are from one villu to another and within a period of 2-3 weeks they may visit 5 or more of these water sources. Thus they tend to remain concentrated in one area around a particular source of water for one to a few days, moving at short intervals to another one.

This latter pattern is demonstrated in Fig. 2 which shows the movements of one herd of 9 individuals during August 1969. In the first two weeks of the month, the herd moved regularly between villus as shown by the arrows in A, concentrating primarily around two villus. Rains began on August 15, breaking a drought of several months. Immediately following the onset of the rain, the herd moved westward into the West Sanctuary and from then until the end of the month its activity was concentrated around three large villus in that area.

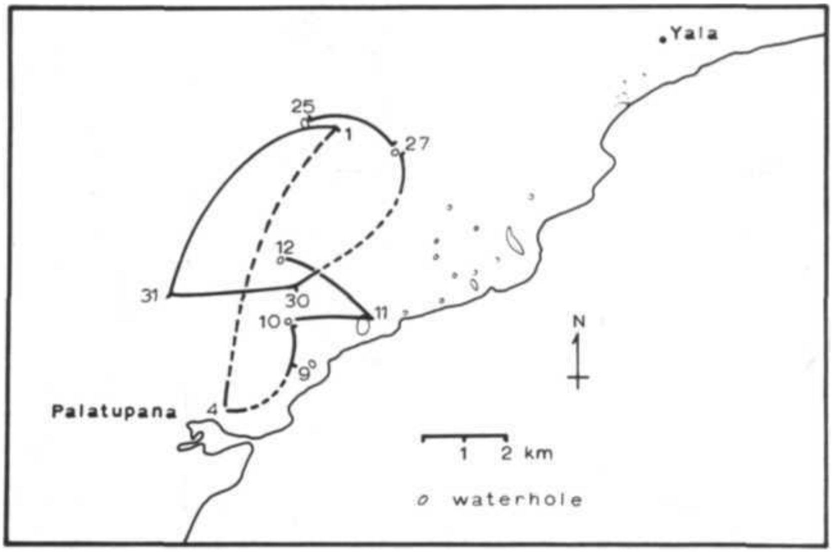

Fig. 3. Movements of a herd of 14 elephants in Ruhunu National Park, July 25-August 12, 1967. Note pattern of movement between water holes.

Movements of elephants in Ruhunu National Park are similar. Figure 3 shows the movement of one group of 14 individuals during July and August 1967 (dry season). Throughout the two weeks that movements were followed, the herd moved from one water hole to another. On three occasions they remained foraging in one area for 2-5 days but on the other days movements were relatively direct and frequent. Feeding accompanied movement between water holes on all days but July 31, when the movement was direct, following a park road. Seasonal trends in this area show a greater concentration along the coast in the wet season accompanied by little daily movement and a dispersal toward the north and west in the dry season with greater daily movement between water holes as outlined in Fig. 3.

Movement patterns shown by elephants in the Gal Oya National Park region differ from those in the other areas. As with the elephants in Ruhunu and Wilpattu National Parks, the Gal Oya elephants have a tendency to use separate parts of their total home range in wet and dry seasons, it is the movements within each of these halves of the ranges that differ. Figure 4 shows the areas covered by one herd of elephants in the eastern sector of Gal Oya National Park during 1968-69. From March to June, 1968, the herd remained in a small area to the southwest of the town of Inginiyagala. They did not, however, move throughout the entire area at frequent intervals. In March their movements were very restricted and they remained feeding in the vicinity of two small bays of the reservoir. In April they moved northward and westward, crossing one arm of the reservoir. By May they had moved south again and early in June they moved northeastward and remained in the area immediately south of Inginiyagala for about 2 weeks. Throughout this entire period (from the end of the wet season to the middle of the dry season), their daily movements were short. They fed in the forest around the reservoir and in the grass zone on the banks of the reservoir itself. They did not move more than 2 km. from the water.

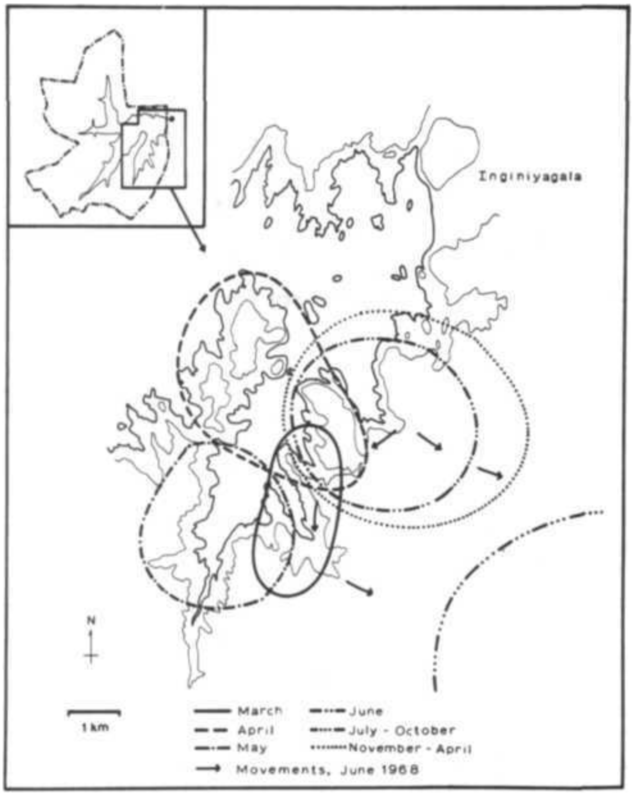

Fig. 4. Movements of a herd of elephants in Gal Oya National Park, 1968-69. Inset shows area of park on main map.

On June 13 and 14, 1968, the herd began to move out of the area they had been in for the past two weeks, part of the herd moving eastward, another part south and east. By June 15 they had left the park and they remained in an area of forest to the southeast of the park until mid-October. In October they returned to the sector of the range they had occupied in June and half of the herd at least remained in this area until April 1969. In April 1969 they again apparently followed the same paths toward their dry season range, but, unlike the previous year, these animals were not observed during the movement.

Thus, the elephants in the Gal Oya region appear to display movement patterns based on three time scales:

(a) daily movements—associated with feeding and to and from water,

(b) seasonal movements—between dry season and wet season home ranges, both of which are shown by the elephants in the other two parks, and

(c) medium-term movements—between sectors of the seasonal home range.

The factors determining these movements appear to be the availability of food and water. Shortage of free water and lack of grass in the West Sanctuary of Wilpattu National Park during the dry season can readily account for the concentration of elephants in the central villu area which contains permanent water and around the rivers (Eisenberg and Lockhart, in press). The seasonal movements of the elephants in Gal Oya appear to be related to availability of food, particularly grass. This, as described by McKay (in press), is in part due to the influence of buffalo which crop the grass around the reservoir to the point where the elephants must scarify the ground in order to obtain any grass. Water does not appear to influence the movements in Gal Oya.

Daily movements are influenced by food and water in that an elephant which requires a large amount of free water daily cannot move too far from a stream or villu or other such source of water. Two patterns are possible: feeding in the vicinity of water (0-2 km) requiring only a short daily movement, and feeding away from water (> 2 km) requiring a long, often rapid, daily movement. The latter case is observed only infrequently and is not maintained for any long period.

The factors determining the medium-term movements in Gal Oya are not so apparent. There is some suggestion that availability of particular food plants may be involved, but at the moment the evidence is inconclusive.

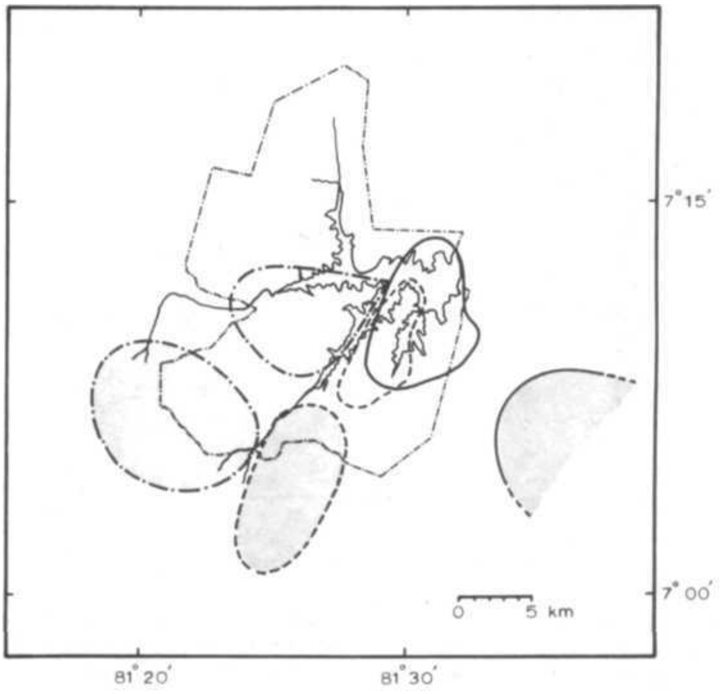

Fig. 5. Seasonal home ranges of three elephant herds in the Gal Oya region. Dry season home ranges shaded, wet season unshaded; note that dry season ranges lie mostly outside the park boundary.

One important aspect of the seasonal movements of the elephants is the relationships between such movements and the park boundaries. As shown in Fig. 5, three herds which use the southern half of the Gal Oya National Park have dry season home ranges which are partly or entirely outside the park. As these dry season ranges are in areas which are being subjected to rapid agricultural development; there is imminent danger that they will become contracted. Evidence from another herd, already surrounded by agricultural land (McKay, in press), shows that elephants appear to maintain their traditional movements even after forest land has been cleared and planted in paddy or other crops. This results in considerable damage to the crops and shooting of elephants. Because of this, it was recommended by McKay (in press) that the boundaries of the park be extended to include the dry season ranges of these herds, rather than make any attempt to restrict the movements of the elephants to a smaller home range.

The only comparable data from mainland Asia are those of Khan (1967) and Singh (1969). Khan (1967) found that a herd of elephants he followed for two years in Malaya showed periodic but non-seasonal movements. Singh (1969), working in Uttar Pradesh, India, found that some herds show seasonal movements while others do not, dependent upon the availability of food and water. Food and water (particularly the former) are responsible for movements of at least some African elephant populations (Buechner *et al.*, 1963). Movements related to rainfall were also recorded by Laws (1969) in Tsavo National Park and by Wing and Buss (1970) in the Kibale Forest Reserve, Uganda.

2. The Water Buffalo

In Wilpattu National Park there are two types of movement patterns shown by the buffalo. Some large herds tend to move from villu to villu in a manner similar to the elephants while a number of smaller groups usually remain in the vicinity of a single permanent villu. As illustrated in Fig. 6 a herd of 52 buffalo spent the period at the end of the dry season (August 1-15, 1969) in the vicinity of 5 villus in the central portion of the park, concentrating primarily around the 2 largest ones. With the onset of rains this herd, like the herd of elephants mentioned above, moved to the larger grassy villus of the West Sanctuary. Four smaller herds, toward the southeastern fringe of the villu zone, remained at the same villus they had occupied during the dry season.

Herds of both types show a seasonal shift in concentration, tending to remain more concentrated around permanent villus in the dry season and dispersing more widely into forested areas in the wet season.

The movement patterns of the buffalo in Gal Oya are shown in Fig. 7. The four groups shown on the north shore of the reservoir for August are wild animals which concentrate in this area during the dry season. They remain in the vicinity of the water making short daily movements into the neighboring forest to browse. During the wet season these herds disperse northward and westward, using temporary water holes and streams for wallowing, only seldom coming to the reservoir.

The remaining four areas outlined on each section of the map show the distributions of buffalo herds which contain large numbers of feral and domesticated individuals. The herds in this area do not maintain the same distinctiveness as do the herds of wild buffalo. Groups of animals will frequently move from one bay to another and recombine with other groups. Figure 7 shows the areas used by these animals during August and March. In both wet and dry seasons these feral and domestic animals remain mostly in the grass zone of the reservoir bank occasionally dispersing slightly into the forest. They tend, however, to remain in the vicinity of one or other of the many shallow bays. There is no seasonal variation in this pattern, the animals merely shift their center of activity from one bay to another. Daily movements are short and consist mostly of a gradual shift along the bank while feeding, occasionally moving into the forest in the early morning, followed by a return to the currently used wallow. The same wallowing site will often be used for several days to weeks.

3. The Chital and Sambar

The movements of both large deer in Wilpattu consist of concentration and dispersal. As described by Eisenberg and Lockhart (in press), the chital tend to concentrate

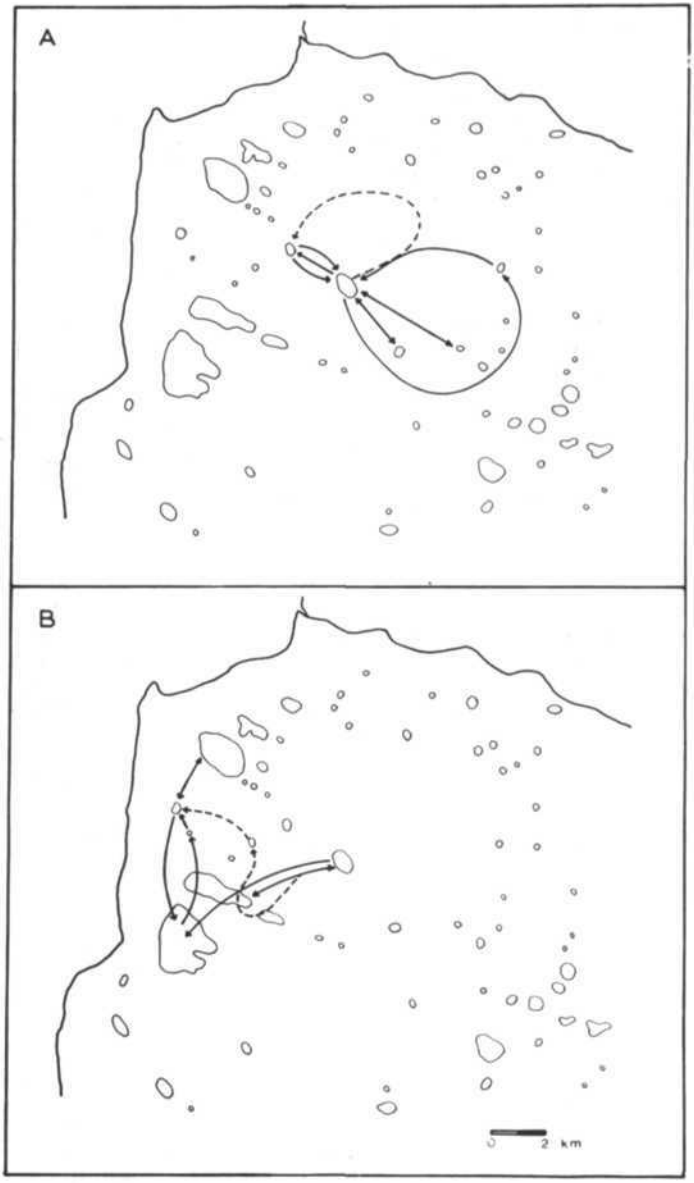

Fig. 6. Movements of a herd of 52 buffalo and 4 smaller herds, Wilpattu National Park, August 1969:

A August 1-15: large herd moves around 5 villus in the central area;
B August 16-31: immediately after rains large herd moves to west sanctuary, smaller herds remaining in the same areas as before.

their activity in the dry season around a permanent water hole or villu. During the daytime they forage in the forest surrounding the villu, moving out into the open again in the late afternoon to graze and drink. At this time of the year large herds form in the grassy areas around the villus. In the wet season the larger herds fragment and

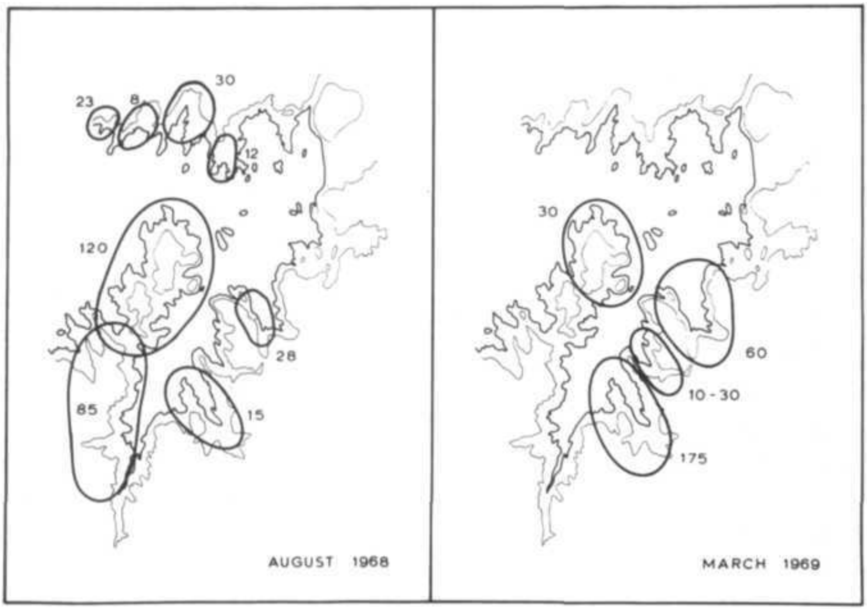

Fig. 7. Areas used by buffalo herds in Gal Oya National Park. In August (dry season) wild herds to north are concentrated by the reservoir. In March (end of rainy season) wild herds have dispersed, while feral herds remain concentrated in different areas.

small groups disperse more widely into the forest, centering their activity around smaller temporary sources of water.

Sambar in Wilpattu show less of a seasonal trend remaining dispersed in small groups whose activity centers around a villu or other source of water throughout the year. In Ruhunu National Park both species show the same patterns as in Wilpattu but in Gal Oya National Park where the numbers of chital are extremely low compared to the other two parks both species remain dispersed showing only a slight tendency to concentrate around the reservoir in the dry season.

4. The Wild Boar

Boar are, like the buffalo and elephant, highly mobile and tend to parallel those species in their movements. In Wilpattu pigs will move from villu to villu but tend to concentrate their activity around one villu during the dry season. In Gal Oya the boar show a more irregular pattern, moving from bay to bay around the edge of the reservoir and from the open areas to the surrounding forest. They do not, here at least, appear to use specific areas on any consistent basis during either wet or dry season, although there is a definite concentration around the easternmost bays of the reservoir during the dry season. This lack of specificity in foraging or wallowing areas may be related to the comparatively high availability of water relative to the home range size of individual groups.

MOVEMENTS AND THE CONCENTRATION OF BIOMASS

Densities and biomass densities were calculated for Wilpattu by Eisenberg and Lockhart (in press) and for Gal Oya by McKay (in press). In calculating biomass densities, weights for elephants were obtained from Kurt and Nettasinghe (1968) and adjusted for the size distribution of the populations. Weights for other species were taken from Phillips (1935).

TABLE I. DENSITIES AND BIOMASS DENSITIES OF TERRESTRIAL HERBIVORES IN TWO OF CEYLON'S NATIONAL PARKS

	Gal Oya National Park (453 km^2)[1]			Wilpattu National Park (580 km^2)[2]		
Species	Density km^{-2}	Biomass Density kg/km^2	% Biomass	Density km^{-2}	Biomass Density kg/km^2	% Biomass
Elephas maximus	0. 232	405. 0	46.9	0.12	217. 2	29. 1
Bubalus bubalis	1. 119	320.0	37. 1	0.27	73.4	9. 8
Cervus unicolor	0. 540	75. 7	8. 8	1.17	157.9	21. 1
Axis axis	0.656	29.9	3.5	5.84	262.8	35.2
Muntiacus muntjak	*	*	—	0.44	5. 9	0. 8
Tragulus meminna	*	*	—	0. 58	1.9	0.2
Sus scrofa	0. 540	14. 8	1. 7	0.30	8. 1	1. 1
Lepus nigricollis	7.72	17.6	2.0	4. 67	14. 9	2.0
Hystrix indica	*	*	—	0. 58	5.3	0.7
Total		863. 0	100.0		747.4	100. 0

[1] McKay (in press).
[2] Eisenberg and Lockhart (in press).

* Present at very low density.
— Numbers not estimated.

Table I shows the annual average for numerical density and biomass density of terrestrial herbivores in these two parks. While the species composition of the two areas is identical, the relative abundance of species differs markedly. Sambar and chital are more abundant in Wilpattu than in Gal Oya and elephant and buffalo are more abundant in the latter area. Wild boar are slightly more abundant in Gal Oya as are hare. In the case of the hare, this difference is undoubtedly due to the higher percentage of grassland in Gal Oya.

The data presented in Table I represent an overall average which would only be a true picture were the species involved equally and evenly distributed throughout the areas censused. When the movements and resulting concentrations of animals are taken into consideration, the maximum biomass densities are as shown in Fig. 8. For Wilpattu the maximum densities were estimated for an area of 25 km^2 including 3 permanent water holes during the July-September drought period. For Gal Oya the maximum densities were calculated for an area of 10 km^2 including 3 bays of the reservoir. The densities were not, however, all calculated for one particular time period. The maximum densities for all species but the elephant were recorded during the dry season, a time when the elephant is absent from this portion of the park.

Thus at Wilpattu the biomass density in the area censused may reach a level as high as 6930 kg/km^2 during the dry season. In the Gal Oya concentration area the biomass density during the same period reaches a level of 2860 kg/km^2—with the elephant absent. The elephants return to this area during the rainy season and they alone contribute about 2600 kg/km^2 for this period. As the buffalo do not disperse widely in this portion of the park, the biomass density during the rainy season may at times exceed 4000-5000 kg/km^2.

Thus, when the movement patterns of the animals are taken into account, it can be seen that the effective biomass density over any given period of time can be several times higher than would be estimated were one to consider only the total annual situation. The converse is also true in that estimates of density and biomass made during periods of concentration do not accurately reflect the overall distribution on an annual or longer-term basis. In order to estimate accurately the carrying capacity and productivity of an area, as emphasized by Talbot (1964), it is essential to

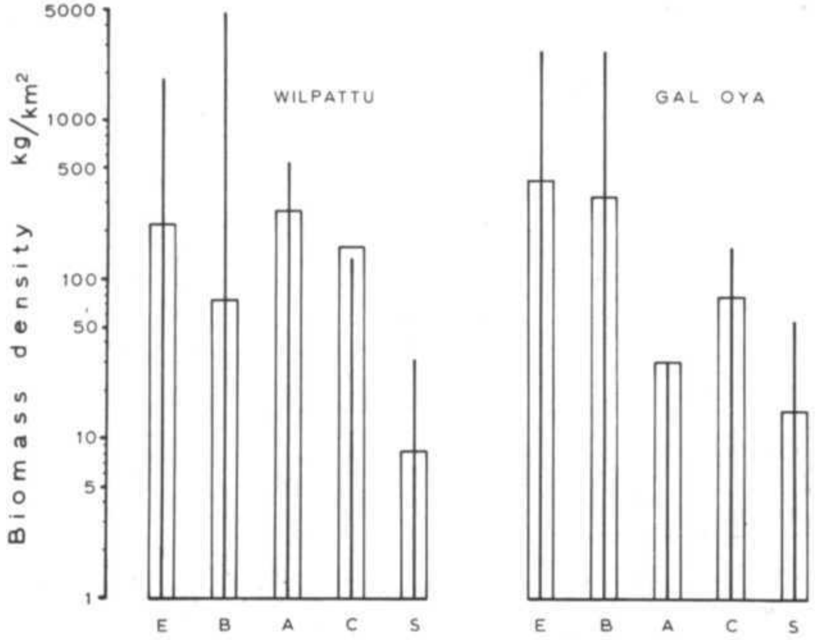

Fig. 8. Biomass densities of major ungulate species in Wilpattu and Gal Oya National Parks, 1968: bars indicate average density; lines indicate maximum concentration.

E = *Elephas;* B = *Bubalus;* A = *Axis;* C = *Cervus ;* S = Sus.

consider both the short term and long term biomass densities. In this way it is possible to arrive at an accurate assessment of the effects of various species on the habitat.

It is unfortunate that most authors give only annual or long-term averages Bourlière and Verschuren (1960) give data from each census along 4 transect lines throughout the period of their study. Even a cursory examination of their data shows that there are not only marked seasonal fluctuations but often rather marked day to day fluctuations especially with regard to highly mobile species such as elephant or buffalo. Perhaps the most complete survey to date is that of Lamprey (1964) which includes monthly estimates over a 4-year period. On the basis of his data, he has divided the species occurring in the Tarangire Reserve into 5 categories, a number of which can conveniently be reduced to 3 major groups: (a) residents, (b) residents with partial dispersal, and (c) migrants.

Another aspect of the study of biomass densities concerns the relative proportions contributed by the different species in the community. From the data presented in Table I and Fig. 8, it is evident that only a small number of the total species are contributing a high percentage of the total herbivore biomass. Table II shows summarized results from a number of studies, giving the number of species which contribute at least 70% of the biomass. In comparing the species compositions of such studies one can see a trend in that mobile species often are among those which contribute most to the biomass. Thus for the Gal Oya study area, the elephant and water buffalo contribute 84%. In Wilpattu the sambar, chital and elephant (two which show a wet season dispersal and one highly mobile) contribute 85% of the average biomass but the elephant and buffalo (both highly mobile) contribute 90% of the biomass in the area of dry season concentration. An examination of the data presented by Lamprey (1964) similarly shows that for his east transect zebra, buffalo and elephant (all migrants) account for 78. 9% of the average biomass. In his west transect these same three species account for only 58. 3% as the giraffe (resident) and impala (dry season dis-

TABLE II. COMPOSITION OF TERRESTRIAL HERBIVORE COMMUNITIES

Region	Total Number of Species	Number Contributing i 70%	Biomass (and %)	Authority
Gal Oya, Ceylon	6	2	(84.0%)	McKay, present study
Wilpattu, Ceylon	9	3	(85.4%)	Eisenberg, present study
Kanha, India	9	3	(89.6%)	Schaller (1967)
Udjung Kulon, Java	6	2	(74.3%)	Hoogerwerf (1970)
Umfolozi, South Africa	18	5	(75.4%)	Mentis (1970)
Tarangire, Tanzania-West	14	5	(83.6%)	Lamprey (1964)
Tarangire, Tanzania-East	14	3	(78.9%)	Lamprey (1964)
Nairobi, Kenya	16	4	(77.2%)	Foster and Coe (1968)

persal) are more abundant there. The same pattern is evident in the data of Foster and Coe (1968) where 55% of the biomass is contributed by 3 highly mobile species: wildebeest, hartebeest and zebra. The somewhat mobile giraffe adds a further 22%.

In discussing the movements of elephants, Buechner *et al.* (1963) (for *Loxodonta*) and McKay (in press) (for *Elephas*) have described the 'seasonal' movements of elephants as a response to proximate conditions of rainfall and food availability. This same pattern appears to be shown by a number of other large ungulates which are major components of herbivore communities. It seems reasonable to assume that the high mobility and the ability to respond to proximate environmental factors rather than be restricted to a rigid annual cycle will be advantageous in areas where rainfall (and thus plant growth) is uncertain and uneven (both temporally and spatially). This will then allow animals, such as elephants and buffalo, which have a high water requirement to maintain high densities in areas that are seasonally arid. It should also be noted that all such species are herd-forming animals. Thus the formation of large herds and, in the case of the elephants at least, a complex social organization will help to facilitate these movements by allowing and promoting the development of traditions. Such traditional use of trails, water holes, etc., is particularly evident among elephants (McKay, in press).

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Paper No. 40

The Development of the Populations of Gazelles in Israel and their Behavioural Adaptations

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ABSTRACT

Two species of the genus *Gazella* occur in Israel, one of them with two subspecies. The subspecific status of the *Gazella dorcas* population occurring in Israel is discussed. Up until now, only four species in all have survived from a former rich fauna of ungulates. Methods for mass-catching of gazelles, which were developed by stone-age men in this area and used until the 20th century, are described, as well as the mass destruction of gazelles with modern arms, which began after the first world war.

The distribution area of *Gazella g. gazella* in Israel is occupied by a dense and increasing human population. The physical and behavioural characteristics of this gazelle, which enabled it to survive under these conditions, even before it was granted protection, are described and discussed, as well as its adaptability. Behaviour and social structure are influenced by surroundings, hunting pressure and population density. In recent times populations of *Gazella g.gazella* have been mainly influenced by human predation (poaching) and pesticides.

The history of the gazelle populations in the southern desert, which comprise two subspecies of *Gazella gazella* and one of *Gazella dorcas,* is described, and their situation there is discussed. These populations, living mainly in level areas, have been much reduced by poaching in recent years, and are also adversely influenced by the bedouin population. Animal predation may also have some influence in this area. In many areas the gazelles are mainly dependent on *Acacia* spp. as a source for food and water during most of the year.

In modern times ungulates, like most other large animals, are able to survive in most areas of the globe only if their populations are protected or managed by man. Species vary in their ability to adapt themselves to changes in the environment and this ability may be critical for their survival. Highly specialized forms which are unable to develop behavioural adaptations are at a disadvantage in the struggle for survival in environments changed by human activities. In this connection, it seems worthwhile to report on the situation of the gazelles in Israel, a country which has undergone intensive development within the last twenty years.

At the present time two species of gazelles, the mountain gazelle *Gazella gazella,* and the dorcas gazelle *Gazella dorcas* (Fig. 1) occur in Israel—the first one with two subspecies, the more common *G. g. gazella* (Figs. 2,3) (Groves and Harrison, 1967; Groves, 1969), and an apparently not yet described desert form.

Ellermann and Morrison-Scott (1951) include Palestine within the distribution area of the Arabian subspecies of *Gazella dorcas, Gazella dorcas saudiya.* The dorcas gazelles of Israel are, however, entirely different from this subspecies and resemble much more the North-East African subspecies *G. d. Isabella.* Apparently the high Transjordan mountain ridge and its steep, rugged western slope, bordering upon the Arava rift valley in the east, separates both subspecies of these mainly plain-dwelling gazelles. Possibly this same mountain ridge has also prevented the penetration of *Gazella subgutturosa marica* into western Palestine. This form had been common in Arabia and Transjordan until the Second World War, but there is little evidence that it ever occurred in Western Palestine. A very old male of this form, which was kept in a local zoo and died at the alleged age of 20 years, was said to have originated from the surroundings of the Dead Sea.

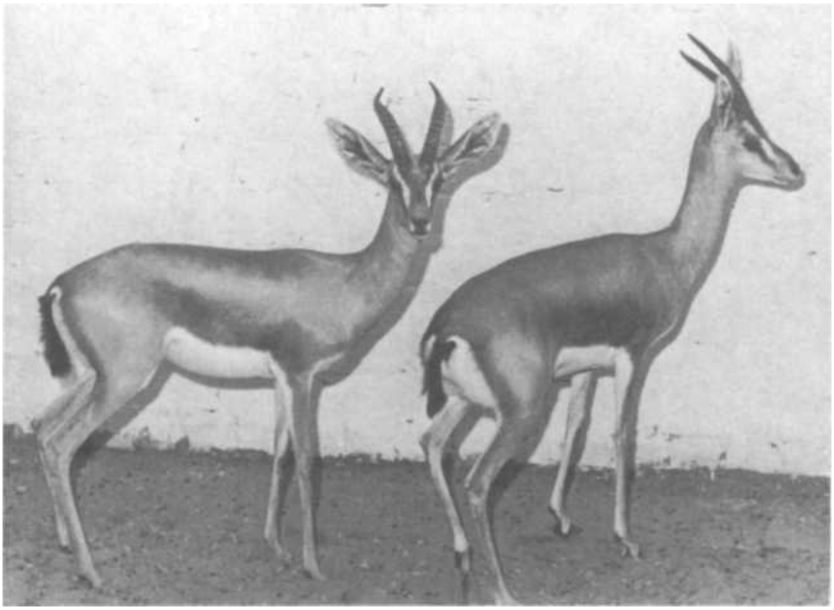

Fig. 1 *Gazella dorcas* (subsp.) from southern Israel male female

Fig. 2 *Gazella g. gazella* male

(Photo. A. Shoob)

Fig. 3 *Gazella g. gazella.* Females on mountain ridge.
(Photo. A. Shoob)

Fig. 4 'Desert kite,' after Yadin (1955).
Three hides, in which perhaps hunters hid, are recognizable in the walls of the smaller enclosure.

The two species of gazelles, together with the wild pig (*Sus scrofa* subsp.) and the ibex (*Capra ibex nubiana*), are the only survivors in this area of a formerly rich fauna of ungulates. Most of these ungulates were exterminated in historical times, the last ones being the fallow deer (*Dama d. mesopotamica*) which existed until the end of the last century (Tristram, 1885) or possibly even until the beginning of the present century, and the roe deer, the last population of which was exterminated on Mt. Carmel at the beginning of the present century (Bodenheimer, 1935; Harrison, 1968).

Of the surviving ungulate forms, three—the ibex, the dorcas gazelle and the desert form of the mountain gazelle—live in the southern desert, where human population is thin, and therefore hunting pressure and competition with livestock have generally been less dangerous than in the northern and central parts of Israel which have been more or less densely populated by humans for many thousands of years. Although in the desert physiological adaptations such as the ability to withstand high temperatures and to survive without drinking water are of decisive importance, in the Mediterranean area behavioural adaptations are crucial as well.

Gazella g. gazella is the only gazelle existing in the northern and central parts of Israel, the approximate southern limit of its distribution being more or less the 150 mm isohyet, which is also the northern limit of *Gazella dorcas*. There is, however, a broad zone where the ranges of both species overlap, and although they generally do not mix, occasionally specimens of both species are seen together.

Gazelles were formerly very common in this area. They were apparently one of the staple foods of stone-age man, representing more than one third of the total meat source during the Pre-Pottery Neolithic A period of Jericho (Bate, 1937;Clutton-Brook,1971).

In other Neolithic settlements gazelle bones were also commonly found. Their importance decreased with the beginning of the domestication of other ungulates, of which especially the goat became the main meat source. In the Pre-Pottery B period of Jericho, gazelles represented only less than 18% of the meat source and by the Middle Bronze period they had decreased to less than 4%.

Apparently during the Chalcolithic period large, triangular shaped corrals were constructed from stones in order to catch gazelles in large numbers (U. Avner, personal communication). These corrals were used by the bedouin in Eastern Jordan until recent times and are called 'desert kites' because of their shape (Rees, 1929): they consist of two walls, several hundred metres to more than one km long, with a distance of from several dozen to several hundred metres between them at one end, whereas at the other end the distance between them is only a few metres. This narrow opening leads into another smaller, closed corral, also surrounded by a stone wall, in which several hides were built or openings left (Figs. 4, 5). In many cases the triangle is directed towards a wadi, and the end extends down the slope of the wadi, so that from the entrance the closed end can not be seen. The latter feature may be important in relation to the keen-sightedness of the gazelles (Fig. 6). In some instances several of these corrals are situated in a row, their broad openings connected with each other, closing a wide stretch of country (Rees, 1929).

These structures were first found in the Syrian desert and in Eastern Jordan, in the area between Djebel Druz and Amman, and south and south-east of Djebel Druz. Recently, similar structures were found in Israel in the southern Arava valley (Meshel, 1968/69) and in eastern Sinai, 30 km north-west of Eilat (U. Avner, pers.

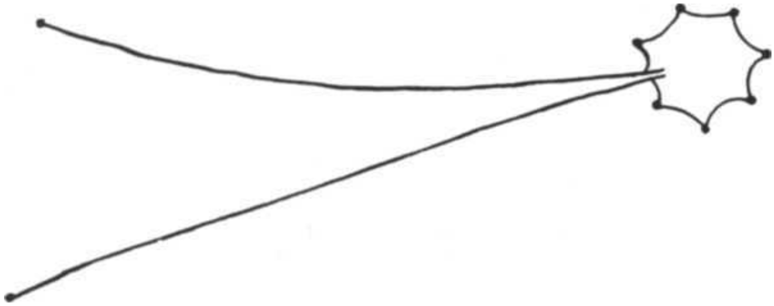

Fig. 5 'Desert kite,' after Yadin (1955). The lower parts of the wall and the trenches into which the gazelles fell, are situated at the tips of the projections of the smaller enclosure.

Fig. 6 Remains of desert kite in eastern Sinai, about 30 km N.W. of Eilat (Photo. U. Avner)

comm.). The desert kites found in Israel and in Sinai are smaller than most of those found in the Syrian desert and in Transjordan (U. Avner, pers. comm.), possibly because the gazelles found in Israel and Sinai, mainly *G. dorcas,* live in smaller herds than *G. subgutturosa,* which was apparently the principal game animal caught in the desert kites east of the rift valley.

The desert kites were interpreted by several authors as corrals into which domestic stock was driven in case of an enemy raid (Yadin, 1955). Meshel (1968/69), however, interpreted them as enclosures intended for trapping gazelles. His opinion is mainly based on a rock-drawing (Fig. 7), discovered in 1953 in the Syrian desert, south-east of Djebel Druz (Harding, 1954), illustrating the herding of animals, probably gazelles, into such enclosures, and on a description by Aharoni (1946), who witnessed the catching of gazelles in such a corral at a time when they were still plentiful in this part of the world. Aharoni's description is so vivid that it seems worthwhile to quote the relevant part of it, translated from Hebrew. No date is given, but circumstantial evidence points to the year 1915.

'Once I made a four-day excursion into the desert with Baron von Wirtenau in order to observe the migration of gazelles. We observed them with binoculars and saw innumerable flocks, one after the other. Our estimate was that we saw more than 10, 000, all of which were returning from north to south. They start their migration in herds of thousands, and the bedouin know this time well and hunt them during the migration.

'I and Y. Hankin, my hunter and reliable companion in my desert travels, witnessed once a shocking spectacle, when 500-600 gazelles were trapped in a corral not far from Racheimah (East Jordan). The length of the corral which we saw was several km. and there are many of them in the desert. I asked several bedouin we met when these structures were erected and all of them gave the same answer: "In old times. The fathers of the fathers of our fathers already found them."

'In order to trap several hundred gazelles at once, the bedouin enclose a large triangular area which extends over many km. In the wall, which is higher than a man, are places which are lower, and before each one a deep trench is dug. When the bedouin saw a migrating flock of gazelles, they drove them from all directions into the broad opening of the corral. The gazelles were not afraid, as the walls, built from desert stone, were similar to their surroundings. When several hundred gazelles had entered the corral, the bedouin closed in on them, running from left and right, shouting ferociously. Then the frightened gazelles tried to escape, jumping over the wall at the lower parts of it, and fell into the trenches outside of them. We saw how many of them were pulled out of the trenches with broken limbs and their bleating in agony was heart-rending. The bedouin, however, were not impressed by the suffering of their victims and cut their throats before they died. Then they loaded the gazelles onto their camels, brought them to their camp, skinned them and salted the meat.'

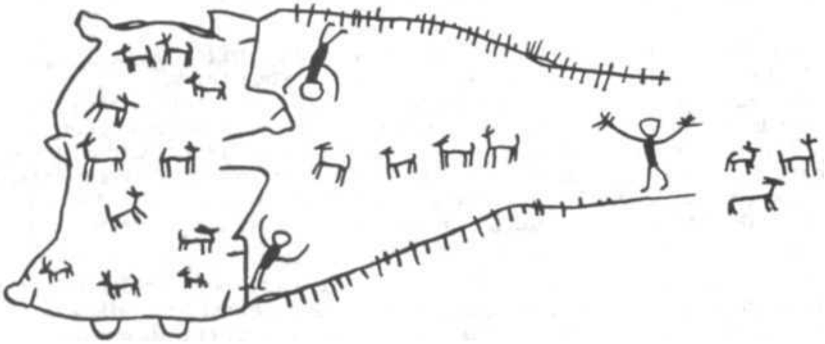

Fig. 7 Rock-drawing of gazelles being driven into desert kite. After Harding (1954)

Fig. 8 Members of Transjordan frontier corps with 10 *Gazella subguttorosa marica, shot* during a mechanized mass-shooting in 1942, east of Amman, near Amman-Bagdad road.

(Photo. M. Gertel, courtesy of G. Ilani)

In other cases the gazelles were perhaps killed inside the end-corral, from places in the walls which are interpreted as hides in which the hunters hid (as shown in Fig. 4).

Aharoni's description, which probably deals with *Gazella subgutturosa marica* which was very common in the desert plains of Transjordan, gives an idea of the former abundance of gazelles. Other descriptions of gazelle hunts in this area, using these stone enclosures, are given by Musil (1928) and by Burckhardt (1831), the latter quoted in Rees (1929).

The human predation described by the above authors, which apparently went on for a long time, did not, however, affect the abundance of the gazelles. Tristram (1885) described them as 'the only large game which is really abundant', for Western Palestine as well.

The survival of gazelles became endangered when, with the First World War, modern rifles became available to the local population in large quantities. The shooting of large numbers of gazelles with automatic weapons from desert-going cars (Fig. 8), after running them down or while dazzling them at night with the headlights, was especially disastrous for the species living on the plains—*G. subgutturosa, G. dorcas* and the desert form of *G. gazella.* The populations of *G. g. gazella* inhabiting the plains were exposed to the same danger, whereas the populations of this form living in hilly country, while also suffering from the constant hunting pressure, were better able to survive.

In 1924, the Mandatory government of Palestine enacted a 'Game Preservation Ordinance' which, besides not being adequate considering the situation of wild life in Palestine, was not enforced at all. The following paragraphs of this ordinance concerned gazelles:

'Game Preservation (Gazelle) Proclamation

(Cap. 64, section)

(1st March, 1924).

1. This proclamation may be cited as the Game Preservation (Gazelle) Proclamation.
2. (1) Gazelle shall not be hunted in any part of Palestine by any person unless he is holder of a licence to hunt game.
   (2) The holder of a licence to hunt game may kill only one male gazelle of each species.'

As three species of gazelles are mentioned in this ordinance, doecas gazelle (G. *dorcas*), desert gazelle (G. *arabica*) and Carmel gazelle (*G. merrili*), this meant that every holder of a licence could shoot three gazelles every year. Towards the end of the mandatory government, however, the number of gazelles surviving in Western Palestine was already much smaller than the number of people holding hunting licences.

Besides this, the game preservation ordinance was largely unknown, even to government officials and the police force, and policemen and members of the Transjordan Frontier Corps used their cars and weapons freely for shooting gazelles (Fig. 8). Descriptions of such shootings were communicated to the author by several people who took part in them between the years 1930 and 1945 in the Syrian and Transjordan deserts. In many cases only parts of the shot animals, generally the thighs, were taken. After such intense and wasteful slaughter there were few surviving gazelles by 1963 (Mountfort, 1965) in Eastern Jordaa

In Western Palestine the situation was no better. Already by 1933, only a few, scattered mountain gazelle populations had survived in the northern and central parts of this country, and they decreased from year to year. The main reason for this decline was that notwithstanding the above-mentioned regulations, everybody who felt like it shot any gazelle on sight. Also, fawns that were found were taken to be reared as pets. Most of these fawns died sooner or later, or developed poorly; in any case, fawn-collecting added to the decrease. By 1940, gazelles were already so rare that the increasing demand for pets could not be satisfied by the local mountain gazelles, and fawns of *Gazella subgutturosa* were imported from Irak, which were sold for from 10 shillings to one pound sterling.

The mountain gazelles survived mainly in hilly country, in areas with low human population density, and in the areas of some Jewish agricultural settlements, where they enjoyed a certain degree of protection. The scattered gazelle populations were not able to develop the social structure as they did afterwards. The most common social groupings observed were single animals, females with fawns, pairs or pairs with a fawn, or rarely and generally in areas where they were not molested, groups of five to, at the most, eight specimens, consisting of one adult male, females and young. These groups lived generally in hilly country in small areas of about one square km, where they would be observed repeatedly, unless they were discovered by hunters. Maturing young males were apparently expelled from the area by the adult buck, as no males older than 15 to 18 months were seen in these groups. No bachelor herds were observed at that time, and only occasionally were 2 to 3 males seen together.

The smaller social units—single animals, females with fawns and pairs—were seen also in areas where there was no protection whatsoever, and in many cases they apparently lived a nomadic way of life as they could not be found continually in the same area. Observation of these gazelles was difficult, however, because of the great flight distance of 700 to 1,000 metres which they had adopted. Perhaps the flight distance was even longer as it is possible that in many cases they perceived the observer before he saw them.

During this period the mountain gazelles underwent a very heavy selection for caution and long flight distance and possibly also for physiological adaptatioa Mountain gazelles drink regularly if water is available. However, they also inhabit areas where no water is available at close range, and where water is found, access to it may be dangerous or impossible because of human occupation. Little is known so far about the water metabolism of the mountain gazelle, but in a preliminary experiment an adult female of 18 kg survived during the summer, exposed to the sun at air temperatures between 24 and 32°C, on airdry food. She was watered once in four or five days, when she would drink 2 to 2½ litres. When water was withheld but a half Kg of succulent food was given daily in addition to the dry food, she did well, and when she was offered water after one month she drank only 200 ccm. Gazelles would easily be able to collect 0. 5 kg of succulent food in most areas they inhabit, even during the dry summer and autumn. As they start feeding before dawn, even dry plants, eaten then, have a high moisture content. Gazelles prefer to rest during the hot noon hours in the shade of trees, if available; but even if no shade is available, most of the radiant heat is reflected by the smooth, glossy summer coat.

Mountain gazelles have several other attributes and adaptations which made their survival possible, notwithstanding the constant and heavy hunting pressure. The English name indicates that this species, contrary to all other gazelles, inhabits mountainous areas. In areas where they are now common, their trails stretch also along steeply inclined slopes of 45°, or even steeper (Fig. 9). Like red deer (Darling, 1937) they prefer to manage the slopes by walking up and down obliquely, but it is astonishing to see how the gazelles, when hard pressed, rush surefootedly along steep slopes at full speed, or run up steep inclines. In this respect they are real mountain ungulates (Fig. 3). However, they avoid stepping on rocks and prefer to walk or run between them; they only walk over rocks if there are flat rock expanses. They jump down terraces which are about 1 m. high; they only jump upwards if they can look over the terraces. Captive specimens easily learn to climb steps but they have some difficulty in going down steps and prefer to jump down, if the flight is not too long. *Gazella subgutturosa* and *Gazella dorcas* have great difficulty in managing steps. Mountain gazelles also inhabit level country. This was shown when, after hunting pressure was discontinued and populations increased and expanded, they spread into the plains. The mountain gazelles prefer open country with some trees and shrubs; however, they also inhabit treeless semi-desert and, on the other hand, open woods. Large areas in Israel are planted densely with Aleppo pines (*Pinus halepensis*). Gazelles pass freely through these dense woods which lack any undergrowth, and use them for shade. On steep, rocky slopes where the pines are not planted so densely and undergrowth survives, gazelle herds may live permanently. They enter orchards and vineyards and cause damage by browsing on saplings and grapevines. Tracks and droppings have even been found in openings in dense Mediterranean shrub forest.

Fig. 9 Trails of *Gazella g. gazella* on mountain slope.
(Photo. A. Shoob)

Fig. 10 Mountain gazelle resting in dug-out form.

The mountain gazelle is very resistant to climatic conditions. Considering related species, it is comprehensible that they do well in the hot and dry Jordan valley. They withstand equally well, however, the low winter temperatures and the cold winter rains in Upper Galilee. Here they live in areas where, during January the average temperature is 6-8°C; at night there are often sub-zero temperatures and snow occasionally covers the ground for several days. Most of the 600-800 mm rainfall occurs during the cold winter months. However, no mortality caused by climatic reasons has been observed. Gazelles may use places protected from rain, such as projecting rocks etc., if available, but are generally exposed to rain. They seek, however, places protected from wind for resting and generally bed down near rocks, bushes etc., on the side protected from wind, in gullies or at least in depressions in the ground, which they may make deeper by digging with the forefeet, in order to obtain maximum protection from the wind while resting (Fig. 10).

Eyesight is excellently developed and gazelle orient themselves mainly according to this sense. Even tame gazelles react at distances of 1 km and more to moving animals, humans and cars. Stationary, strange objects are perceived and sometimes observed for a long time. Stationary humans are also perceived and sometimes stared at for some time before the gazelles take flight. Their eye-sight in the dark is, however, much poorer than during the day, this fact perhaps being the reason for their mainly diurnal activity.

The adaptability of the mountain gazelle to new situations is considerable. They learned to live with fences and get through them by crawling underneath—an interstice of about 20 cm or even less between the ground and the fence being sufficient. They are able to jump well, for stotting gazelles jump occasionally 1 m high and panicked ones even higher, but they very rarely jump even low fences. They can easily pass through the 30 cm interstices between the barbed-wire strands of cattle fences, stopping short and climbing through, but when in full flight they pass through almost without stopping. Only in very rare cases have gazelles been wounded on such occasions. They are adept at locating easy passages through fences. Females seem to be more inquisitive than males, and more interested in occurrences in the surroundings.

Mountain gazelles are also adaptable in their food habits; they graze and browse and feed on a very great variety of plants, generally feeding in a goat-like manner, so that several or even many different species are found in their stomachs. Occasionally they feed mainly on one species, mostly in monoculture fields of cultivated plants. When browsing they tend to stand on their hindlegs in order to reach higher branches much less than the dorcas gazelle (see Fig. 14). They have certain food preferences, but few plants are rejected altogether. Even some plants which are poisonous and not accepted by most herbivores, such as Solanaceae, oleander (*Nerium oleander*) and leaves of the fig (*Ficus carica*) are eaten. A preferred food-plant is the grass *Cynodon dactylon,* a common weed. Occasionally, mountain gazelles dig with the front feet in order to feed on the rhizomes of this grass.

Mountain gazelles react promptly to alterations in hunting pressure by changing their flight distance. The existence of poaching in an area is distinctly reflected in the behaviour of the gazelles. They distinguish well between dangerous and non-dangerous objects. In many cases gazelles are not disturbed in their normal activities by tractors working in the fields but keep a long distance from jeeps which are generally used by poachers.

The reproductive capability of the mountain gazelle is not very high, as only one fawn is born. Normally, the first fawn is born when the dam is two years old. However, a percentage of the females, so far unknown, produce the first fawn already at the age of one year. Possibly the number of early-maturing females depends on environmental conditions. In one sample of 79 females checked during the main fawning season there were 26 one-year-old females, of which 19 were pregnant or suckling, and 53 females two years old or older, of which 45 were pregnant or suckling. In this population, therefore, the larger part of the young females were already active reproductively. A number of cases are on record, of gazelles in captivity as well as in nature, where suckling females were already pregnant again, so that they produced two fawns in one year. It is still not known how often females in nature bear two fawns in one year.

Fig. 11 Two mountain gazelle fawns laid up in the same hide.

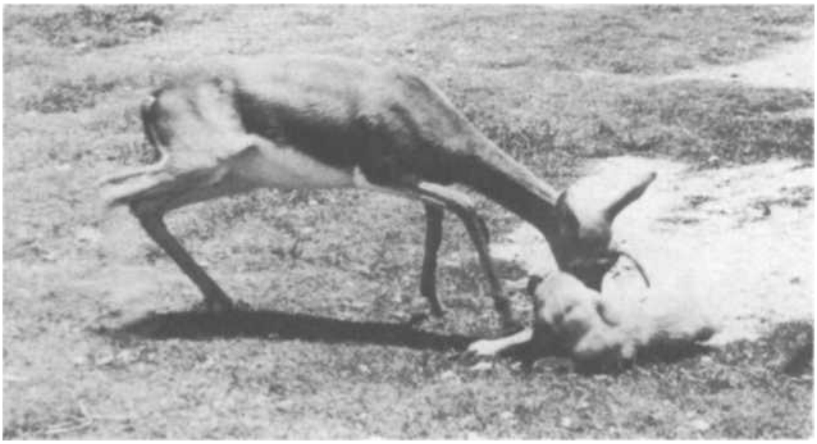

Fig. 12 Nursing mountain gazelle attacking small dog.

The fawns spend several weeks in hiding and begin to accompany their dams only when about one month old. The young fawns are strongly attracted to dark places, and this tendency leads them to well-hidden places among high vegetation, in dense shrubs, between rocks etc. Occasionally two fawns may use the same hide (Fig. 11). Fawns are also found in open fields, if born there; and are even then not easily seen because of their protective coloration. Nursing females tend to be more aggressive than usual and may well be able to defend their fawns against small predators (Fig. 12). Fawn survival seems to be good. If a young fawn is lost, the dam generally becomes oestrous. This accounts for a certain spreading of fawning. The main fawning season is April-May, but fawns and pregnant and suckling females have been recorded in every month. Dispersal of fawning seems to be more common in areas with irrigated agriculture. In the research zoo of the Tel-Aviv University it has been found that nursing females still fawn on an average once in nine and a half months (65 cases).[1] As pregnancy is six months, and as the fawn is weaned at three months, it seems that females, under good feeding conditions, become oestrous soon after the fawn is weaned. All these facts indicate that the mountain gazelles are able to increase reproduction under favourable environmental conditions.

It was probably the versatility and adaptability of the mountain gazelles which enabled them to survive in a densely settled country, notwithstanding the relentless hunting pressure. However, their numbers have decreased continually (Maps la and lb). These maps are not based on counts, but only on rough estimates obtained from observations and records of tracks and droppings. Information received from local inhabitants was used only as a basis for investigation since it was found to be unreliable in many cases.

It was equally difficult to estimate the number of mountain gazelles surviving at the end of the Mandatory government in 1948. Certainly not more than 500 survived, but possibly their number was much smaller—even as few as 300. Large areas, especially the plains, were at that time void of gazelles. This decrease in the gazelle population was concomitant with an increase in the human population: the latter growing from about 1,200,000 in the years 1933-35 to about 1,800,000 in the years 1946-48, the larger part concentrated in northern and central Palestine, the distribution area of the mountain gazelle.

The situation changed with the foundation of the State of Israel. Because of demographic alterations, the number of hunters and poachers decreased considerably in the area of Israel and as a first step towards the enacting of a new 'wild animal preservation law' all hunting was forbidden for one year. Hunting of a number of species, including gazelles, remained entirely forbidden. The 'wild animal preservation law', enacted in 1955, affords complete protection to most species of wild mammalsand birds, including all gazelles, so that gazelles were legally protected as from 1948. Only where gazelles caused damage to agriculture have permits to shoot gazelles been issued. As this practice encouraged poaching, the gazelles that cause damage are now shot by rangers of the Nature Reserves Authority (established in 1964). The carcasses of these gazelles are generally used for research.

Species with high reproductive capabilities, such as the wild pig (*Sus scrofa*) and the chukar partridge (*Alectoris graeca*) soon responded to the discontinuation of the hunting pressure in 1948 and as early as 1950 a remarkable increase was noted. The mountain gazelles soon responded by a decrease in their flight distance, but, because of their lower reproductive capability, were slower to respond by an increase in their populations. They did respond, however, in due course. The small, isolated remnant populations increased and spread and gazelles appeared in areas where for dozens of years none had been seen. They also spread to the plains and now live in entirely flat country. Mountain gazelles are now found in most areas of northern and central Israel, and even not far from Tel-Aviv. They are only absent from the most densely settled areas of the coastal plain and none or very few are found in areas inhabited by Arabs and Druzes, apparently because of poaching. The increase of mountain gazelles was most conspicuous between the years 1950-1965. It has slowed down in recent years, mainly because of increased poaching, for the growing gazelle populations stimulate human predation. The number of licensed hunters is small in Israel. In 1970, 2, 500 permits were issued, of which 65% went to Arabs and Druzes and 35% to Jews and members of the Diplomatic Corps (report for the year 1970/71 of the Nature Reserves Authority). The number of poachers, who are, however, mainly occasional, is probably larger. Poachers of gazelles are not numerous, but their effect on the gazelle populations is conspicuous and is soon recognized by the increase in the flight distance and the decrease in the population concerned. In 1969, three poachers were arrested by rangers of the Nature Reserves Authority; in 1970 eleven, and during the first 6 months of 1971 eight. These numbers may indicate an increase in

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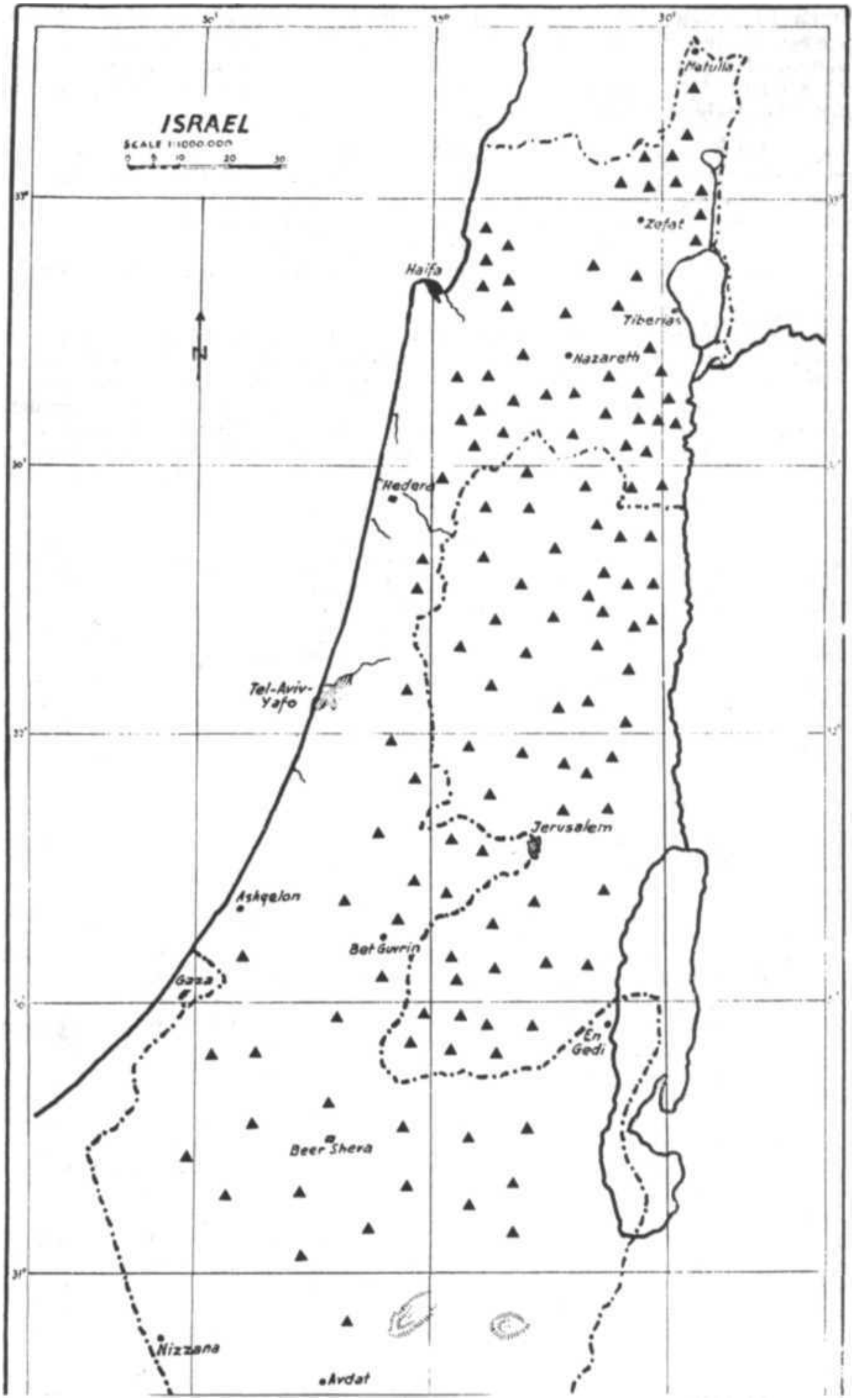
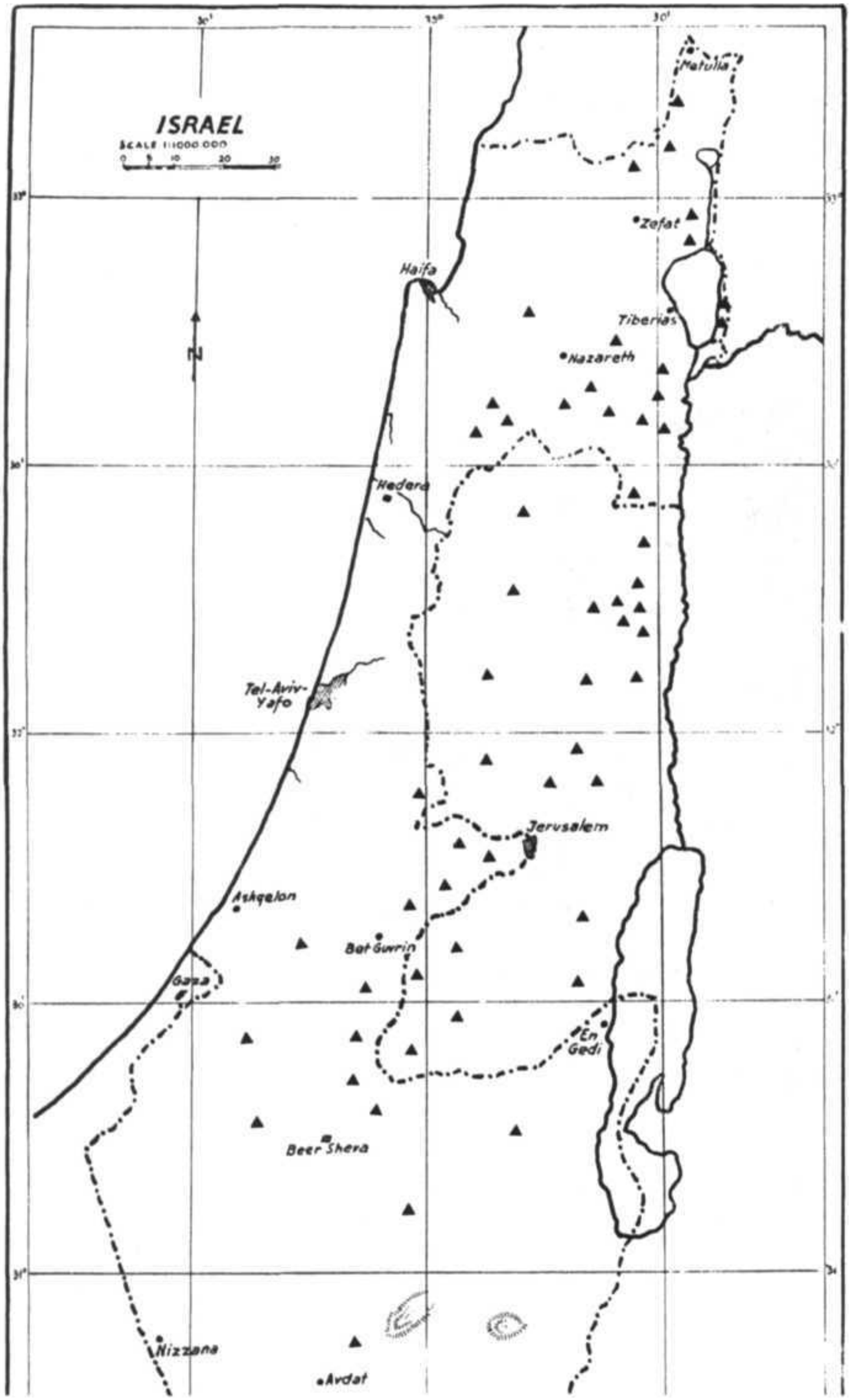
[1] Successive births were spaced from 6 to 19 months. In many cases females became oestrous soon after parturition.



Map 1a. Distribution of *Gazella g. gazella* in Western Palestine, 1033-35.
▲ = about 10 gazelles.



Map 1b. Distribution of *Gazella g. gazella* in Western Palestine, 1946-48.
▲ = about 10 gazelles.

poaching as well as the increasing efficiency of the rangers dealing with the poachers. Unfortunately, only small financial fines (the largest so far was equivalent to $100) are imposed by the law-courts for poaching of gazelles and only in a few cases are the weapons confiscated (U. Tzon, pers. comm.).

In most cases observed, females were the pioneers of the expanding gazelle populations. Single females or females with fawns were generally the first to be observed in formerly gazelle-free areas. As females before parturition separate from the herd, this behaviour pattern may be the cause of their invading new areas. Besides, females are more inquisitive than males, as has been found from observations of the herd of mountain gazelles kept at the research zoo at the Tel-Aviv University. This zoo is surrounded by a high wall and inside the door is a wire-netting door in order to prevent the animals from leaving the compound. If the door is left open, females have often been observed standing near the wire-netting door and watching the activities going on outside (Fig. 13). This behaviour has never been observed in males, which display much less interest in matters that do not concern them directly.

Fig. 13 Inquisitive female mountain gazelle in the research zoo of the Tel-Aviv University.

Gazelle populations expanded at a pace of up to three km per year. In some cases, expansion rates of five km per year have been recorded, but possibly in some of them gazelles that had not been observed earlier were already present in the area.

The present distribution of mountain gazelles is shown in Map 2. The areas indicated by numbers in this map are those in which counts of gazelles have been carried out in recent years, and the numbers of gazelles counted are indicated with the years in which the count was carried out.

Based on these counts, which were carried out only in relatively small areas, the population of mountain gazelles on the whole could be conservatively estimated to amount to at least about 3, 000 specimens.

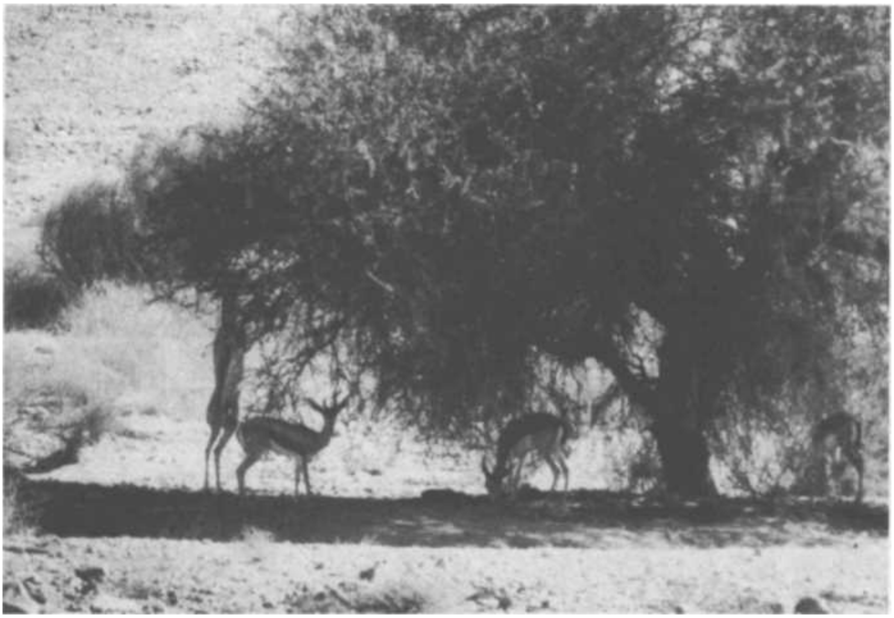
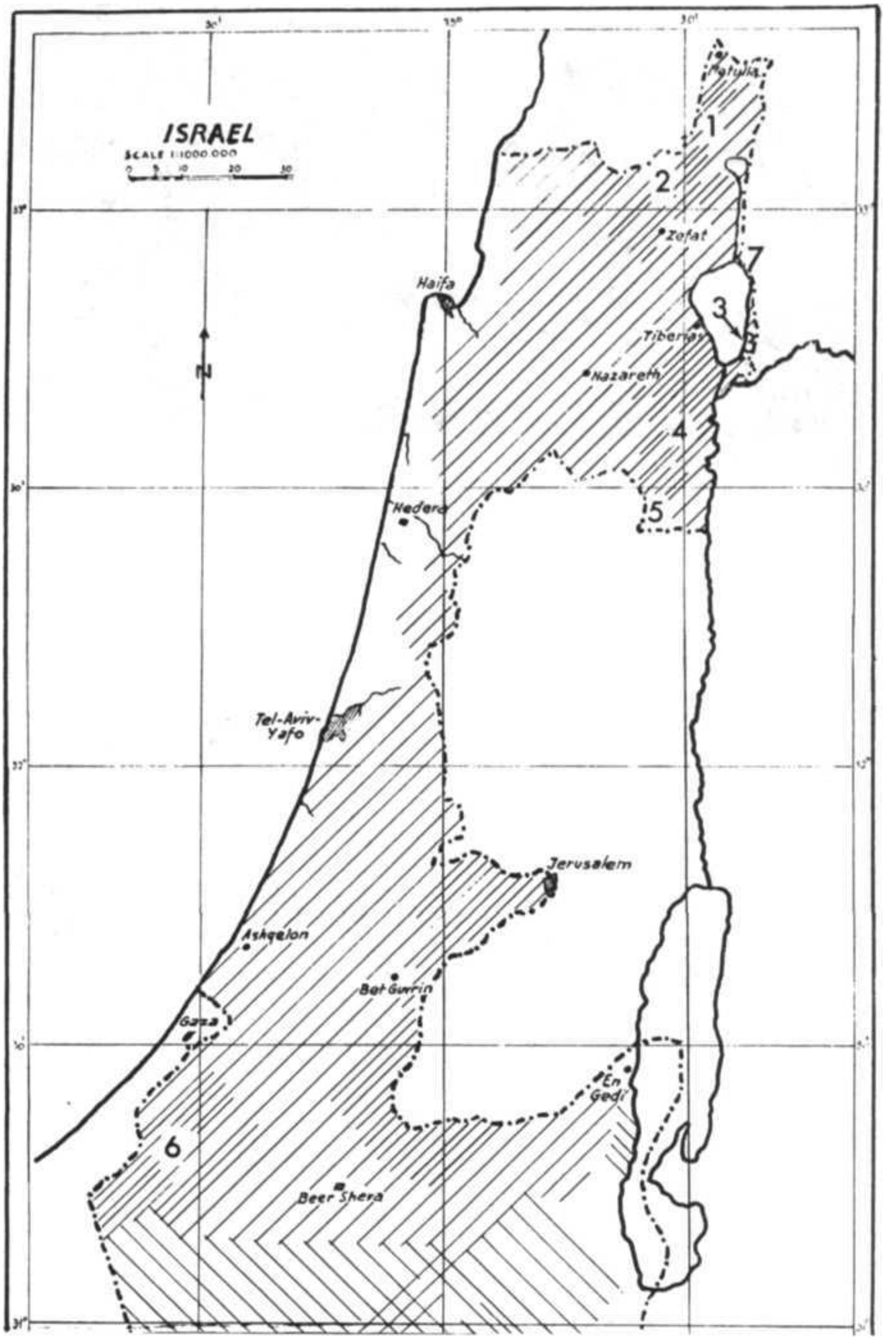


Fig. 14 Family of *Gazella dorcas,* adult male, two females and young buck under *Acacia tortilis* tree in the Arava valley. The adult male browses, standing on the hind legs, the females collect seed-pods from the ground. (Photo. and courtesy of P. Merom)

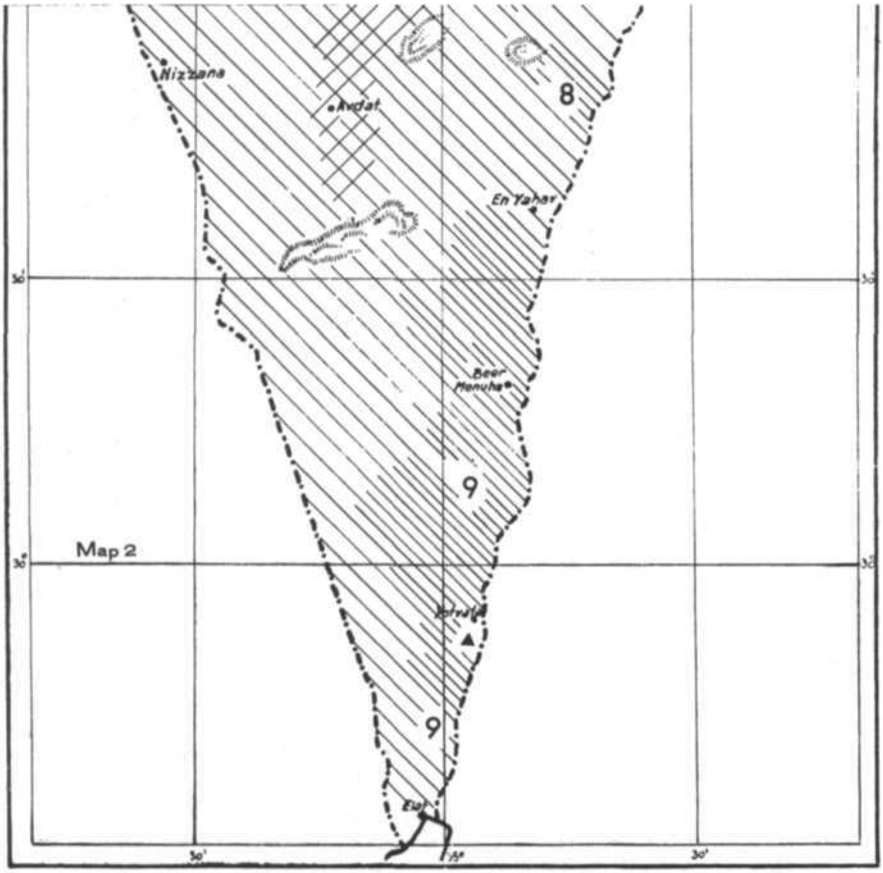
Whereas during the time of the Mandatory government human population increased and mountain populations decreased, both populations increased after 1948. The human population is now more than 3, 000, 000, almost all of which live in the northern and central part of Israel. This area is also inhabited by the mountain gazelle and the human density in these areas is almost 300 per sq. km. Notwithstanding this dense human population, mountain gazelle populations are still increasing. Of course, this increase is most conspicuous in areas with lower human concentrations.
In recent years mountain gazelles have again demonstrated their tendency and ability to expand their distribution. After the six-day war of 1967, they began to appear in areas of Western Jordan and Golan (formerly Syria), which had been without gazelles because of overhunting. Gazelles appeared at first in areas close to the borders of Israel and are penetrating further from year to year.

With increasing population density, the social structures of the mountain gazelles have changed and become similar in many respects to that of *Gazella thomsoni* and *G. granti* as described by Walther (1964, 1965, 1968). Territorial males, the flight distance of which was in many cases much smaller than that of the rest of the population, established themselves. Bachelor herds and female herds appeared: small ones in the beginning, later larger ones. In an area in which a high population density (an average of 17 per sq. km) was reached, bachelor herds comprising up to 70 males and also large female herds were observed. Here also mixed herds of males and females were observed more often than in areas with smaller populations. In areas with a more broken landscape of small valleys and steep slopes with a denser cover of shrubs and trees only small bachelor and female herds are found. Polygamous groups are seen more often in this kind of biotope, possibly because the home range of female herds is small, influenced by landmarks, and is identical with or overlaps the territory of a territorial male. Nevertheless, there seems to be a certain connection between the male and the females, because in many cases they are seen continually together.

With increasing gazelle populations the damage caused by gazelles to agriculture has increased as well. This damage is occasionally considerable, and as the moun-



Map 2. *Distribution of gazelles in Israel in recent years.*



(a) *Gazella g. gazella*
(b) *Gazella dorcas* subsp.
denser hatching indicates areas with denser populations
(c) ▲ *Gazella gazella*-desert form
(d) The numbers indicate areas in which counts have been carried out. The approximate size of the areas, the year in which the counts were carried out and the numbers of gazelles counted are given below. A possible error of about 10% should be taken into consideration.

1	75 sq. km.	(1968)	269	*G. g. gazella*
2	45 sq. km.	(1966)	82	" " "
	110 sq. km.	(1968)	212	" " "
3	20 sq. km.	(1968)	176	" " "
4	90 sq. km.	(1967)	1355	" " "
		(1970)	1487	" " "
5	40 sq. km.	(1968)	223	" " "
6	350 sq. km.	(1966)	256	" " " + 5 *Gazella dorcas*
7	To this area about 350 *G. g. gazella* were transplanted from area 4 in 1970 after the count had been carried out			
8	200 sq. km.	(1966)	52	*G. dorcas*
		(1971)	114	" "
9	2000 sq. km.	(1964)	292	" " (incl. about 35 *Gazella g.* subsp.)
		(1965)	275	" " " " " " " "
		(1966)	314	" " " " " " " "
		(1971)	468	" " + 32 *Gazella g.* subsp.

Counts by courtesy of U. Paz and G. Ilani, Nature Reserves Authority.

tain gazelles are omnivorous feeders, no crop is safe from them. A grazing herd, passing over a newly planted vegetable field, feeding on the young plants, makes it necessary to plant the whole field again. Young cereals and young cotton plants are among their favorite food plants and severe damage may be caused. In orchards and citrus groves trees may be severely damaged and even killed by the hornrubbing of males. So, notwithstanding their low average population density of only one mountain gazelle per 3 sq. km in that part of Israel inhabited by them, the absolute protection granted them by law has been called into question time and again by farmers.

Life in agricultural areas is, however, not without dangers for the gazelles. Animal predation is rare and human predation occurs mainly only in areas with a high population density of gazelles. Pesticides, however, take their toll. Many gazelles have been poisoned by rodenticides (thallium sulphate, fluoracetamide) which are applied in Israel excessively (Mendelssohn, 1971a). Gazelles are able to collect single grains from the ground, and are therefore easily poisoned by ingesting poisoned grain. In an experiment on rodent control in an area of 12 acres, exactly 10 wheat grains poisoned with a fluoracetamide solution were distributed per sq. m, and three dead gazelles were found the next day. Occasionally, farmers or pest control officers poison gazelles on purpose by distributing heaps of poisoned grain in the fields. More than 50 gazelles have been poisoned in this way in one day in one place. Despite the legal protection for gazelles, such cases have not been prosecuted. As mountain gazelles living in agricultural areas are exposed also to insecticide pollution they carry high levels of organochlorine residues. Levels between 2. 9 and 89. 7 p.p.m. have been found in their body fat (D. Ben-Shaul, pers. comm.). Mortality by all these pesticides may be high. A ranger of the Nature Reserves Authority found within one year in his area of about 100 sq. km, 23 dead gazelles (Palti,pers. comm.).

In those areas of Palestine which belonged to Jordan after 1948, overhunting apparently continued, for very few mountain gazelles survived there until 1967, and those only in desert areas south-east of Jerusalem. Even chukar partridges and doves were found to be extremely rare in western Jordan. In a very good mountain gazelle area, Wadi Faria,east of Nablus, where a gazelle population of at least several dozens still existed in 1945, none were found to survive in 1967.

In the southern desert (the Negev), the development of the gazelle populations was different from that in the northern and central part of Israel. Originally gazelle populations in this area were probably large, as indicated by the already mentioned presence of stone enclosures used for catching gazelles in the southern Negev and eastern Sinai. Little is known about the gazelle populations in this area during the time of the Mandatory government. Their flight distance was very high, about one km, indicating an intense hunting pressure. This hunting pressure was exerted by the bedouin as well as by the police force, many members of which were recruited from bedouin tribes. The northern parts of the Negev have a higher rainfall and therefore a higher population density of bedouin than the southern parts. Therefore in the northern areas gazelles were rarer and apparently nomadic, evading the wandering herds of the bedouin.

Even today an inverse relationship exists between gazelle and bedouin populations. In areas occupied by bedouin, gazelles are rare or absent; they increase in areas evaluated by bedouin, if no other form of poaching exists. Their disappearance in areas occupied by bedouin may not be solely due to poaching, which is difficult to control in bedouins, but also because gazelles avoid the presence of livestock. Even tame gazelles, used in the field for studying grazing and browsing behaviour, become extremely nervous even at a distance of several hundred metres from herds of cattle or sheep.

In the Arava valley, extending between the Dead and the Red Seas, and in the southern Negev, rainfall is 50 mm or less. The bedouin population there was therefore less dense and occupation in many cases periodical, as these areas were visited only temporarily with herds of camels and goats which browsed on halophytic shrubs and acacia trees. In these areas acacia trees (*Acacia tortilis, A. spirocarpa*) grow in plains and valleys which receive the run-off from adjoining slopes. Because of the low bedouin population density and the less severe competition with livestock, more gazelles were found here than in the northern Negev. *Gazella dorcas* as well as the desert form of *Gazella gazella* inhabit mainly plains and broad valleys and are rarely found in hilly areas. The broken ground inhabited in the north by the mountain gazelle, is used in the Negev by the Nubian ibex *(Capra ibex nubiana)*.

In areas with acacias the gazelles depend mainly on them; they browse on the leaves and twigs and collect the seed-pods which drop from the trees. Part of the browsing is done in *Litocranius* (gerenuk)-like fashion, standing on the hindfeet (Fig. 14). Gazelles in the Negev apparently do not feed on halophytic plants. They seem to be independent of water, even in areas without acacias, for they are found in areas where no water is accessible to them. In areas with acacias they tend to be resident, as has also been found in Africa (Brouin, 1950).

The reproductive season of the gazelles in the Negev is more restricted than in the north. Fawns are mainly born from March to May. So far it is not known if females of the desert gazelles are also able to produce fawns when one year old. Among the behavioural differences between dorcas gazelles and mountain gazelles, it is worthwhile mentioning the fact that in the former the fawn is laid up for a much shorter period and follows its dam at a much younger age than in the latter. This behaviour may have survival value in surroundings where the dam may have to move over large areas in order to feed.

It is possible that there is animal predation on gazelles in the Negev, for wolves (*Canis lupus pallipes*) and caracals (*Felis caracal schmitzi*) occur. Gazelles entering narrow valleys in order to feed on acacia trees, as they occasionally do, may be exposed to predation by leopards (*Panthera pardus nimr*). Animal predation does not, however, influence the gazelle populations in the desert conspicuously. Human predation, on the other hand, has been much more decisive. As in the north, so also in the Negev the gazelle populations declined during the time of the Mandatory government. It is difficult to estimate how many survived at the time of the foundation of the State of Israel in 1948, but their number was probably not more than 500 to 600. During the war of 1948, many of the bedouin emigrated and therefore hunting pressure was considerably reduced; but on the other hand, soldiers of the Israeli army had begun to shoot gazelles in the Negev during the war in 1948, and continued to do so after the war. The gazelles in the Negev, therefore, did not enjoy the protection afforded to the gazelles in the north by the above-mentioned prohibition after the foundation of the State of Israel.

The poaching was even worse than that done formerly by bedouin, as the gazelles were chased with cars and shot down with automatic weapons. Therefore, a group of conservationists applied to the army authorities, and in 1951 all hunting in the Negev was forbidden to the army personnel. This prohibition worked well. The gazelle populations increased and their flight distance decreased so much that by 1956 it was possible to see gazelles in some areas at distances of several dozen metres from the road, quietly browsing or resting. By 1956 their numbers had increased to an estimated 1, 500-1, 800. In the very favourable area of Hazeva, south of the Dead Sea, about 500 gazelles lived in an area of about 100 sq. km., about two-thirds *Gazella dorcas* and one-third the desert form of *Gazella gazella.*

After the war of 1956, however, extensive poaching by army personnel, mainly in the higher ranks, began again. Cars and machine guns were freely used and in the beginning large numbers of gazelles were killed because of their small flight distance. The flight distance increased quickly, indicating the changed situation. The intensive slaughtering of gazelles in the Negev at that time can well be compared to what went on in other countries of the Near East (Talbot, 1959). Whole areas were almost or completely depopulated. Eventually gazelle populations were reduced to approximately the same level as in 1948. For some unknown reason the desert form of *Gazella gazella* was hit by this poaching much harder than *Gazella dorcas,* and few of them survived. For instance, in the surroundings of Hazeva, where these gazelles had been common, apparently none survived. Possibly *Gazella gazella* reach a lower maximum speed than the lighter-built *Gazella dorcas* and are therefore more vulnerable to hunting by cars.

The social structure of the desert gazelles deteriorated in these dispersed, harassed populations, as had been the case with the mountain gazelles.

The established tradition of gazelle poaching continued until eventually the then Commander-in-Chief was approached, and he prohibited poaching by army personnel in 1965. This prohibition proved to be effective. Recovery of gazelle populations was, however, much slower than after the discontinuation of poaching in 1951, and some formerly well populated areas are still void of gazelles. This may be due to the several successive drought years which occurred during this period, as well as to the revival of poaching in recent years.

A number of counts were carried out in the years 1964-71 in the southern Negev (see Map 2), indicating a slow increase.

What are the prospects for the future of the two gazelle species in Israel ? It is evident that their existence depends on the attitude of the people towards them. The experience of the past, as well as experience in the surrounding countries and experience with other ungulates in other parts of the world, have clearly shown this fact. In Israel, animal predation is negligible compared with human predation. Legal protection is important but poaching seems to be increasing, perhaps because the law-courts do not impose deterrent penalties.

Although the number of poachers seems to be small, the damage caused by each of them or by a group of them in destroying and dispersing gazelle populations is considerable. Control of poaching is difficult because offenders have to be practically caught red-handed. Control of poaching is especially difficult among the bedouin population, which, like some other sectors of the population, has no understanding whatsoever of conservation and whose attitude has been aptly described by Talbot (1959). The Nature Reserves Authority does not plan to issue permits for cropping surplus gazelles as the supervision of legal hunting would also be difficult and permitted hunting might stimulate poaching.

Poaching, however, is not the only danger threatening gazelles. Although gazelles are popular with the public in general, they are not so with those farmers whose crops are damaged by gazelles, for the damage may be considerable. Fencing of orchards with gazelle-proof fences has begun in some places only recently. It has been found, however, that mountain gazelles quickly learn to use gates left open. Occasionally, irate farmers try to poison gazelles and have unofficially been encouraged to do so by certain pest control officers. Grain poisoned with endrine or with fluoracetamide is used for this purpose and since gazelles collect even single grains from the ground, this method is successful.

As gazelles do much feeding on cultivated plants, they ingest considerable amounts of pesticides, the residues of which are found in their tissues, as has already been mentioned. These amounts were also found in gazelles shot by rangers of the Nature Reserves Authority for research purpose in an area which is largely natural pasture. As gazelles are attracted to agricultural crops, part of them had probably fed in orchards, cotton and vegetable fields. Mortality from pesticide poisoning occurs, as has already been mentioned, but so far has not endangered the existence of the gazelles. Few gazelles are run over on roads, as they are reluctant to approach them.

As it is the declared policy of the government to establish agricultural settlements in the desert, the problem of gazelle damage and of pesticide pollution will become more acute there too.

If all these factors are considered together, the future of gazelles in Israel may still be regarded as safe. It will not be possible, however, for their population to reach a density comparable for instance to that of the roe deer in Central Europe.

As a conservation measure, in 1970 the Nature Reserves Authority transplanted about 350 mountain gazelles from the Ramot Yissakhar area, south-south-west of the Sea of Galilee, to the Yahudiya area, north-east of this lake (Map 2 area 7), a distance of about 80 km. The Ramot Yissakhar area has the densest gazelle population in Israel, about 1, 500 having been counted there in February of 1970, in an area of about 90 sq. km. The Yahudiya area, on the other hand, as well as the whole of the Golan, was found to be entirely void of gazelles in 1967. This transplantation has been criticized because of possible differences between the gazelle population of Ramot Yissakhar and the one surviving in the area south-east of the sea of Galilee, the latter of which began, after the six-day war in 1967, to expand towards the Yahudiya area. On the other hand, the establishment of additional populations may be considered of advantage in safeguarding endangered populations.

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Paper No. 41

Seasonal Changes in the Feeding Behaviour of Barren-ground Caribou on the Taiga Winter Range

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ABSTRACT

Barren-ground caribou populations in Canada remained stable during the past decade following a marked decline. The Kaminuriak caribou population was chosen for a study of whether the capacity of the taiga winter ranges limits caribou populations and of what effect wildfires have on this capacity.

Caribou feeding patterns on the taiga were adapted to forage availability which changed with depth and hardness of snow. As forage availability changed during early, mid- and late winter and spring periods, caribou responded by moving to more suitable pastures. Caribou concentrate on sedge and horsetail forage in early winter; terrestrial forage in protected tree cover during mid-winter; arboreal in the presence of a sun crust in late winter; and terrestrial on bare hillsides and exposed flats in spring. Forage near treeless areas where caribou could escape wolves was favoured in mid- and late winter. The diversity of cover types is partly maintained on the taiga range by wildfires. A complete snow cover protects forage supplies at any one site against heavy use. In spring, however, forage supplies were depleted by caribou on sites from which the snow first disappeared. Correlation of daily and seasonal caribou feeding patterns with measurements of snow depth and hardness, and use and availability of forage illustrated the pertinence of behaviour observations in the assessment of range capacity.

INTRODUCTION

The barren-ground caribou population in Canada was estimated at 30, 000, 000 shortly after the turn of the century (Seton, 1912). The 3, 000, 000 proposed by Hoare (1927) and supported by Clarke (1940) may have been a more realistic figure. Initial surveys, however, placed the figure at slightly over 600, 000 in 1949 (Banfield, 1954). A serious decline in numbers was suggested by a second series of aerial surveys during the winter of 1957-58 when less than a quarter million caribou remained (Kelsall, 1960). A dramatic population decline had apparently occurred. Reasons given for the decline included over-harvest, predation, several years of high calf mortality due to inclement weather at calving time and forest fires on the taiga. No firm conclusions were reached. The caribou decline tapered off after 1958, but no substantial increases were indicated by surveys 10 years later (Parker, 1971). The caribou failed to increase in response to hunting restrictions and wolf control. It appeared that other aspects of caribou ecology restrict population increases and this prompted an intensive caribou investigation.[1]

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[1] In 1966, the Canadian Wildlife Service in co-operation with governmental agencies from Manitoba, Saskatchewan, Alberta and the Northwest Territories initiated an intensive 3-year study of the ecology of the Kaminuriak barren-ground caribou population. This investigation of the taiga winter range relationships was one phase. Three others included movements, distribution, mortality and population surveys by G. R. Parker; age and sex structure by F. L. Miller; and physical condition and reproductive performancy by T. C. Dauphiné, Jr.

My part in this investigation was to determine the role of the taiga winter range in the ecology of the Kaminuriak caribou population which normally winters in northern Manitoba and northeastern Saskatchewan. Most of my effort was devoted to the measurement of abundance and distribution of forage plants and their use by caribou. It became evident, however, that the relationship of snow cover to foraging behaviour of the animals was an important aspect of the problem. That relationship is the subject of this paper.

Taiga winter ranges have been studied in Canada (Pruitt, 1959 and Scotter, 1968), Alaska (Skoog, 1956, 1968), Sweden (Skuncke, 1963), Finland (Helle, 1966) and Russia (Andreev, 1954; Sablina, 1960 and Karaev, 1961). Lichens have generally been considered as the primary winter forage in North America whereas in Eurasia, sedges (*Carex* spp.), horsetail (*Equisetum* spp.) and evergreen shrubs, as well as lichens, are forages important to reindeer. Evergreen shrubs are important winter forage of woodland caribou in Newfoundland (Bergerud, 1971). The emphasis on lichens in discussions of the winter diet of barren-ground caribou prompted Scotter (1964) and Kelsall (1968) to comment on the limited capacity of the taiga, especially as affected by wildfires, to support large caribou populations.

METHODS

Data presented here were collected during field studies in early April 1966; mid-January to early March, and late November to mid-December 1967; and during the second half of February and mid-April to early May 1968. The winter season was divided into four periods based on progressive changes in the depth and hardness of snow: (1) The early winter period from when caribou entered the taiga in late October or early November until snow depths in open canopy conifer stands reached 50 cm, which is within the range of snow depths (50-60 cm) at which caribou begin to have trouble walking (Pruitt, 1959). (2) The mid-winter period from when caribou movements were restricted by snow depths of more than 50 cm until a sun crust formed in undisturbed, semi-open conifer stands. (3) The late winter period from when sun crusts formed until bare spots appeared in the snow cover. (4) The spring period from the appearance of bare patches until caribou left the taiga.

I used a spotting scope and binoculars to observe caribou behaviour. I measured snow depths in various cover types and used a snow penetrometer to measure hardness. Fences were built around sites of intensively used feeding craters to prevent further use. Individual craters within the enclosures were marked with tripods of poles. Three crater enclosures were built in mid-winter, 1967, and four during each field trip in early, mid- and late winter, 1967-68. Rumen samples were collected from caribou killed in November and in April during each winter from April 1966 to April 1968.

I observed and measured the capacity of the range to support caribou during summer seasons from 1966 through 1970. At crater enclosures I observed how the forage had been used and watched its recovery. Ground cover and standing crop of terrestrial lichens were measured on 25 unprotected plots (25 × 5 m) and in six fenced plots (32 m square) on taiga winter range. I measured the percentage of lichens in the ground cover with a 50 × 20 cm Daubenmire frame (Daubenmire, 1959) at 20 randomly located quadrats within each unprotected plot. Dry weight of the standing crop of lichens was determined for each plot using 20 randomly located 1 dm^2 divots extracted with a brass, circular sampler. Lichens were separated from other material in the divot sample, dried and weighed on a Mettler H6T electric balance. Ten quadrats and ten divots made up the sample from each fenced plot.

RESULTS

Feeding Behaviour and Movements

Early winter

After the rut, caribou entered the taiga in several waves from the north and northeast (Parker, 1970). They frequently migrated on frozen lakes and streams although they were not usually restricted by deep snow on land until mid-December. By December 13, 1967, I measured snow depths of 50 cm in open and semi-open stands (Fig. 1). The snow was deep along shores of lakes and streams while shallower snow was measured in dense conifer stands where snow accumulated on branches.

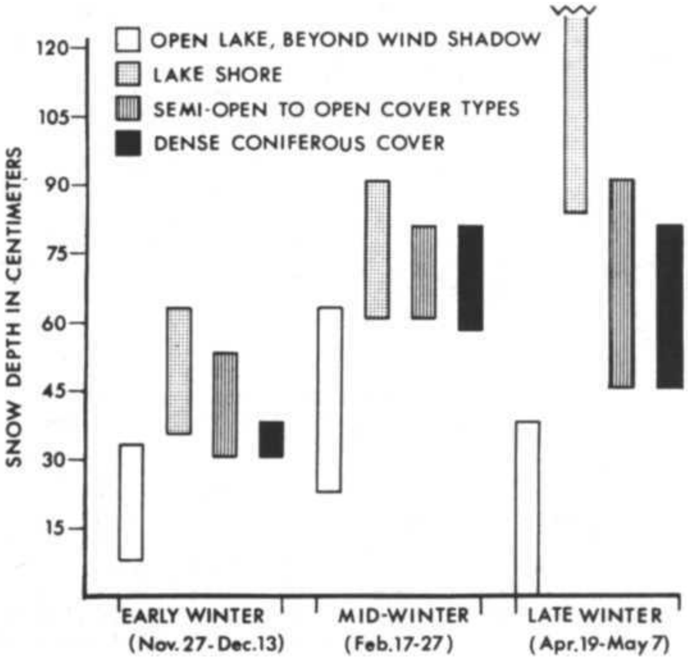

Fig. 1 Range of snow depths measured in four broad cover types within the distribution of the Kaminuriak caribou population during the early, mid- and late winter periods of 1967-68.

Caribou migrated most frequently in early morning and at dusk although major migrations continued throughout daylight hours and into the night. The momentum of major migrations occurred during clear, cold periods. Migrational movements were not observed when temperatures remained above — 18°C (0°F). In 1967, major migrations were observed at the end of November and again after December 11 (see Fig. 4 on p. 748).

In early winter, caribou fed most consistently at dawn and in late afternoon. During feeding periods singles, pairs and small bands were distributed over large areas through various types of cover and topography. They regrouped on lakes and streams in early morning and at dusk. Although caribou fed extensively on terrestrial lichens and low shrubs they appeared to concentrate on water sedge (*Carex aquatilis*) and water horsetail (*Equisetum fluviatile*) stands located on alluvium along shores and shallow bays. Caribou fed consistently at those sites in late afternoon despite the formation of a hard crust from repeated use (Figs. 2 and 3).

No agonistic behaviour was observed at sedge and horsetail feeding sites. Individual animals occasionally dug feeding craters side by side but they were not observed grazing in the same crater. On one occasion I watched eight caribou dig 15 craters during a 20-minute period.

Except for intensive use of sedge and horsetail stands, caribou grazing was widely distributed. Sedge and horsetail plants were not permanently damaged by the intense use. Grazing of the terrestrial lichens was light and widespread. Caribou remove the entire lichen podetia when feeding and the overall reduction of lichens in marked craters was not measurable. Caribou browsed and trampled on *Ledum groenlandicum*

Fig. 2 A heavily cratered site where caribou foraged on *Equisetum fluviatile* and *Carex aquatilis* in January.

(Photo. D. R. Miller)

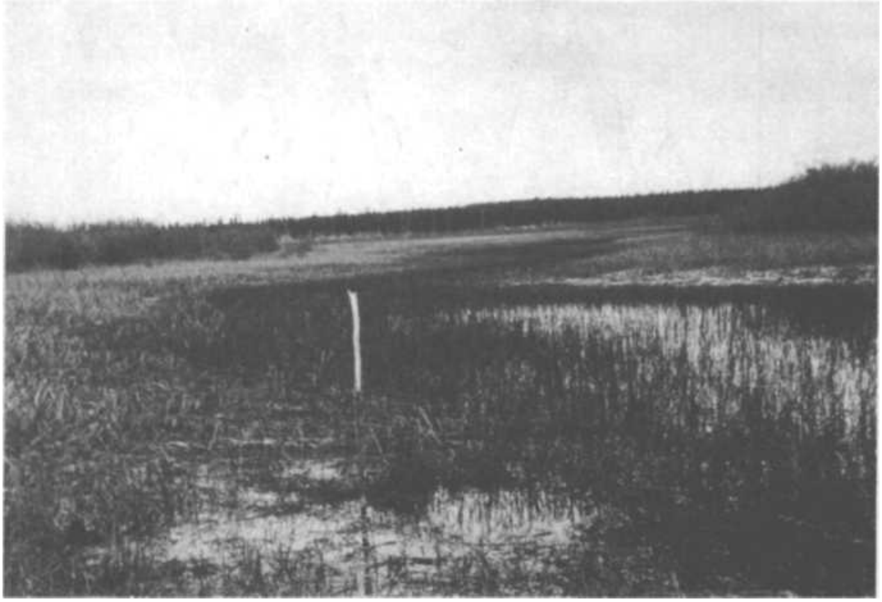

Fig. 3 A lush stand of *Equisetum fluviatile* in the main channel bordered by *Carex aquatilis.* The stake marks location of a square metre sample of *Equisetum* that measured 115 grams dry weight (1150 kg/ha). Fig. 2 above was photographed from the far shore as seen here.

(Photo. D.R. Miller)

plants but usually only the leaves were removed. The terminal buds were rarely damaged and new leaves appeared during the next summer. Mountain cranberry (*Vaccimium vitis-idaea*), bog billberry (*V. uliginosum*), velvet-leaf cranberry (*V. myrtilloides*), leather leaf (*Chamaedaphne calyculata*) and black crowberry (*Empetrum nigrum*) were lightly browsed.

Mid-winter

The feeding habits and movements of caribou were restricted to forest cover types when snow depths exceeded 60 cm in treeless and sparsely treed areas. The accumulation of deep snow along lake and stream shores and in wind shadows made forage in such sites unavailable. In February 1967 and February 1968 (Fig. 1), snow depths of 60 to BO cm were measured on lake shores. The variation between snow depths in open canopy and closed canopy cover types was much less in mid-winter than it had been in early winter. Accumulation of snow on evergreen branches was not as common during mid-winter as early winter, no doubt because of more frequent high winds.

In mid-winter caribou movements did not vary in relation to temperature fluctuations, as they had during early winter. Temperatures remained below —18℃ between mid-January and March 1. 1967, and caribou migrated steadily during dusk of the coldest days. During the second half of February 1968, however, they also migrated steadily despite temperatures which varied between —43℃ and —4℃ (—46°F and 25°F) (Fig. 4). In 1968, the aggregations of caribou were larger and the migration continued throughout the day with no apparent increase in intensity at dusk.

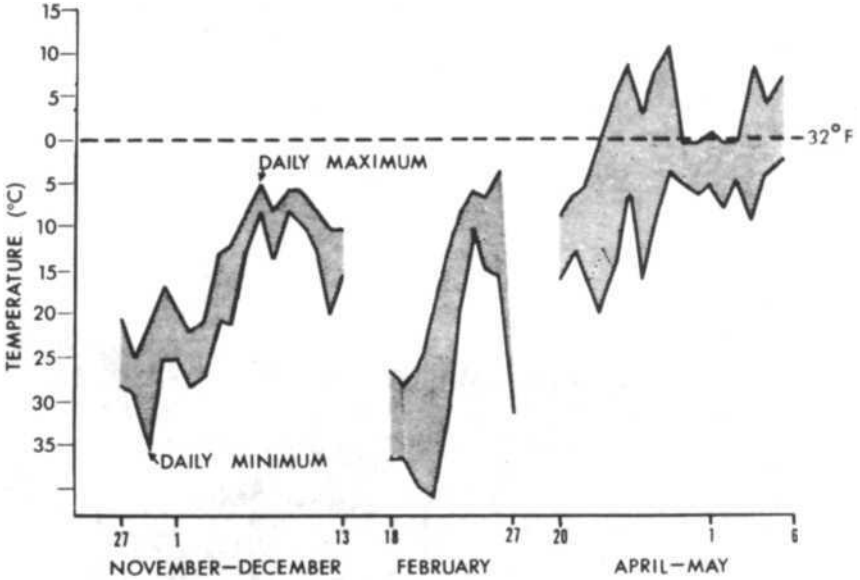

Fig. 4 The daily range of temperatures recorded within the distribution of the Kaminuriak caribou population in the taiga during the early, mid- and late winter periods of 1967-68.

Caribou feeding behaviour in mid-winter underwent a gradual transition from that of early winter. As snow increased and crusts formed on exposed sites from the effects of wind, caribou foraged more in treed areas, especially in semi-open conifer stands. Less use of sedge and horsetail stands occurred, evidently because they were less available. Caribou foraged in larger bands as snow depths restricted movements. Observations of singles and pairs decreased as snow depth increased during mid-winter of both 1967 and 1968. The most conspicuous behavioural change, however, was the concentrated use of forage supplies close to lakes, rivers and other treeless areas. Relatively little use was made of forage supplies farther than about a kilometer from such areas even though snow conditions were favourable. In 1967, when the main caribou band continued migration into new areas throughout the mid-winter period, they foraged close to the migration routes along bogs and fens as well as lakes and streams. In 1968, when caribou migrated in a circular fashion during mid-winter, they foraged close to the lakes and streams over which they travelled. Presumably, proximity to treeless areas is a form of protection against predators. Terrestrial lichens constituted the forage most used in mid-winter with leaves and twigs second in importance (Figs. 5 and 6).

Fig. 5 Trail of caribou band during mid-winter in deep soft snow, showing muzzle depressions made in search of forage (arrowed) and subsequent cratering activity (top righthand corner).

(Photo. D. R. Miller)

When movements were restricted by snow conditions caribou bands functioned more as single units, especially in flight. The animals fed, moved and rested together. In forested areas it was very difficult to approach a band without causing it to flee to a treeless area. There, caribou were much more tolerant of men, dogs and wolves than in forests but still reacted as a band.

Between early winter and mid-winter the area of range used was greatly reduced. Measurements of the physiological condition of caribou, however, showed no evidence of nutritional deficiency (Dauphiné, 1970). Later examination of sites utilized in mid-winter showed that they had been grazed lightly. The snow cover had protected individual stands against heavy use.

Late winter

Snow characteristics on treeless sites changed dramatically in late winter. In 1968, snow depths on lake shores reached 200 cm and more, while those in forests changed little from mid-winter (Fig. 1). On lake ice and southern exposed banks sun crusts formed and broke down, and snow depths diminished rapidly.

In the late winter period of 1968. temperatures fluctuated in clear weather from about 9°C (48°F) during the day to about –21°C (–3°F) at night (Fig. 4). The fluctuations were less pronounced during cloudy days. Caribou utilized arboreal forage supplies when it was cold and terrestrial forage when warm. Arboreal lichens and twigs of

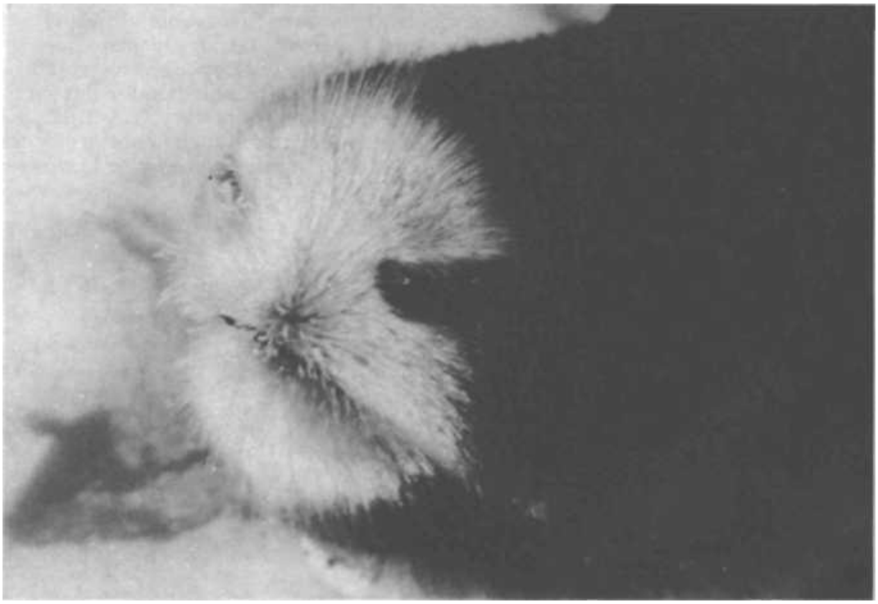

Fig. 6 Densely haired caribou muzzle which permits the animal to extend its nose into soft snow with a minimum of compacting effect.

(Photo. D. R. Miller)

willow (*Salix* sp.), birch (*Betula* sp.) and alder (*Alnus crispa)* were major forage items during the late winter. Terrestrial lichens and evergreen shrubs were used mainly at midday when the crust was modified by thermal radiation at exposed sites. Bands remained as units during movements to and from feeding sites. No antagonism was observed between foraging caribou during this period. However, close observation of animals feeding on arboreal lichens was not possible.

During late winter caribou greatly reduced arboreal lichen supplies close to treeless areas. Some deciduous shrubs and trees on the shores of lakes and streams were also quite heavily browsed but they largely recovered during the following growing season.

Spring

The appearance of patches of bare ground on exposed southern slopes and banks and at former feeding craters was accompanied by a sudden change in caribou feeding patterns. Caribou concentrated on these bare patches and fed on terrestrial lichens and evergreen shrubs. These exposed forage sites were repeatedly utilized.

Movements of caribou to and from forage sites were no longer band activities. Individuals occasionally left and returned to resting sites. Immature animals, in particular, foraged long after other members of the band had returned to rest on the lake ice. It was much easier to approach caribou foraging at inland sites in spring than during the winter seasons.

At inland sites, threat displays and antler clashes were common between caribou attempting to feed at the same crater. By contrast, on the bare banks of lakes and eskers caribou foraged side by side without exhibiting any antagonism.

Later examination of enclosed feeding craters showed that the use of terrestrial lichens and evergreen shrubs on southern exposed banks, eskers, ridges and flats during the spring period had been intense. The forage plants were damaged by repeated use and trampling. The effect on terrestrial lichens and evergreen shrubs was still apparent two years later. Fortunately, caribou usually spend only a few weeks in the taiga after bare patches appear in the snow cover. Most of the damage to forage supplies on these southern exposures occurs along main corridors of the spring migration to the tundra calving grounds.

Caribou-wolf interactions

I usually observed wolves close to areas occupied by caribou. In early winter wolves did not appear to influence caribou movements: no kills or tracks of pursuits were observed. In mid-winter however, when snow depths restricted movements of caribou, they travelled more in bands and remained close to treeless areas presumably in response to wolf harassment. Wolf kills, tracks of pursuits and cripples from wolf attacks were observed during mid-winter especially in February 1968, when caribou were relatively sedentary. Caribou-wolf interactions reached a height during late winter 1968, when wolves killed an average of three caribou per day during an 18 day period at one 20-square-mile lake (Fig. 7). Most of those kills occurred on the lake at night or in early morning, and according to tracks in the snow, many of the attacks originated in tree cover. Although we spent little time searching inland, seven out of 147 caribou that we found killed by wolves were off the lake within 100 m of shore. These observations suggest that caribou feeding patterns during mid- and late winter and spring were largely determined by the need to detect and escape wolves.

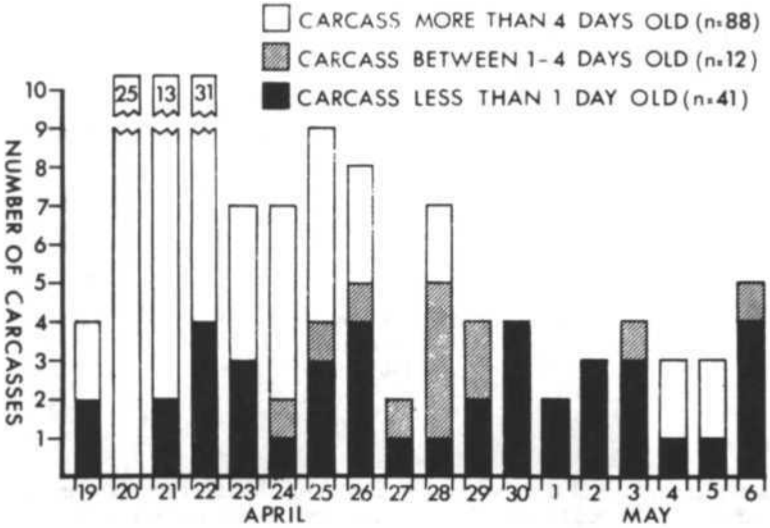

Fig. 7 Number of wolf-killed caribou carcasses, according to the estimated time of kill, found daily at Hara Lake, Saskatchewan between April 19 and May 6, 1968.

Rumen analyses

Rumen analyses from November and April samples showed a predominance of lichens in the diet during the early and late winter periods (Fig. 8). Leaves and twigs were important components in the winter diet during both periods while grass and grass-like plants were important only during early winter. The results of the rumen analyses were consistent with observations of feeding behaviour.

Terrestrial lichen reserves

Measurements of the standing crop of terrestrial lichens in caribou winter range on upland and lowland conifer stands revealed substantial reserves of forage. This was true of both fenced and unfenced plots. However, standing crop measurements are not an indicator of the capacity of the range to support caribou without corresponding information on availability of the forage to caribou and the importance of terrestrial lichens in seasonal diets. Large quantities of terrestrial lichens, especially with high proportions of the climax species *Cladonia alpestris* and *C. rangiferina*, suggest that many of these lichen stands are protected from caribou use by snow cover.

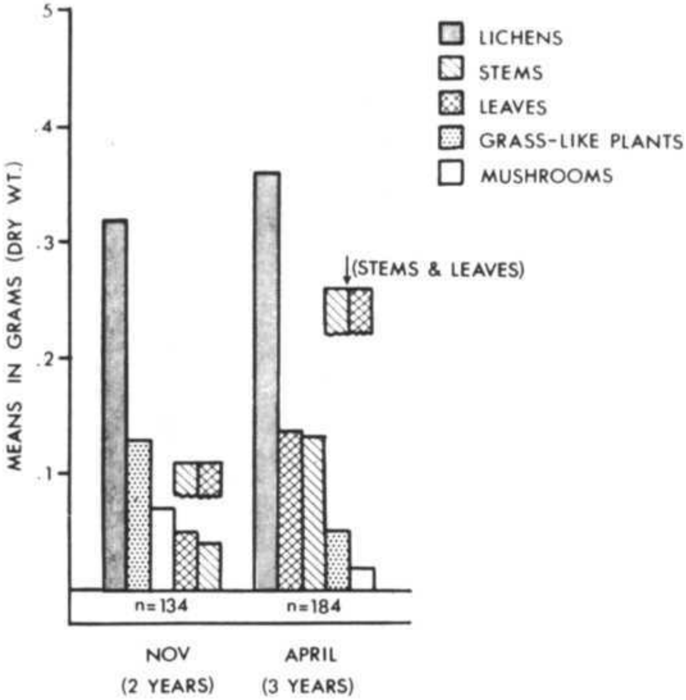

Fig. 8 The relative quantities of the five major forage items found in caribou rumens collected regularly in November and April from April 1966 to April 1968.

DISCUSSION

Caribou make efficient use of forage resources by using different habitats and plant species in different snow conditions. Concentrated grazing on snow-free sites in spring when serious depletion of forage may occur, appears to be an exception. However, annual changes in migration routes and of winter ranges used tend to guard against greatly reducing productivity of lichens on exposed sites.

Wildfires play a role in maintaining the heterogeneity of habitats and plant species which caribou require under different conditions of snow cover.

Snow and its effect on forage availability determines the use which caribou make of the taiga range. Formozov (1946) showed the importance of snow in the ecology of mammals and birds, and Nasimovich (1955) showed the role of snow in the life of ungulates in the U.S.S.R. Pruitt (1959) demonstrated some relationships of snow to the winter ecology of caribou, and Henshaw (1964) showed how wintering caribou responded to major climatic and nival factors in northwestern Alaska. This study adds to the earlier investigations by illustrating how caribou adapt their food habits on the taiga in response to seasonal changes in the snow cover.

A general sequence of caribou feeding pattern responses to varying snow conditions can be illustrated for what is considered as an average winter in the Taiga (Table 1). The range of modifications to this guide of forage use is as variable as annual changes in precipitation, temperature fluctuations, wind and caribou densities. Time sequences for any one season are also variable between winters and in some winters

TABLE 1. GENERAL CARIBOU BEHAVIOUR AND FORAGE USE RELATIONSHIPS CORRELATED WITH PERIODIC CHANGES IN THE SNOW COVER ON TAIGA RANGES

Season	Snow Condition	Movement*	Social behaviour when foraging	Forage sites most used	Forage groups most utilized
Early winter	Shallow and soft, < 50 cm	M	Scattered in small bands, members (other than doe-fawn pairs) independent	River and lake shores Open canopy	Sedges, horsetails, lichens and shrubs
Mid-winter	Deep and soft, > 50 cm	M or S	Medium-sized bands, members dependent	Open conifer canopy close to treeless areas	Terrestrial lichens and evergreen shrubs
Late-winter	(a) Deep, sun crust	S	Large bands, members dependent	Open and closed conifer canopy close to treeless areas	Arboreal lichens and deciduous shrubs
	(b) Depth diminishing, alternate crust and no crust condition	S	Medium-sized bands, members dependent	Open canopy close to treeless areas	Terrestrial lichens and evergreen shrubs
Spring	Appearance of bare patches	M	Scattered in small bands, members independent	Open canopy on southern exposures	Terrestrial lichens and evergreen shrubs

* M—Mobile, bands migrating S—Sedentary, bands not migrating

a whole season, especially mid-winter as described, may not occur. This extreme variability of winter environments in taiga ranges and the associated adaptability of caribou to these environmental changes ensures a scattered distribution of forage use that minimizes chances for damage of any one forage source or any one segment of the taiga. Forage availability is the key to caribou use of forage supplies on taiga winter ranges and Table 1 shows the general pattern of this use as related to seasonal changes in snow cover characteristics.

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Paper No. 42

The Question of Polygamy at an Unbalanced Sex Ratio in the Moose

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ABSTRACT

During normal conditions there may be about 55-58 percent males in the secondary sex ratio of moose, but usually a heavier hunting pressure on the bulls causes a predominance of females in hunted populations. In some high-density areas in Alaska extreme bull-cow ratios of approximately 10 : 100 have been recorded without obvious effects on reproduction. In contrast to this, there is evidence that the reproductive ability of certain European moose populations decreased markedly when there were more than two females per adult male. The moose is 'conditionally polygamous', as the bull stays with one cow for several days until her estrus is over and then he goes searching for other females in the receptive stage. The noted dissimilarities between the Alaskan and the European populations are probably mainly due to the much higher population density in Alaska. Also some behaviour differences exist between North American and European moose. For instance, the cow moose seem to be more active and ambulatory during the rut in North America than in Europe.

INTRODUCTION

The moose (*Alces alces*) is one of the very few cervids that forms no harems. A bull stays with a female until she is bred and leaves her thereafter. Yet one bull may mate with more than one cow during the rutting season. Thus it is not a disadvantage to have a certain predominance of cows in the population; the question is how unbalanced a sex ratio could be allowed before reproduction would be affected. On this, opinions diverge widely.

SEX RATIO

Calculations on the sex ratio in moose from embryo and calf counts have given results of between 55 and 58 per cent males (Pimlott, 1959; Markgren, 1970). It has also been suggested that condition or age of the mother would have some influence on the sex of the offspring (cf. Heptner and Nasimowitsch, 1967; Bannikov, 1970), but my data from Sweden do not show any such clear tendency. Normaly there is a slight preponderance of males in the secondary sex ratio of moose. Because of a heavier hunting pressure on the bulls, however, the sex ratio in hunted populations is practically always in favour of the females.

REPRODUCTIVE PATTERNS AT UNBALANCED SEX RATIOS

I was told by R. A. Rausch (in litt.) that extreme bull: cow ratios of approximately 10: 100 have been recorded in an Alaskan area after many years of hunting of only males. Yet calf production was not greatly affected.

Experiences from Europe differ markedly from this, probably very much due to lower population densities. In the U.S.S.R., Bannikov (1970) recorded that when there were more than two females per adult male the reproductive ability of the population decreased markedly. In Sweden we have noted that in some northern low-density areas where for many years there has been a heavy hunting pressure on bulls, whilst cows have been protected or very moderately harvested, the expected population increase failed to accrue. Furthermore, abnormally late calving occurs here which implies that a number of cows were not bred during their first estrus. The birth of calves late in the season is undesirable, because they are subjected to great winter mortality or will only survive the winter in bad condition.

COURTSHIP AND MATING CHARACTERISTICS

Some behaviour sequences in the rut of American moose were described by Altmann (1959). There is a stage of active searching when the bull and also the cow are traveling around and calling. The courtship begins with a period of posing performed by the bull near the cow. After this the driving or following stage is in evidence. Finally mating occurs several times during the short receptive period of the cow. Digging of rut-pits, fighting with rivals, mock-battles, etc., may be observed in various parts of the rutting period but particularly in the early phases.

This main pattern seems to be the same also for European moose, but every behaviour element is not identical in all subspecies. I recorded this in comparing my experiences of European moose (*Alces a. alces*) with the findings by Geist (1963) on North American moose (*Alces a. andersoni*). Apparently, there are also some basic dissimilarities in the rutting behaviour complex. In Sweden the cow moose does not stroll far and wide in a searching stage. Usually, she remains in the summer range together with her calves and will be sought there by the bull. Even the calling seems different. No one has ever reported a loud, plaintive rutting call from a Swedish cow moose.

POPULATION STRUCTURE AND POLYGAMY

Observations on one bull moose mating with many cows have been made in enclosures (e.g. see Serafinski, 1969). When evidence of extensive polygamy is found also in free-ranging populations, as in Alaska, it is obvious that the population density must be high. Similar thoughts were expressed by Heptner and Nasimowitsch (1967) who stated that the moose is 'conditionally polygamous' (*bedingt polygam*). The bull has a courtship programme to carry through and he will generally stay with one cow for several days. The receptive stage of the cow lasts less than 24 hours, and in the same region the majority of females come into estrus within a limited period. In sparse populations each bull could not possibly find, court and mate with more than a few cows in the same season. Furthermore, when the bull population is heavily hunted there will be a greater percentage of young animals (yearlings) who show little searching activity compared with mature bulls.

In the Alaskan example the density was said to be between 5 and 10 moose per square mile on an average. In Sweden such a density may be found only in a few restricted localities. The average density is mostly below 2. 0 animals per square mile of forested area. The figure for northernmost Sweden, where these problems are actual, is as low as 0. 4. It is doubtful whether a series of protected seasons for cows could be recommended in such a region as an instrument for raising the numbers. At least it seems rather certain that the general quality of the population will not be positively influenced in this way.

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Paper No. 43

Food Selection by Dall's Sheep (*Ovis dalli dalli* Nelson)

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ABSTRACT

Feeding observations were done on a band of captive Dall's sheep with emphasis on the dominant ram.

The captive band, which is held in a large enclosure at the Yukon Game Farm at Whitehorse, originated from the 'Sheep Mountain' population at Kluane Lake, S. W. Yukon Territory, which is presently under study. The floristic composition of the enclosure communities and of those at the Kluane Lake winter range were comparable. Feeding observations were done at approximately monthly intervals over a one year period. Forage composition was expressed as number of 'interactions' per plant species per day. Variation in forage composition from month to month was explained on the basis of changing phenology of the food plants and different snow depths in the communities. Fluctuations in the daily forage intake of the ram was explained on the basis of changing digestibility of the forage, degree of fatness of the animal, severez–interfering—snow depths, and distortions introduced by supplementary feeding. Diurnal activity rhythms were found to be highly correlated with daylength. The beginning of feeding in the morning more or less coincided with sunrise, while bedding down for the night took place on the average of an hour after sunset. Food selection of the captive band was found to be similar to that of the wild population. Pellet group counts of the dominant ram were higher than values given in the literature for closely related species. The growth curve of the ram over the observation period showed the periodicity characteristic for ungulates, as has been demonstrated for members of the deer family.

INTRODUCTION

This paper reports on the feeding behaviour of a band of captive Dall's sheep, in particular on the forage consumed by the dominant ram.

Observations were made at approximately monthly intervals over the period of one year. The band is held in an enclosure at the Yukon Game Farm in Whitehorse. The size of the enclosure is about 40 acres. The sheep lived almost entirely on natural food. The captive sheep are privately owned; they are not experimental animals as such. Nothing was done to endanger their well-being. Supplementary food was provided during the worst of the winter, even though this somewhat interfered with our observations. Fig. 1 is a simplified map of the area and Table I lists some important ecological factors of the major vegetation types within the enclosure.

These observations were done concurrently with an ecological investigation of the wild Dall's sheep on 'Sheep Mountain' at Kluane Lake, Yukon Territory. The distance between these two sites is about 150 miles.

The purpose of the investigation was: (a) to compare food selection between the captive band and the wild population, since the floristic composition of the Sheep Mountain winter range and the enclosure communities is very similar; (b) to set some standards by which to judge feeding observations done on wild sheep.

Observations were recorded as number of bites (interactions) per plant species per time interval. Much more detailed observations were possible with the captive band, and it therefore served as a reference.

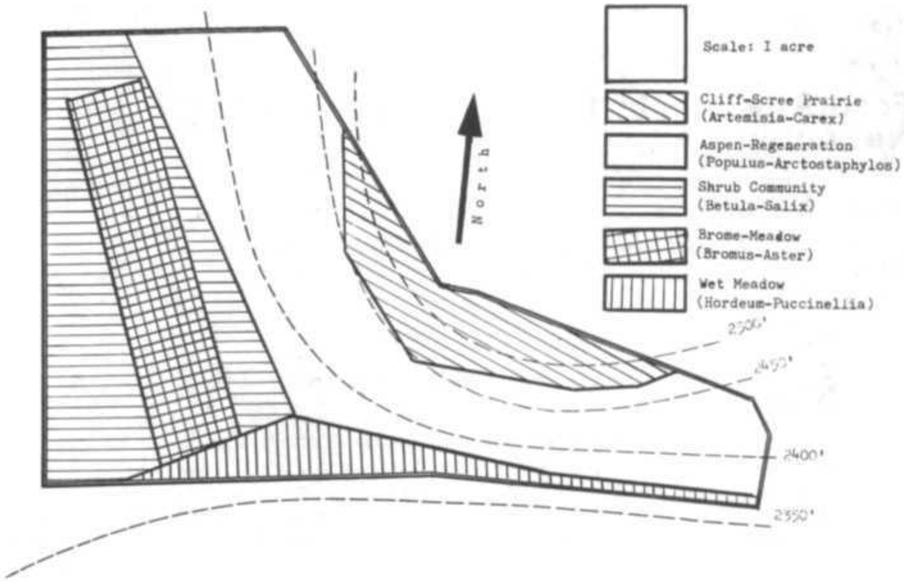

Fig. 1. Map of sheep enclosure at Yukon Game Farm (Whitehorse).

DEFINITIONS

The following terms have been used in this paper:

Herbage: the total vegetative matter available to the sheep.
Forage: that part of the herbage, which is utilized.
Browse: the woody part of woody vegetation (not its leaves) used by sheep.
Interaction: a bite performed by a sheep on a plant species when feeding.
Feeding period: an activity period when the sheep is primarily involved in feeding.
Tree: woody vegetation in excess of four feet in height.
Shrub: woody vegetation up to four feet in height.
Herb: non-woody vegetation.
Grass and grass-like vegetation: members of the grass-, sedge- and rush families.
Forb: herbaceous vegetation other than grass and grass-like vegetation.
Selection: the utilization of a plant species in excess to what would be proportional to that species' abundance.
Avoidance: the utilization of a plant species to a lesser degree to what would be proportional to that species' abundance.

DESCRIPTION OF PLANT COMMUNITIES

Five plant communities are recognized:

(a) Cliffs, scree-slopes and boulder fields, amounting to 4 acres and rising up to 130 feet above the valley floor, in the north-eastern portion of the sheep range. Grassland vegetation, dominated by *Artemisia frigida* and *Carex stenophylla,* covers this area.
(b) Dense Aspen regeneration is found on the lower slopes down to valley bottom. The major associates are *Populus tremuloides* and *Arctostaphylos uva-ursi.* This is the largest vegetation type in the enclosure totalling 18. 7 acres. This site was formerly occupied by mature white spruce-aspen forest, which burned in 1958.
(c) Shrub vegetation, dominated by *Betula glandulosa* and *Salix glauca* covers the more mesic sites in the valley floor. This vegetation type originally covered the western half of the enclosure; part of it was cultivated (see Brome Meadow) and 8. 1 acres remain at present in the original state.

TABLE 1. ECOLOGICAL CHARACTERISTICS OF ENCLOSURE COMMUNITIES

Community	Acreage	Altitude	Slope	Aspect	Hygrotope*	% Cover Trees†	% Cover Shrubs‡	% Cover Herbs	% Cover Mosses Lichens	Stones Rocks	% Cover Litter§
Cliff-Scree Prairie (Artemisia-Carex)	4.0	2500' to 2420'	$\bar{x}$ = 35v r = 0%-90%	South	2	0%	0.6%	40.3%	0.6%	23.4%	1.4%
Aspen-Regeneration (Populus-Arctostaphylos)	18.7	2450' to 2370'	$\bar{x}$ = 15% r = 0%-30%	South	3	34.0%	26.0%	34.8%	11.4%	2.6%	42.0%
Shrub—Community (Betula-Salix)	8.1	2380' to 2370'	0%	–	4	1.0%	37.0%	43.0%	24.0%	0%	29.0%
Brome-Meadow (Bromus-Aster)	5.5	2375'	0%	–	4	0%	2.1%	53.6%	16.0%	0%	28.0%
Wet Meadow (Hordeum-Puccinellia)	3.7	2370'	0%	–	5	0%	4.4%	62.4%	5.6%	0%	18.0%

* index of moisture regime, after Krajina (1969)
† woody vegetation above 4 feet in height
‡ woody vegetation less than 4 feet in height
§ includes remains of herbaceous vegetation as well as stumps and windfalls

TABLE 2. FLORISTIC COMPOSITIONS OF ENCLOSURE COMMUNITIES

	Cliff-Scree Prairie	Aspen Regeneration	Birch-Willow Shrub	Brome Meadow	Wet Meadow	Sheep Mt. Winter Range†
Carex stenophylla subsp, eleocharis	12.0					
Artemisia frigida	10.2					d
Carex filifolia	4.7					d
Lappula myosotis	1.1					0
Potentilla pennsylvanica	.8					0
Pentstemon Gormani	.7					f
Poa glauca	.3					0
Saxifraga tricuspidata	.2					0
Potentilla Hookeriana	.1					f
Anemone multifida	.1					0
Festuca baffinensis	<.1					0
Calamogrostis purpurascems	3.1	.6				d
Populus balsamifera	<.1	.5				a
Agropyron yukonense	.7		<.1			a
Rosa acicularis	1.1	5.6	.1			f
Populus tremuloides (<4')	.5	20.0	.2			f
Arctostaphylos uva-ursi	.7	11.6	11.2			d
Fragaria virginiana subsp, glauca	.2	.2	.6			–
Galium boreale	.5	.3		.1		r
Oxytropis deflexa	.1		.1	<.1		r
Agropyron subsecundum	.7				4.2	r
Bromus Richardsonii	.1		.7	37.0	3.6	–
Achillea lanulosa	1.1	.9	2.3	1.1	1.5	0
Shepherdia canadensis	.3	3.4	.3	.4	.4	f
Epilobium angustifolium subsp, angustifolium	<.1	9.2	10.2	.8	.7	f
Salix glauca subsp, desertorum		1.8	10.4	1.3	1.9	0
Betula glandulosa		.6	27.4	.9	.7	0
Hedysarum alpinum		.7	1.9	.6	.2	0
Astragalus alpinus		.2	2.6	.5	.2	r
Gentiana propinqua		.3	.9	.4	.3	0
Calamogrostis canadensis		1.4	.1		<.1	r

Pyrola secunda	.1				r
Amelanchier alnifolia	.2				0
Viburnum edule	.3				0
Populus tremuloides (>4')	34.0	1.0			f
Carex concinna	.5	.3			r
Linnaea borealis	3.0	.5			f
Salix myrtillifolia		6.4	.2	1.2	–
Agropyron borealis		1.5	1.2	1.2	r
Aster sibiricus		1.1	9.6	1.0	r
Calamogrostis neglecta		1.0	1.8	4.4	r
Hierochloe odorata		<.1	.2	1.2	r
Juncus arcticus subsp, ater		<.1		.8	0
Pinus contorta		1.2	.1		–
Picea glauca		.2			d
Equisetum scirpoides		.2			0
Agrostis borealis		1.6			–
Trisetum spicatum		.1			f
Carex praegracilis		.2			–
Pentstemon procerus		.2			–
Solidago multiradiata		.1			0
Agropyron violaceum subsp, andinum		.4			0
Poa arctica			.1		–
Puccinellia deschampsioides			.3	19.0	a
Hordeum jubatum			<. 1	23.0	a
Deschampsia caespitosa			.2	1.8	a
Arctagrostis latifolia subsp, arundinaeesa:				2.0	–
Equisetum arvense				2.6	r
Lomatogonium rotatum				.3	r
Erigeron acris				.3	–
Beckmannia erucaeformis				.2	–
Taraxacum lacerum				.1	r
Stellaria longifolia				.1	r

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* expressed as percent foliage cover

† Rating of foliage cover as d = dominant, a = abundant, f = frequent, 0 = occasional, r = rare.

(d) Brome meadow, amounting to 5. 5 acres, was established within the shrub community in 1964. *Bromus Richardsonii* is still the dominant species; while the native *Aster sibiricus* is uniformly distributed within this type, members of the original community invade it from its margins.

(e) A narrow strip of 'wet meadow,' dominated by *Hordeum jubatum* and *Puccinellia deschampsioides*, occupies the moist sites along the southern boundary of the enclosure. This is the smallest community amounting to only 3. 7 acres.

Before feeding observations began in August 1970 plant collections were made and the floristic composition of the communities was determined.

FLORISTIC COMPOSITION OF ENCLOSURE COMMUNITIES

Analysis of the vegetation followed the Braun-Blanquet school of phytosociology (Braun-Blanquet, 1964; Krajina, 1933) with the following modification: species significance, here referred to as foliage cover, was estimated to the nearest per cent. The plots, each 10 meters by 10 meters, were randomly located in each community. Separate analyses were done for trees, shrubs and herbs.

Table 2 gives the floristic composition of the five enclosure communities, each foliage cover value being the mean from 10 plots. Plant nomenclature follows Hulten (1968). Table 2 also lists the status of the species on Sheep Mountain in the Kluane Lake area. Only a rating is given, since vegetation analysis has not been completed for that area. Fifty-one of the 62 species identified in the sheep enclosure are also found on the native winter range, which reveals the similarity of these two areas.

Since foliage cover as such is not a good indicator of 'available herbage' because of different heights and different densities of species, an 'available volume' was calculated. Brome grass, being the dominant of a very uniform, artificial community, was used as the standard. It was given an 'available height' factor of one and a density factor of one; the other species were rated in relation to Bromus. For 'available height' the height of the vegetation up to 5' was used, this being the maximal height a sheep can reach under normal conditions. For trees therefore, only the lowest one foot was within the 'available height' zone. 'Available height' ranged from 0. 2 for low herbs like *Equisetum scirpoides* to 3. 0 for tall shrubs like *Betula glandulosa* and *Salix glauca.* 'Density' took into account the number of stems per unit area, the size of the leaves and the number of layers of leaves. It was determined by considering the amount of ground surface visible through the foliage. The cover of *Bromus Richardsonii* is fairly 'open,' therefore most species were given a density factor greater than 1. Density ranged from 0. 8 for the delicate and thin-stemmed *Equisetum scirpoides* to 2. 5 for species like *Arctostaphylos uva-ursi* and *Linnaea boralis,* whose foliage forms a continuous dense mat through which no soil is visible.

Using the foliage cover values in the respective communities, the acreage of the community, available height and density, an 'available volume' was calculated which will more truly represent the contribution of each species to the total available herbage, than foliage cover would by itself. An example will demonstrate the method: *Calamagrostis purpurascens* is present with 3. 1% foliage cover in the cliff community and with . 6% in the aspen forest (Table 2). The acreages of these two communities are 4 and 18. 7 respectively. *Calamagrostis purpurascens* is slightly taller than brome and was given an available height factor of 1. 2. It is also denser than brome and was given a density factor of 1. 2 (Table 3). The available volume was calculated as follows: 3.1 × 4 × 1. 2 × 1. 2 plus. 6 × 18. 7 × 1. 2 × 1. 2 equals about 34. 0. The total available volume of all species amounted to 5531. 8, thus *Calamagrostis purpurascens* contributes 0. 61% to the total herbage and ranks 15th in the scale of herbage producers.

Table 3 lists available height, density and available volume for each species, as well as the percentage it contributes to the total herbage and its rank as a herbage producer.

The first 3 species contribute more than 50%, the first 10 species more than 80% of the total herbage. More than ½ of the number of species contribute less than 0. 1% each. This is characteristic of many plant associations.

TABLE 3. CONTRIBUTION OF INDIVIDUAL SPECIES TO 'AVAILABLE VOLUME'

	'Available Height'	Density	'Available Volume'	Percentage of total 'available volume'	Rank
Carex stenophylla	0.3	1.5	21.5	0.39	22
Artemisia frigida	0.7	2.0	24.5	0.44	20
Carex filifolia	0.3	2.5	14.2	0.25	26
Lappula myosotis	0.7	1.3	4.0	0.07	38
Potentilla pennsylvanica	0.7	1.5	3.4	0.06	39
Pentstemon Gormani	0.4	1.2	0.1	<0.01	56
Poa glauca	0.7	1.2	1,0	0.02	44
Saxifraga tricuspidata	0.7	1.5	0.8	0.01	49
Potentilla Hookeriana	0.4	1.7	0.3	<0.01	56
Anemone multifida	0.5	1.2	0.1	<0.01	56
Festuca baffinensis	0.8	1.2	0.2	<0.01	56
Calamogrostis purpurascens	1.2	1.2	34.0	0.61	15
Populus balsamifera	2.0	2.0	37.3	0.68	14
Agropyron yukonense	1.0	1.0	3.2	0.06	39
Rosa acicularis	1.2	1.2	158.6	2.85	8
Populus tremuloides (seedl.)	2.0	1.5	1129.8	20.30	1
Arctostaphylos uva-ursi	0.3	2.5	233.4	4.18	6
Fragaria virginiana	0.3	1.5	4.3	0. 08	37
Galium boreale	1.0	1.2	9.8	0.17	30
Oxytropis deflexa	0.3	1.5	0.7	0.01	49
Agropyron subsecundum	1.0	1.0	18.5	0.33	24
Bromus Richardsonii	1.0	1.0	218.8	3.93	7
Achillea lanulosa	1.0	1.2	60.8	1.09	11
Shepherdia canadensis	2.0	2.0	282.2	5.06	5
Epilobium angustifolium	1.3	1.5	510.4	9.18	4
Salix glauca	3.0	2.0	790.4	14.15	3
Betula glandulosa	2.0	2.0	959.9	17.21	2
Hedysarum alpinum	0.8	1.2	31.3	0.56	17
Astragalus alpinus	0.2	2.0	11.2	0.20	28
Gentiana propinqua	0.3	1.0	4.9	0.09	35
Calamogrostis canadensis	1.2	1.2	39.1	0.69	13
Pyrola secunda	0.3	1.5	0.9	0.02	44
Amelanchier alnifolia	2.0	1.0	7.5	0.19	33
Viburnum edule	2.0	1.0	11.2	0.20	28
Populus tremuloides (tree)	1.0	0.7	450.7	8.09	1
Carex concinna	0.3	1.2	1.0	0.02	44
Linnaea borealis	0.2	2.5	30.2	0.54	18
Salix myrtillifolia	0.4	2.0	46.0	0.83	12
Agropyron borealis	1.2	0.8	18.5	0.33	23
Aster sibiricus	0.3	1.3	23.5	0.42	21
Calamogrostis neglecta	1.0	1.0	34.2	0.61	15
Hierochloe odorata	1.0	1.0	6.0	0.11	34
Juncus arcticus	0.8	1.2	3.3	0.06	39
Pinus contorta	2.0	1.5	29.5	0.53	19
Picea glauca	2.0	1.5	4.8	0.09	35
Equisetum scirpoides	0.2	0.8	0.3	<0. 01	56
Agrostis borealis	1.0	0.7	9.1	0.16	32
Trisetum spicatum	1.0	0.7	0.6	0.01	49
Carex praegracilis	0.7	1.7	1.9	0.03	43
Pentstemon procerus	0.8	1.0	1.3	0.02	44
Solidago multiradiata	0.8	1.0	0.6	0.01	49
Agropyron violaceum	1.0	1.0	3.2	0.06	39
Poa arctica	0.8	1.0	0.4	0.01	49
Puccinellia deschampsioides	1.2	1.3	112.6	2.02	9
Hordeum jubatum	0.9	1.3	100.0	1.80	10
Deschampsia caespitosa	1.2	1.3	12.0	0.22	27
Arctagrostis latifolia	1.2	1.2	9.6	0.17	30
Equisetum arvense	0.6	1.0	1.6	0.29	25
Lomatogonium rotatum	0.8	0.8	0.7	0.01	49
Erigeron acris	0.8	1.0	1.0	0.02	44
Beckmannia erucaeformis	1.0	1.0	0.7	0.01	49
Taraxacum lacerum	0.4	1.2	0.2	<0.01	56
Stellaria longifolia	0.2	0.8	<0. 1	<0.01	56

It should be kept in mind that vegetation analysis was done during July, when most species have reached the maximum of their annual production. Strictly speaking, Table 3 is representative only for that time. However, since sheep eat dried plants, pick up leaf hay and dig for roots in late winter, there is some validity to the values reported in Table 3 for the fall and winter seasons as well.

Utilization of the sheep enclosure

Feeding observations began after completion of the botanical analysis in August 1970, and were continued at approximately monthly intervals until August 1971.

During the observation time the number of sheep in the enclosure varied from 6 to 13, the average was 11. At present (October 1971) the composition of the band is as follows: 4 sheep (3½ years old) 2 ♂♂: 2 ♀♀; 1 ♀(2½ years); 4 sheep (1½ years) 2 ♂♂: 2 ♀♀; 2 lambs (½ years) 1 ♂:1 ♀.

When first released into the enclosure, about a year before observations started, the sheep did not graze it uniformly. They stuck close to the fence and hardly ever ventured into the aspen forest. Gradually their range expanded and the first major breakthrough came when the cliffs were discovered. The cliffs were subsequently used as bedding sites, escape terrain and lambing grounds. To get to the cliffs from the fence all other communities have to be traversed. Possibly for this reason all communities were subsequently used for feeding. However, even to this date the aspen forest is not used as much as the other vegetation types. Feeding takes place mainly along the edges and along trails leading up to the cliffs. Whenever the sheep do go into dense aspen they appear nervous, their feeding is hasty and they spend a lot of time looking and listening. They hardly ever stay more than an hour at a time.

These sheep act as one band. The nucleus is made up of 4 mature animals (2 ♂♂: 2 ♀♀), now 3½ years old, which were caught as day-old lambs, bottle-raised and released into the enclosure as yearlings. Four of the remaining sheep are their lambs, the others are animals caught as lambs in the wild. Whenever wild sheep were released into the pasture they joined the group after 2 to 3 weeks and tamed down. The size of the enclosure is such that the sheep were always aware of the activities of others even if dispersed at the time. For the most part, however, things were done together. Getting up in the morning, bedding down for the night, holding mid-day 'siestas' were group affairs. They usually fed together in the same community, and for this reason it is safe to say that feeding observations are representative for the band, even though detailed observations were only possible on one animal at a time. Only during October and November was this close association disrupted. The mature rams then spent a lot of time by themselves—kicking, head-rubbing and fighting, or they chased the ewes and broke up the band.

The dominant ram was chosen as the 'observation animal.' He is docile, can be approached closely and even handled, which is not possible with most of the other sheep. Feeding observations always covered the entire daily feeding period. Species lists had been prepared for each community and observations were made by walking at a distance of 3 to 4 feet beside the ram, counting the number of bites and making notes of the species involved. A bite—also referred to as an interaction—is a relatively constant amount. The variation is much smaller than in the often applied 'animal minutes.' It was found that during one minute the number of bites may be as low as 2 or 3 and as high as 50. On the other hand, an interaction is determined by the 'capacity' of the animal's mouth and the nature of the forage (height and density of vegetation, size and thickness of leaves). It was never observed to be less than a single leaf or bud and cannot possibly be more than the animal can grasp at a time. This method of assessment was found to be reliable; there were only a few cases when a bite could not be properly determined. The following are examples. *Salix glauca* catkins are among the first signs of spring: very little other green vegetation is available at the time. Sheep feed on these catkins not by picking them individually, but by taking into their mouths the terminal 4 to 6 inches of a willow twig and stripping it by a quick side-ward motion of the head. By this method several catkins, leaf buds and often bark are stripped off at a time (Fig. 2). This method of feeding on willows was not observed later when leaves had expanded. Another example is feeding on *Astragalus alpinus.* This legume is a very delicate, thin-stemmed, much-branched, prostrate plant, which often grows intermingled with the basal leaves of

Fig. 2. Ram stripping catkins and expending leaf buds from *Salix glauca* branches.

two bunch grasses *(Hordeum jubatum* and *Puccinellia deschampsioides*). It remains green late into the fall—possibly because of the protection by its 'host' plants—and is selected particularly at that time. The usual feeding procedure of 'grasp and jerk' is not very rewarding on this species. The sheep start working on one side of a bunch grass, carefully taking the legume into their mouth and very gently nibbling and pulling—almost sucking—their way through the bunch grass, until most of the legume has been worked into their mouth. This procedure may take up to one minute and is done without looking up. In these cases 'interactions' were difficult to determine and the assessment was made by taking into account the time spent feeding in this manner and the average number of interactions per time interval during the entire feeding period.

Considering that there were 62 potential food plants, this method of keeping track of individual species may appear difficult. It should be realized, though, that at any one spot in a community there are usually less than half a dozen species, and only one or two are abundant. An example may demonstrate the procedure: 'September 19/70, 18 :15, the band is feeding in the brome meadow, the observation ram has just urinated, thus giving the observer time to bring up his check sheets and to set the counter on zero. Time 18 : 17, the ram begins feeding again. The counter keeps track of the total number of interactions, while the observer keeps track of the use of 'rare' species. Time 18 : 24 m the ram stops feeding, looks around and rubs his flank with his muzzle. These few seconds are sufficient to keep up with the notes. Total number of interactions during this interval was 220. The observer had counted 10 interactions on *Aster sibiricus* and 2 on *Poa arctica,* the remainder (220-10-2) 208 interactions, must have been on *Bromus Richardsonii.* The counter is reset on zero and the observer is ready for another run.' Even when feeding intensively shortly after rising in the morning, sheep make breaks of sufficient length to allow an observer to keep notes. Urinating and defecating (when following urinating), stretching, rubbing the hide, looking around or walking to another feeding site, all interrupt feeding for long enough duration. There is only one prerequisite for this method, the observer must be thoroughly familiar with the potential food plants at all phenological stages. The method works better in low and sparse vegetation than a complex community, and it is only applicable for animals which can be approached.

A second day in the enclosure was spent with phenological measurements. Representative members of each species were checked to determine the percentage of 'green' matter and old matter, usually the day after feeding observation. The sheep was also caught for weighing.

The results of the feeding observations are summarized in Table 4. The number of interactions on each species is given for each observation day. The table also gives daily and annual summaries of interactions per species, the percentage each species contributes to the total forage and its rank as a forage producer. Figure 3 is a graphical representation of the annual cycle of forage intake by the experimental ram, expressed as number of interactions per day. Caution is necessary when reading it, since the weight of plant matter consumed per interaction was not constant. It was lower in late May than at other times, since sheep were feeding extensively on low, newly emerging vegetation at the time. Even though much food is consumed at the time, which is also evident from the amount of time spent feeding, it may not be much more than on other dates. Interpretation is complicated by supplementary feeding from late December to early March. A 'hand-full' of grain, estimated as half a pound per animal per day, was fed around noon time. Since the sheep were holding siesta at that time, and since this supplement was 'consumed' in a few minutes, it is doubtful that it interfered with their diurnal rhythm; however, it did introduce a safety factor. It probably prevented the sheep from trying harder to get food. It is reasonable to assume, that the number of interactions per day in January

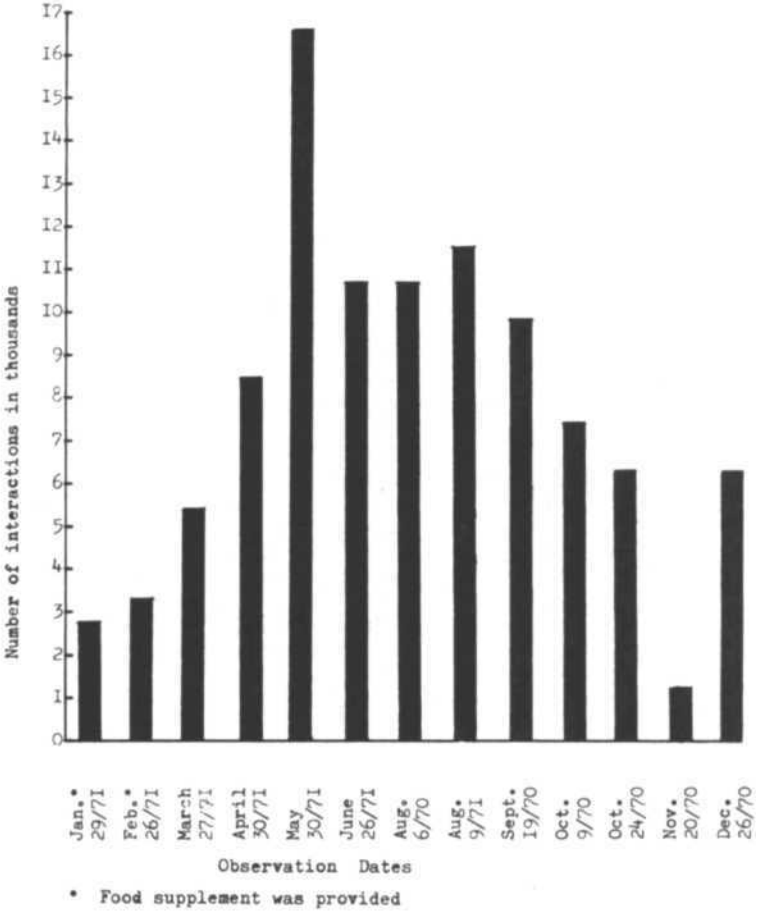


Fig. 3. Fluctuation in daily forage by Dall ram over the annual cycle.

and February would have been somewhere close to the values for December and March, if no supplement had been given and if deep snow conditions had not greatly reduced the feeding rate, since available daylight hours increase after December and the digestibility of forages is comparable. Eadie (1970) gives a diagram of the annual cycle of digestibility for a hill pasture of domestic sheep in northern Scotland. Even though the absolute values may be different since different species are involved, the trends of the curve should be similar in the Yukon; the only difference being a more contracted season because of a higher latitude. In Scotland digestibility is lowest through January and February. It begins to increase with the first emergence of green vegetation in early March, and the peak of digestibility is reached in mid May. From then on there is a rather steady decline as the vegetation matures and dries up. When all vegetation has dried up in December there is very little further change in digestibility. Phenological observations suggest that the comparable dates for the Yukon are as follows: first emergence of green vegetation in late April and probably correlated increase of digestibility; peak of digestibility most likely reached in the early part of June, when most vegetation is in the growing stage, but before flowering sets in; maturation and drying-up take place at a faster rate in the Yukon, all vegetation being dry by the end of October. October will also be the end of the sharp reduction of digestibility, further reduction to March, due to leaching, being minimal in the cold and dry winters of the Yukon.

Blaxter (1962), Blaxter *et al,* (1961) and Hughes *et al.* (1964) have shown that the factor most highly correlated with voluntary food intake by sheep is digestibility of the forage. Ferguson (1956) has shown that there is an inverse correlation between voluntary food intake by sheep and their degree of fatness. From collections we know that rams have the greatest amount of subcutaneous fat just before the onset of the rutting season in late October.

With these facts in mind Fig. 3 is a reasonable representation of the fluctuation in food intake by the Dall ram over the annual cycle, as long as the distortions are considered which were introduced through supplementary feeding, severe snow depth, and low weight per number of interactions in May compared to other times of the year. Figure 4 gives the contribution of 'broad' vegetation types to the diet of the observation ram. For this purpose the forage species were divided into (a) grass and grass-like vegetation, (b) forbs, (c) shrubs and trees, and (d) dry bark.

Figure 5 reveals selection for 'green' forage. It lists the percentages of green matter in the forage and in the herbage for the observation dates. The snow conditions encountered by the captive band are given in Fig. 6.

Food selection will be discussed briefly for each observation day, and a general discussion of the trends observed will be given after.

January 29/71: Total interactions for the day 2830, total time spent with feeding 6 hours 7 min. Average snow depths varied from 31 cm in the cliffs to 45 cm in the wet meadow. The average number of interactions per hour was reduced to 1/3 of the May and June values (about 500 for January and February compared to 1500 in May and June, when ram was feeding continuously in brome meadow). Most feeding took place in 'tramped-down' areas in the cliffs and in the brome meadow and along the trails between them. No feeding was observed in the wet meadow where the snow cover was thickest. Browse and dry leaves of trees and shrubs and dry bark peeled off windfalls (Fig. 7) made of 50% of the forage. Most of the herbaceous forage came from spots with 'shallow' snow in the cliffs (*Artemisia, Carex, Calamagrostis).* Green matter in the forage was made up by *Arctostaphylos* and *Linnaea,* dug out along the forest trails.

February 26/71: Total number of interactions for the day 3325, total time spent feeding 7 hours 55 min. Except for the cliffs, where strong winds had removed some of the snow from exposed ridges, snow cover was at its worst for the winter. Average snow depths ranged from 10 cm in the cliffs to 52 cm in the wet meadow. When feeding in the brome meadow much more time was spent by ram on digging craters and trenches than on actual grazing. The feeding pattern was similar to that of January, in that most grazing took place in the cliffs and in the brome meadow. Forest and shrubs were only utilized along the trails leading through them, and the wet meadow was avoided. Feeding on trees and shrubs was not quite as heavy as in January, and

TABLE 4(a). COMPOSITION OF FORAGE OF DALL RAM OVER THE ANNUAL CYCLE

TABLE 4(b). COMPOSITION OF FOREAGE OF DALL RAM OVER THE ANNUAL CYCLE.

	Jan. 29/71	Feb. 26/71	March 27/71	April 30/71	May 30/71	June 26/71	Aug. 6/70	Aug. 9/71	Sept. 19/70	Oct. 9/70	Oct. 24/70	Nov. 20/70	Dec. 26/70	Sum		Rank
Carex stenophylla	155	165	715	1065	2580	20		205	20	105	125		145	5300	5.27	6
Artemisia frigida	255	245	2250	355	375				5	1150	475	65	575	5750	5.73	4
Carex filifolia	35	45	160	325	525	15		95	5	15	5		25	1250	1.24	20
Lappula myosotis															0	58
Potentilla pennsylvanica				55	5					10			5	75	0.07	44
Pentstemon Gormani	15	5	20		25									70	0.07	44
Poa glauca	55	75	95	155	105	225	35	20	15	5		10		795	0.79	27
Saxifraga tricuspidata															0	58
Potentilla Hookeriana			5	15										20	0.02	50
Anemone multifida					25	15								40	0.04	48
Festuca baffinensis	20	55	15	25	105	25	10			5	25	15	20	320	0.32	33
Calamogrostis purpurascens	310	365	710	425	1050			65		2565	565	375	1065	7495	7.45	2
Populus balsamifera (leaves)	105	100		155	705	65	165	75		150	50	15	200	1785	1.78	14
(browse)	25	30											85	140	0.14	14
Agropyron yukonense	45	60	300	225	55	10		30			25		145	895	0.89	24
Rosa acicularis	45	20	105	85	405	125	425	560	150	25	25	15	20	2005	1.99	12
Populus tremuloides (leaves)	205	130		55	350	40	50	10		1210	100	115	150	2415	2.40	9
(browse)	50	25											45	120	0.12	9
Arctostaphylos uva-ursi	205	115	325	115	10	25	10			5	20	25	105	960	0.96	23
Fragaria virginiana					55	850	65	220						1190	1.18	22
Galium boreale						20				5				25	0.02	50
Oxytropis deflexa					100	85	15	5						205	0.20	38
Agropyron subsecundum	50	105	115	155	75	105	45	75	135	55	260	10	105	1290	1.28	18
Bromus Ricliardsonii	305	910	75	1870	5505	1350	4850	4050	4935		1955	410	2250	28465	28.40	1
Achillea lanulosa					590	1310	125	785	75	10	60		90	3045	3.03	8
Shepherdia canadensis				35	5					10				50	0.05	46
Epilobium angustifolium	45			25	745	1720	1470	1445		15	70			5560	5.54	5
Salix glauca (leaves, etc.)	260	105		55	205	1655	2085	1490	125	55	55	25		6090	6.06	3
(browse)	50	15	120											185	0.18	3
Betula glandulosa (leaves, etc.)	55	20			10	50	305	260	25	5				730	0.72	25
(browse)	25	25	50											100	0.10	25
Hedysarum alpinum						5	85	515	175	15	40			840	0.84	28
Astragalus alpinus						320	310	370	425			5		1425	1.42	17
Gentiana propinqua						5	30	10	15	5	10			75	0.07	44
Calamogrostis canadensis	60	55	230	65	105			150		165	55		185	1070	0.11	42
Pyrola secunda						15	10		5					30	0.03	49
Amelanchier alnifolia	15	25			15			25						80	0.08	43
Viburnum edule	5	20			25	85		40						175	0.17	39
Carex concinna				5			10					5		20	0.02	50
Linnaea borealis		65	65	655	10					450				1245	1.24	20
Salix myrtillifolia (leaves)		100		150	525	1030	115	305	40	45	75	15		2400	2.40	10
(browse)		15												15	0.01	10
Agropyron borealis	20	50	20					120		15		20		245	0.24	35
Aster sibiricus						450	75	515	225		15		5	1285	1.28	18
Calamogrostis neglecta	25	55		55	475	195	305		415		250	45	105	1925	1.91	15

Hierochloe odorata		25		155	25	15	55		105		35		50	465	0.46	30
Juncus arcticus				25	45	5	50		175					300	0. 0	34
Pinus contorta														0	0	58
Picea glauca														0	0	58
Equisetum scirpoides									50	235	100			385	0.41	31
Agrostis borealis	38	10		100	15				50				25	235	0.23	36
Trisetum spicatum		5		15	5						5		25	55	0.05	46
Carex praegracilis				15					20					40	0.04	48
Pentstemon procerus						10		5						15	0.01	54
Solidago multiradiata							10							10	0.01	54
Agropyron violaceum					105	20		5					85	215	0.21	37
Poa arctica				20	85	15			5	40	125		45	335	0.33	32
Puccinellia deschampsioides				425	550	420			1250	265	655	15		3580	3.58	7
Hordeum jubatum				275	625	175			625	115	445	15		2275	2.27	11
Deschampsia caespitosa				125	275	165			735	125	350	20		1795	1.79	16
Arctagrostis latifolia				25	105	35			175	105	145	5		595	0.59	29
Equisetum arvense				605	55			15		130				805	0.80	26
Lomatogonium rotatum														0	0	58
Erigeron acris														5	<0.01	57
Beckmannia erucaeformis				150										150	0.15	41
Taraxacum lacerum						25				5				25	0.02	50
Stellaria longifolia						15								15	0.01	54
Mosses				150										150	0.15	40
Dry Bark	355	285	165	205				10	10	165	75	25	625	1920	1.94	13
Sum	2830	3325	5540	8420	16655	10720	10710	11475	9990	7280	6195	1250	6180			
														100570		

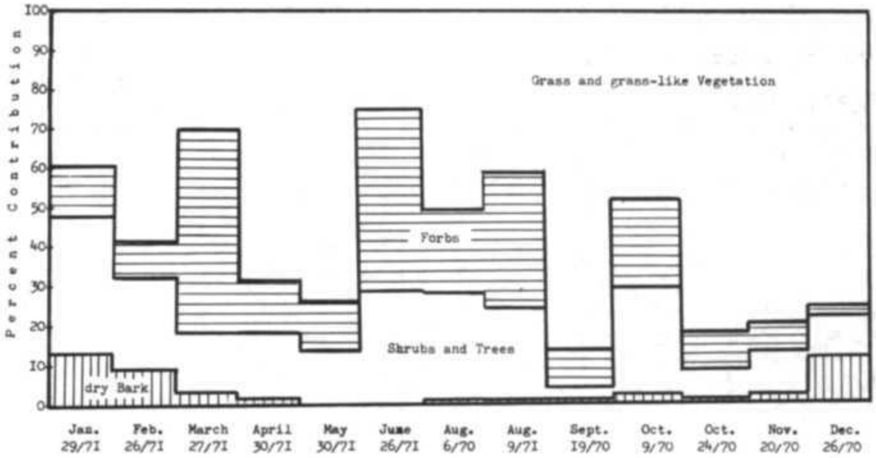


Fig. 4. Contribution of 'broad' vegetation types to forage over the annual cycle.

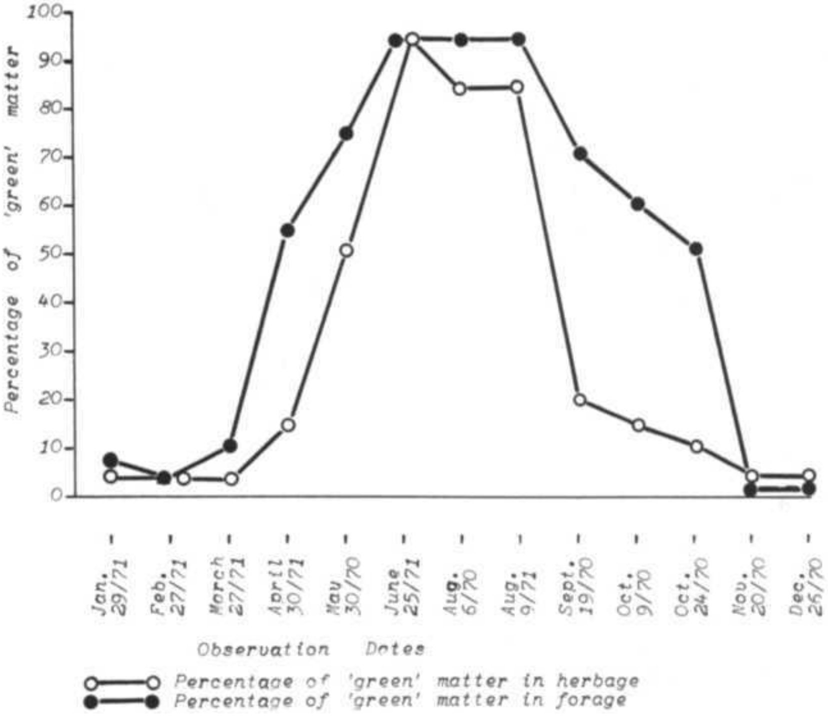
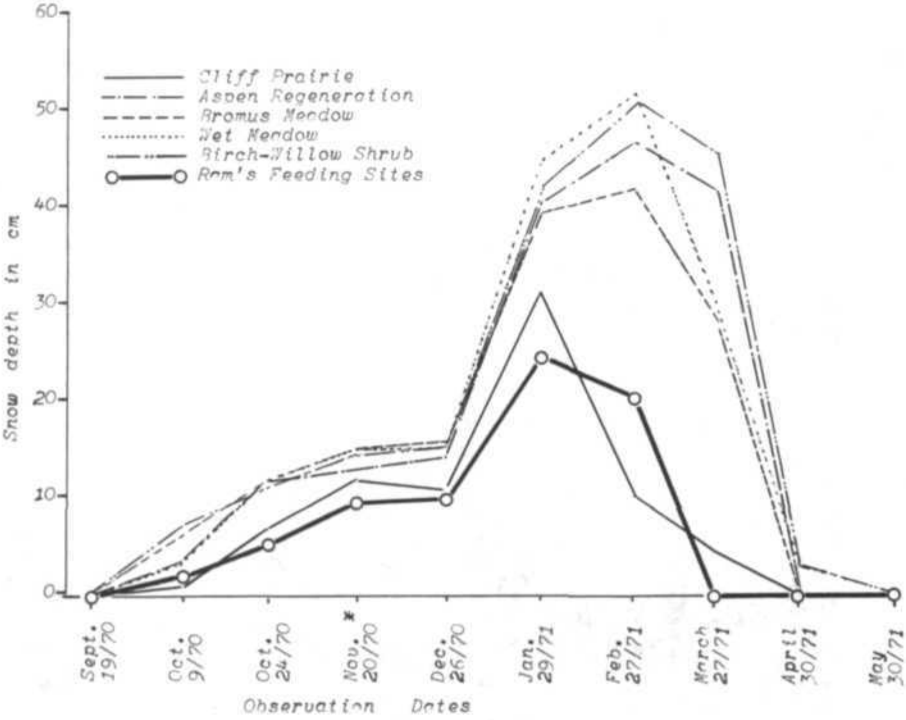


Fig. 5. Selection of 'green' forage.



* Date for mature ewe (ram did not feed that day)

Fig. 6. Average snow depths in communities and in ram's feeding sites.

Fig. 7. Ram peeling dry bark from windfalls in mid winter.

there was a corresponding increase in the utilization of grasses. There was the usual contribution by the 'evergreens' *Arctostaphylos* and *Linnaea* and the peeling of dried bark from windfalls. It is doubtful that any nutritive value could be obtained from the latter. It appeared to be a pastime activity, since digging craters was too unrewarding a procedure.

March 27/71: Total number of interactions for the day: 5540, total time spent with feeding 10 hours 43 min. The first prolonged thawing period had removed most of the snow from the cliffs and had cleared patches around large boulders in the highest part of the aspen forest. Most feeding took place in these snow-cleared areas (Fig. 8).

Fig. 8. Ewe feeding on vegetation recently cleared from snow after first thawing period in spring

Average snow depths in the other communities still ranged from 28 cm to 46 cm. Compared to the previous months there is a great increase in the percentage of forbs in the ram's diet (50%), this increase comes almost entirely from heavy grazing pressure on *Artemisia* in the cliffs. There was also increased use of the other species of the grassland community in the cliffs (*Carex stenophylla, Carex filifolia, Calamagrostis purpurascens*) and a reduction in the use of *Bromus.* There still was no use of the wet meadow, where the snow depth averaged 30 cm. Characteristic for this time was the digging for roots. The soil had thawed to a depth of about 10 cm on south-facing aspects in the cliffs and the sheep spent considerable time digging for *Artemisia, Pentstemon Gormani* and *Agropyron yukonense* roots.

April 30/71: Total number of interactions for the day: 8420, total time spent with feeding 11 hours 22 min. Snow had almost disappeared, except for a few shaded spots in the aspen and willow communities (see Fig. 6). For the first time this season all communities were utilized by the band. Grasslike vegetation contributed 70% of the forage of the observation ram. The first signs of green emerging vegetation were observed. The cliff community and the wet meadow appeared to be the most advanced sites, phenologically, and these got the highest grazing pressure. Selection of green forage is at no time more apparent than now and in October (see Fig. 5). *Poa glauca, Carex filifolia, Carex stenophylla. Festuca baffinensis* had emerging leaves up to 2 cm long, and this was also the case with *Hordeum jubatum, Puccinellia deschampsioides* in the wet meadow. These species were used heavily. Other indication for selection of fresh vegetation was the use of the emerging pale fertile shoots of *Equisetum arvense* and the stripping of willow catkins in the manner described earlier (Fig. 2). Increased grazing was also observed on the 'evergreen' *Linnaea borealis,* previously covered by deep snow. It was estimated that the percentage of green matter in the available herbage was at the time not more than 15%, while the percentage of green matter in the ram's food was between 50 and 60% (see Fig. 5).

May 30/71: Total number of interactions for the day: 16655, total time spent with feeding 12 hours 57 min. More time is spent feeding now than at any other time of the year; and most likely, the amount of forage consumed is also highest. The composition of the forage is almost identical to that of late April even though the amounts have increased. Increased feeding was observed on *Bromus, Epilobium, Achillea,* which emerged during the month, as well as on *Populus* spp. and *Salix* spp. which have now expanding leaf buds. It was estimated that 50% of the herbage consisted of green matter, compared to about 75% of the ram's forage. Winter carry-over was taken accidentally, because of the close association of old and fresh vegetation particularly in the bunch grasses. Because of the great proportion of *Bromus* in the forage, whose newly emerging shoots are only about 2 cm high at the time and far apart, it is reasonable to assume that the weight per interaction is smaller at this day than for the other observation days. This may explain the unexpectedly high number of interactions.

June 26/71: Total number of interactions for the day: 10720, total time spent with feeding 12 hours 21 min. Some feeding was observed in all communities, but the use of the cliffs and of the aspen forest was confined to the times when the sheep walked to and from their bedding sites. Characteristic for the time is the heavy utilization of forbs, contributing almost 50% to the ram's forage, many of which had not emerged in late May, the more important ones being *Fragaria, Achillea, Epilobium, Astragalus* and *Aster.* There is less use of grasses than at any other time of the year. Willows, on the other hand, receive more grazing pressure than at other times. Along trails sheep often 'ride down' willows, thereby getting leaves normally out of their reach (Fig. 9). At this time of the season almost all forage and herbage consist of green vegetation.

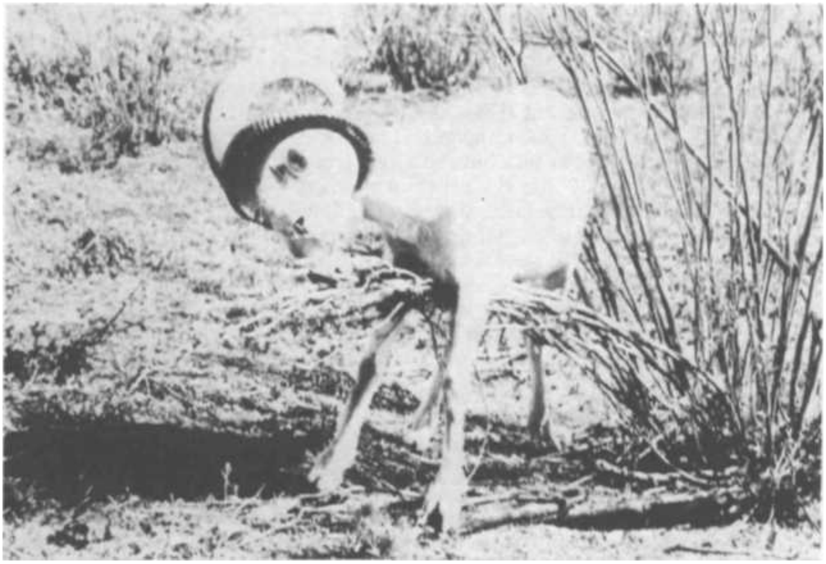


Fig. 9. Ram riding down *Salix glauca* branches, thus increasing the 'volume' of forage available.

August 6/70: Total number of interactions for the day: 10710.

August 9/71: Total number of interactions for the day: 11475, total time spent with feeding 9 hours 32 min. These two dates, which mark the beginning and the end of the observation period will be discussed together since the observations made were very similar. On both days there was no use made of the wet meadow and very little of the cliff communities. As in late June, forbs contributed a major portion to the forage, but the percentage decreased to 22% and 35% respectively. Besides those mentioned for June, the late-emerging *Hedysarum alpinum* is heavily used. On both days there was also a great amount of feeding on *Rosa acicularis* leaves. It is interesting that a great proportion of the feeding on forbs and low shrubs took placed in shaded locations where the species were found in a 'younger' phenological stage. The utilization of shrubs and trees is comparable to the June figures, both in amount and composition. *Bromus* was the most important grass on both August observation days, contributing 45% (Aug. 6) and 35% (Aug. 9) to the forage of the ram. The first signs of drying up of vegetation are apparent at this time; the green matter in the herbage was estimated at 85%, while the forage was still all green.

September 19/70: Total number of interactions for the day: 9990, total time spent feeding 8 hours 41 min. From the latter part of August to the middle of September there is a drastic reduction in the amount of green matter in the available herbage, and selection of green vegetation becomes again apparent at this time. All communities were utilized, but feeding in the cliffs was limited to the time of walking to and from the bedding site. The proportion of grasslike vegetation in the forage was higher than at other times of the year (85%), the reason being that most grasses still had green basal leaves, while the foliage of trees and shrubs was completely dry by now; much of it had already fallen off. Some of the taller forbs had also dried up (*Achillea, Epilobium*). Brome contributed almost half the daily forage intake; heavily utilized were also basal leaves of the bunch grasses *Puccinellia, Hordeum,* and *Deschampsia.* Forbs, which were still green at the time and selected, were *Astragalus, Hedysarum* and *Juncus.* It was estimated that the percentage of green matter in the herbage had dropped to 20%, while the percentage of green matter in the forage was still about 70%, (see Fig. 5).

October 9/70: Total number of interactions for the day was 7280, total time spent feeding 7 hours 37 min. Snow had fallen a few days earlier, but all communities, except the brome meadow, had snow-free patches under dense shrubs, stumps and windfalls. Most feeding took place in these clear patches. All communities were utilized, but in contrast to the summer months there was again heavy grazing pressure on the prairie communities in the cliffs. There was very little use of the brome meadow, and this may be explained by the fact that this area had a continuous snow cover of 6 cm. The proportion of trees and shrubs in the forage is unexpectedly high through heavy use of aspen. Young aspen had been cut in early June while the leaves were in the expanding stage, to thin out the very dense stands. The leaves dried up and remained on the trees. While the other aspen leaves went through the usual phenological sequence of maturation, drying and falling, these leaves were 'frozen' in an early phenological stage as leaf hay and became very appealing to the sheep at this time. Selection was for species which still had some green leaves: *Artemisia, Calamagrostis purpurascens, Calamagrostis canadensis,* and *Puccinellia,* and for the 'evergreens' *Linnaea* and *Equisetum scirpoides.* When feeding in only a few cm of snow, sheep prefer to use their muzzles to move it aside. The use of front legs for this purpose was not observed until the snow was at least 8 to 10 cm deep.

October 24/70: Total number of interactions for the day: 6195, total time spent with feeding 8 hours 11 min. There was continuous snow cover now in all communities, the average being 7 cm for the cliffs up to 12 cm in the wet meadow. All communities were utilized, grasslike vegetation making up 80% of the ram's forage. The composition of the forage was similar to that of October 9/70, except that more use was made of the brome meadow (*Bromus, Calamagrostis neglecta*) and much less use of aspen leaf hay, which by this time had been almost consumed. There was again selection of species which had green matter left (*Artemisia, Calamagrostis purpurascens, Puccinellia, Deschampsia, Hordeum* and *Equisetum scirpoides*). It was estimated that by this time the percentage of green matter in the herbage had dropped to 10% while approximately half of the food was still green.

November 20/70: Total number of interactions for the day 1250, total time spent feeding 0 hours 51 min. During three days stay in the game farm this was the only day when any feeding at all was observed by the two mature rams, and it was limited to 51 minutes in the early morning when they were leaving the bedding sites. Some use was made of all communities. The rams walked from cliffs through aspen, shrubs and brome meadow to the wet meadow, where prolonged fighting started. Feeding while walking was hasty and limited to vegetation above the snow line. A mature ewe, observed on November 2/70, took 4550 interactions. The composition of her forage was comparable to that of the ram's of November 20/70. All vegetation had dried up by now, and green matter in the diet had to come from evergreens.

December 26/70: Total number of interactions for the day was 6180, total time spent with feeding 6 hours 16 min. The average snow cover ranged from 11 cm for the cliffs to 16 cm in the brome meadow. The typical feeding pattern, characteristic for the winter period of deep snow, was established now. Most feeding took place in the cliffs, which usually had the shallowest snow depth and where the snow was more easily removed because of the inclining slopes; next in importance was the brome meadow, where feeding took place in tramped-down areas and by expanding already existing craters and trenches. Use of the aspen forest and the birch-willow shrubs was limited almost entirely to narrow strips along the trails leading from the brome meadow up to the cliffs. No use at all was made of the wet meadow, which usually had the deepest snow cover and was out of the way of the sheeps' travel. At this time snow depth began to interfere with feeding by reducing the maximum rates (continuous feeding in brome meadow) from a high of up to 1500 in May and June to about 900 interactions per hour. Green matter at this time came from bearberry, dug out along forest trails. The first use of 'browse' was observed this season. The use of leaves of woody vegetation was confined to feeding above the snow line (Fig. 10).

Fig. 10. Ewe taking dry Aspen foliage in early winter.

GENERAL TRENDS IN FEEDING BEHAVIOUR

Over the annual cycle grasses and grass-like vegetation contributed 59% of the forage of the observation ram, forbs about 19%, shrubs and trees about 17. 5% and dried bark windfalls about 3. 5% (see Fig. 4). Variations in feeding between months can be explained on the basis of different phenological stages of the plant species and different snow depths of the communities.

Whenever possible the forage included a great diversity of species, 38 being the highest observed on a single day. Of the 62 potential food plants in the enclosure only 5 were never touched.

Whenever possible feeding took place in areas with no snow, very little snow, or above the snow level. Feeding in deep snow was avoided.

Whenever possible, also, sheep selected green forage, preferably a species in its youngest phenological stage. Some green matter was found in the forage of the ram over the entire annual cycle, even though considerable digging was required to get at the evergreens at the forest floor in winter. Conifers were not used. The term 'evergreen' is here used in a general sense and includes the following species: *Pinus contorta, Picea glauca, Equisetum scirpoides, Linnaea borealis* and *Arctostaphylos uva-ursi.* Karaer (1961) has shown that some green forage is essential for the survival of Russian reindeer throughout the winter; it is possible that this may also be the case for sheep. Arnold (1964),Eadie (1970) and Martin (1964) found that domestic sheep select green more succulent vegetation in preference to old and dry plants, as long as enough pasture is available for selection. As was observed in our study, domestic sheep aim at filling their stomach; if this is not possible through the use of preferred species alone, others are utilized.

In general flowers and flowering heads are preferred to leaves, and leaves are preferred to stems. These observations support findings made by Arnold (1964),Eadie (1970) and Fontenot and Blaser (1965). However, there were many exceptions to this rule. The awned heads of *Hordeum jubatum* were never taken. While inflorescences of grasses which are rather 'fleshy' and have large seeds (*Bromus Richardsonii, Poa arctica, Agropyron yukonense, Hierochloe odorata* and *Beckmannia erucaeformis*) were selected, those with thin, feathery inflorescenses and tiny seeds (*Calamogrostis* spp., *Puccinellia deschampsioides* and *Deschampsia caespitosa*) were very little utilized. In delicate, thin-stemmed species like *Poa glauca, Festuca baffinensis* and *Carex filifolia* the entire plant was taken. Which forage is 'liked best' becomes apparent at the end of a prolonged feeding period, shortly before the sheep beds down to ruminate. The rumen is filled and the animal becomes highly selective. Individual flowers of *Epilobium angustifolium* and *Achillea lanulosa* are picked, as well as the flowering heads of *Bromus Richardsonii* and *Agropyron yukonense* and the entire legume *Astragalus alpinus.* The individual forage items may be many meters apart at this time.

As has been pointed out, selection is very much influenced by the amount and type of forage available. Phenological changes as well as grazing by the sheep themselves continuously change these factors.

A good example was the utilization of *Calamogrostis purpurascens,* a rather coarse grass growing in the cliffs and upper part of the aspen forest. Phenologically speaking, this species is an 'early bird,' and its newly emerging leaves are heavily utilized in late April and May, when little other green vegetation is available. As the season progresses the leaves become longer and coarser and flowering clumps develop. By this time many other species have emerged. In the latter part of May only the tips of the leaves of *Calamogrostis* are taken and for the remainder of the summer, when more succulent forage is available, *Calamogrosotis* is avoided. When the vegetation is drying up in September and October the lowest basal leaves of *Calamogrostis* remain green for a long time and the sheep again take to the species. It is the most utilized forage plant during October because of this delayed drying up of its lowest, most protected leaves. *Calamogrostis* continues to be heavily utilized, because from now on snow restricts feeding intensity and selection. It is a tall bunch grass which protrudes out of the snow for a long time; besides, it grows in communities which usually have the shallowest snow cover. During the early part of the winter the dry leaves, previously avoided, are utilized and the coarse flowering clumps are left behind. These are taken in the latter part of the winter when snow conditions are most severe and forage is scarce. In March, after the first snow melt, even the stubbles previously left behind and covered by snow are grazed down to the level of the soil. With the emerging of new shoots in the latter part of April a new 'selection cycle' starts.

The method of assessing forage composition by counting the number of interactions per plant species has been tried for domestic sheep by Arnold (1964). His maximum rates are higher than ours. He reports:'... we have found that the number of bites per minute changes with both the quantity and quality of pasture on offer, being highest on short, green pasture in winter (60-80) and lowest on abundant dry pasture in summer (25-40).' The highest rates in my study were observed to be 45 to 55, when the ram was feeding in continuous, dense, emerging vegetation in May and June.

Attempts were made to estimate the weight per interaction by walking beside the ram and imitating his feeding behaviour. Samples of 100 interactions were collected at a time, oven-dried and weighed. The procedure was repeated in different communities and at different times of the year. The range observed was from . 1 gr. to . 4 gr. per interaction dry weight. Leathery leaves of *Populus balsamifera, Salix* spp. and Bearberry contributed the heaviest interactions while thin-stemmed grasses like *Poa glauca* and *Festuca baffinensis* made up the light samples.

These values fall within the expected range, since Palmer (1944) reported that Dall's sheep require 6 lbs. dry weight per day. The distribution of forage producers (Table 2) shows a similar trend as the distribution of herbage producers (Table 3); however the ranks of the species within these distributions varies greatly.

To get some idea of preference or selection, the following simple method was applied. If we consider the ideal (unrealistic) case that each species is utilized exactly proportional to its abundance, then its rank as a forage producer should be the same as its rank as a herbage producer, and the difference between the ranks should be zero. Deviations from zero would mean either selection or avoidance, depending on whether the deviation is negative or positive. The greater the deviation the greater the degree of selection or avoidance. This method was applied for the 62 species in the enclosure. Table 5 shows the calculations. The rank of a species in the herbage distribution was given a positive value, that in the forage distribution a negative one. Therefore, the resulting difference—if positive—means selection or preference, if negative—means avoidance. The results are graphically shown in Fig. 11. It is emphasized that this

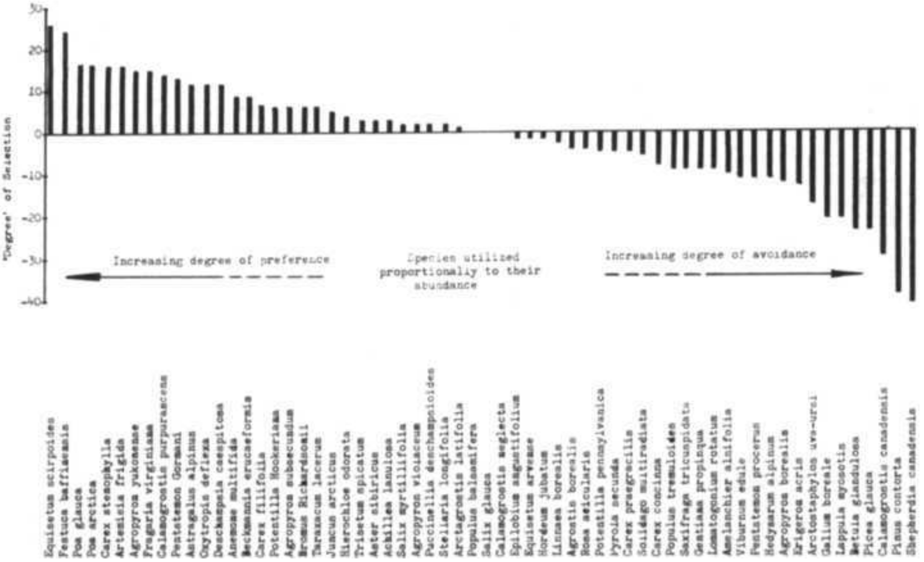


Fig. 11. Preference scale.

TABLE 5. RANK OF SPECIES ON PREFERENCE SCALE

	Rank in Herbage (+)	Rank in Forage (-)	Difference	Rank on preference scale	Utilization on Sheep Mt.†
Carex stenophylla	22	6	16	4	–
Artemisia frigida	20	4	16	4	3
Carex filifolia	26	20	6	10	3
Lappula myosotis	38	58	–20	29	0
Potentilla pennsylvanica	39	44	–5	20	1
Pentstemon Gormani	56	44	12	7	1
Poa glauca	44	27	17	3	3
Saxifraga tricuspidata	49	58	–9	23	0
Potentilla Hookeriana	56	50	6	10	1
Anemone multifida	56	48	8	9	1
Festuca baffinensis	56	33	23	2	3
Calamogrostis purpurascens	15	2	13	6	2
Populus balsamifera	14	14	0	16	2
Agropyron yukonense	39	24	15	7	3
Rosa acicularis	8	12	–4	19	2
Populus tremuloides	1	9	–8	22	1
Arctostaphylos uva-ursi	6	23	–17	28	1
Fragaria virginiana	37	22	15	5	–
Galium boreale	30	50	–20	29	1
Oxytropis deflexa	49	38	11	8	1
Agropyron subsecundum	24	18	6	10	0*
Bromus Richardsonii	7	1	6	10	–
Achillea lanulosa	11	8	3	13	2
Shepherdia canadensis	5	46	–41	33	0
Epilobium angustifolium	4	5	–1	17	1
Salix glauca	3	3	0	16	0*
Betula glandulosa	2	25	–23	30	1
Hedysarum alpinum	17	28	–11	25	2
Astragalus alpinus	28	17	11	8	2
Gentiana propinqua	35	44	-9	23	1
Calamogrostis canadensis	13	42	–29	31	0*
Pyrola secunda	44	49	–5	20	0
Amelanchier alnifolla	33	43	–10	24	1
Viburnum edule	28	39	–11	25	1
Carex concinna	44	50	-6	21	0*
Linnaea borealis	18	28	–2	18	1
Salix myrtillifolia	12	10	2	14	–
Agropyron borealis	23	85	–12	26	0*
Aster sibiricus	21	18	3	13	1
Calamogrostis neglecta	15	15	0	16	0*
Hierochloe odorata	34	30	4	12	0*
Juncus arcticus	39	34	5	11	0*
Pinus contorta	19	58	–39	32	–
Picea glauca	35	58	–23	30	0
Equisetum scirpoides	56	31	25	1	1
Agrostis borealis	32	36	–4	19	–
Trisetum spicatum	49	46	3	13	2
Carex praegracilis	43	48	–5	20	–
Pentstemon procerus	44	54	–10	24	–
Solidago multiradiata	49	54	–5	20	1
Agropyron violaceum	39	37	2	14	0*
Poa arctica	49	32	17	3	–
Puccinellia deschampsioides	9		2	14	0*
Hordeum jubatum	10	11	–1	17	0*
Deschampsia caespitosa	27	16	11	8	0*
Arctagrostis latifolia	30	29	1	15	–
Equisetum arvense	25	26	–1	17	0*
Lomatogonium rotatum	49	58	–9	23	0*
Erigeron acris	44	57	–13	27	–
Beckmannia erucaeformis	49	41	8	9	–
Taraxacum lacerum	56	50	6	10	0*
Stellaria longifolia	56	54	2	14	–

* These species are associated with moist habitats not normally frequented by sheep.

† The following rating was used for Sheep Mountain: — absent, 0 no use observed, 1 rare use, 2 average use, 3 extensive use.

is only a very simple and crude method to show selection as observed in the field; it should not be used mathematically. Since the intervals between ranks in the forage and herbage scales are not of equal magnitudes they cannot be so in the preference scale either.

Table 5 also gives a rating of species utilization on Sheep Mountain, for those common to both sites. Species associated with moist habitats should not be used in comparisons, since wild sheep do not use such areas. Otherwise there is a great similarity between the preference scale for the enclosure and the observations made in the wild. In both areas there was no use of conifers and very little use of *Shepherdia.* Others, like *Arctostaphylos, Betula* and *Populus tremuloides* only showed limited utilization. *Rosa, Linnaea, Epilobium, Populus balsamifera, Achillea* and *Aster* were used proportionally to their abundance. Preferred species were 'dry land' grasses and herbs in both sites (*Artemisia, Festuca, Poa glauca, Carex filifolia* and *Agropyron yukonense.* It is very interesting that the captive band, whose mature members had no feeding experience in the wild, developed a very similar 'taste.'

Unfortunately, observations of this nature are not possible anymore, since the sheep enclosure is stocked beyond its carrying capacity and signs of overuse are apparent. Along much-used trails preferred shrubs have practically been eliminated and a browse line has formed on those beyond the reach of sheep. The forbs *Epilobium, Achillea* and *Aster* and all legumes were hardly allowed to get to the flowering stage, and a reduction in their cover values can be expected the next season.

DIURNAL RHYTHM

For the most part the beginning of feeding in the morning coincides more or less with sun rise (Table 6, Fig. 12). There is some indication that sheep rise early, up to 1 hour before sun rise on clear days, and remain bedded down longer on overcast days, particularly during rain and snow storms. The wild Dall's sheep population at Kluane Lake behaves similarly. This supports the findings of Gwynne *et al.* (1970) on Soay sheep at St. Kilda and those of Hunter (1954), who observed Hill sheep in Scotland.

TABLE 6. DIURNAL RHYTHM OF DALL RAM IN RELATION TO SUN-RISE AND SUN-SET

Observation Dates	Beginning of Feeding	Sunrise	Difference (minutes)	Bedding down for night	Sunset	Difference (mins.)
January 29/71	09-30	09-26	4	17-30	17-02	28
February 26/71	09-06	08-10	–54*	19-01	18-18	43
March 27/71	07-03	06-41	–22	21-00	19-33	87
April 30/71	05-20	04-58	–22	21-45	21-00	45
May 30/71	04-30	03-46	–54*	22-45	22-12	33
June 25/71	03-20	03-29	9	23-51	22-37	74
August 9/71	04-50	04-56	6	21-49	21-15	34
September 19/70	06-20	06-37	17	20-15	19-10	65
October 9/70	07-45	07-26	–19	19-20	18-08	72
October 24/70	07-00	08-05	65	19-00	17-24	96
November 20/70	09-23	09-16	–7	17-11	16-16	55
December 26/70	09-06	10-12	66	16-30	15-51	39
			$\bar{X}$ = –0.3		$\bar{X}$	55

* overcast mornings

Geist (1971) found that in winter sheep tended to rise much later in the morning than in summer. Very intensive feeding begins soon after rising and continues for 2 to 3 hours. During early summer, when the emerging grass is still short, up to 1500 interactions have been recorded per hour during this intensive feeding period. Finally, the sheep slows down and becomes very selective. Individual flowers (fireweed, yarrow) and heads of grasses (brome) as well as preferred legumes are taken, often many yards apart. This selective feeding may continue for 10 to 15 minutes, after which the animal beds down and begins to ruminate. Bedding down may take place anywhere, typical 'bedding sites' are only used at night and sometimes during the mid-day 'siesta.' Subsequent feeding periods are usually shorter, except for the last one before bedding down for the night, which may also be as long as 3 hours or more.

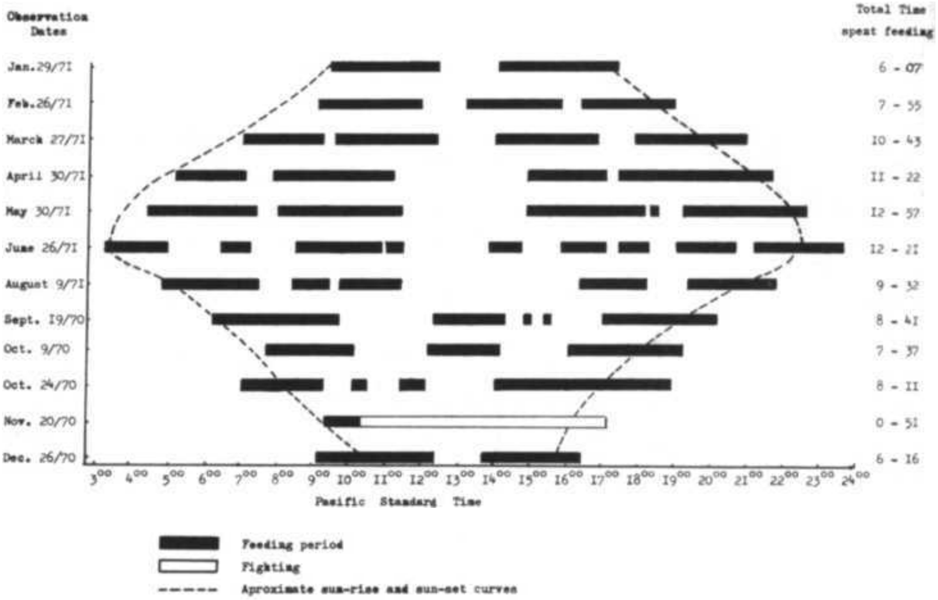


Fig. 12. Feeding periods of Dall ram over the annual cycle.

Bedding down for the night always takes place well after sun set, the average being 55 minutes. Similar findings were made by Geist (1971) on Stone's sheep. It appears that sheep feed as long as they can see. The number of daily feeding periods is proportional to day length. During winter there is an early and a late feeding period interrupted by a relatively short siesta. As day gets longer, there are more breaks, but the only true resting period, when ruminating is followed by 'dozing' and sleeping, is a fairly long mid-day break here referred to as 'siesta.' Only this siesta is predictable, all sheep take part in it. Other minor breaks appear to serve only to ruminate and make room for more food. Not all sheep may take part in it at the same time. Even in mid-winter a siesta is held. The low digestibility of the forage at the time does not allow the sheep to spend the few available daylight hours on continuous feeding.

No feeding was observed at night. Twenty-four hour periods were spent with the sheep during the summer months, and periodic checks with spot lights were made at other times of the year.

There is no agreement in the literature as to whether night-time feeding occurs or not. Crofton (1949)—as cited by Hunter (1954)—remarks that hill sheep graze and move very little during the hours of darkness. Of the hill sheep observed by him only 10% were grazing at night, while 90% were grazing during the day. Wallace (1884) found that hill sheep do not eat during the short summer nights, but do eat in the long winter nights between the hours of 11 p.m. and 2 a.m. Tribe (1950) reviewed this subject and concluded that moving about as well as feeding does occur.

It is likely that no generalization is possible on this point. Studies done in different parts of the world, with associated differences in day lengths, seasons, quality and quantity of pastures, type of animal and physiological state of animal cannot be strictly compared. As far as wild sheep are concerned, familiarity with the terrain, presence or absence of predators and weather conditions (clear vs. overcast nights, snow depths, etc.) will be additional complicating factors.

RATE AND QUANTITY OF DEFECATION BY THE OBSERVATION RAM

Ever since the original work by Bennett, English and McCain (1940) considerable use has been made by wildlife investigators of pellet group counts as a management tool for big game censuses, population trends and competition studies (Riney, 1957; Rogers *et al.*, 1958). Some of the problems involved with this technique have been discussed by Robinette *et al.* (1958) and the entire subject has recently been reviewed by Neff (1968). My project was not designed to deal with this aspect of sheep biology, but since no reports on Dall's sheep defecation rates and amounts are available in the literature, and since our findings deviate greatly from what has been reported for closely related ungulates, the observations are worth mentioning. During the summer months the experimental ram was kept under observation for 24-hour periods. The time of defecation was noted and the number of pellets per group was counted whenever possible. If the ram was feeding at the time, the location was marked and returned to later for counting when the ram rested. Counts were not attempted when pellets fell on steep slopes, littered forest floor or into high grass. Intervals reported between defecations are based entirely on observations during feeding periods. It is difficult to record these intervals during resting periods, since the sheep don't get up for defecation. They may rest in high vegetation, in close proximity to another sheep, or on favoured bedding sites in several inches of previous droppings, all of which make exact determination of defecation time difficult. Making a sheep get up whenever defecation was suspected usually caused a lot of disturbance in the entire band. Subsequent behaviour was often not natural; in most cases the animal walked away and began to feed. This method was only tried once (September 19 to September 20/70), and subsequently abandoned. Table 7 lists the results.

TABLE 7. DEFECATION RATES AND AMOUNTS OF DALL RAM

	May 30/71	June 26/71	Aug. 6/71	Aug. 9/71	Sept. 19/71	Oct. 9/71	Oct. 24/71
Number of defecation periods per 24 hours							
	41	37	35	34	29	31	30
Number of pellets per defecation period							
X	76 ± 20	77 ± 32	73 ± 22	85 ±47	78 ± 29	77 ± 17	75 ± 30
r	63 – 95	55 – 115	50 – 86	36 –145	57– 100	60 – 84	59 – 102
n	13	23	11	18	12	8	8
Time interval between defecation periods*							
X	37 ± 27	30 ± 45	32 ± 25	31 ± 42	34 ± 51	35 ± 47	39 ± 52
r	19 – 62	2 – 72	9 – 75	1 – 67	1 – 103	9 – 93	10 – 114
n	12	25	23	20	21	11	12

* Time given in minutes

The number of pellets per group is fairly stable over the six months observation period, the daily means ranging from 73 to 85. There was no seasonal trend in the deviations observed. The number of defecation periods per 24 hours was highest in late May (41) and declined gradually as the season advanced, to 30 in late October. The time interval between defecation periods increases over the season, being shortest in late June (30 min.) and longest in late October (39 min.). The late May mean (37 min.) is still fairly high. It should be recalled that at this time a considerable portion of the ram's forage still consisted of 'old' vegetation. These trends are to be expected. High forage intake in early summer results in a great number of defecations (Neff, 1968) and in a fast rate of passage, due to the high digestibility of forage at this time (Eadie, 1970; Blaxter, 1962; Lambourne, 1957). As the season advances, digestibility decreases. This is apparent from larger intervals between defecations due to a slower rate of passage. Food intake goes down, and there is corresponding decrease in defecations as summer goes by. This relationship, however, is not directly proportional, since digestibility decreases. It takes approximately 3000 interactions (food intake) to result in a defecation in mid summer, but only about 2200 interactions in late fall.

The defecation rate is slower at night, and limited observations suggest that the intervals between defecations become longer as morning approaches. During the night of September 19 to 20/70 six intervals were measured; the mean was 80 min., the range 61 to 170 min. The corresponding figures for daytime were x — 34 min., r — 1 to 103 min. It is interesting that these observations deviate considerably from reports in the literature on closely related ungulates. Longhurst (1954) reports for domestic sheep a mean defecation rate per day of 13. 3 when feeding on grain, stubble and hay, and a rate of 15. 0 to 16. 0 when feeding on green grass. Ogren (1959) gives a mean rate of 12. 7 for Barbary sheep (*Amnotragus lervia*). Neff (1968) reviewed the observations done on many ungulates ranging from deer to moose. The lowest mean given in his paper was 8. 0 pellet groups per day for mule deer on summer range; the highest mean was 23. 1 pellet groups per day for black-tailed deer feeding on native forbs. Strict comparisons, however, are not possible since the authors do not give the number of pellets per group.

GROWTH AND WEIGHT OF OBSERVATION RAM

To compare the growth of the captive sheep with their wild cousins, which have the advantage of a vertical migration to alpine summer range, the sheep were caught and measured at approximately monthly intervals, usually the day after feeding observations. Details of that project will be dealt with separately.

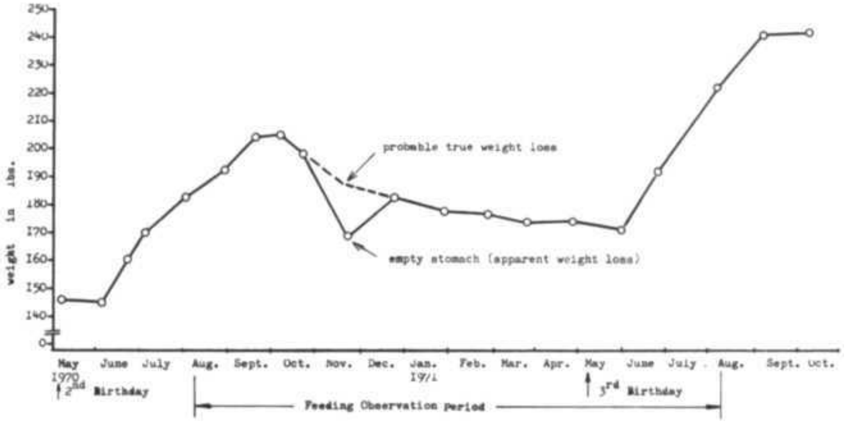


Fig. 13. Growth of Dall ram during observation period.

Figure 13 gives the growth curve of the observation ram. Periodicity of growth, typical for ungulates, is apparent. Detailed work on this subject has been done by Wood *et al.* (1962) and Wood and Cowan (1968) for deer, by McEwan and Wood (1965) and McEwan (1968) for reindeer and caribou, and by Heptner and Nasimowitsch(1967) for moose. None of the investigators dealing with sheep weights and growth (Aldous *et al.,* 1958; Forrester and Hoffman, 1963; Hansen, 1965; Blood *et al.,* 1970) give continuous data over the annual cycle, but Blood *et al.* (1970) indicate that weight loss does occur during winter.

The observation ram reached a maximum weight of 208 lbs. when 2 years and 5 months old (early October/70) and a maximum weight of 242 lbs. when 3 years and

5 months of age. He lost 17% of his maximum October weight during the winter. The food supplement provided probably prevented him from losing 25 to 30%, which are the values obtained from wild sheep. In both observation years the lag between the first appearance of green, nutritious vegetation and the correlated increase in weight was about six weeks.

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Paper No. 44

Dominance Relationships as a Possible Regulating Factor in Roe Deer and Reindeer Populations

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ABSTRACT

The purpose of this paper is to emphasize the possible role of dominance behaviour as an indirect mortality factor for roe deer and reindeer under severe environmental conditions. Both species suffer from food shortage in winter and it is suggested, supported by some evidence, that dominant individuals are the prime utilizers of the available food, both natural and artificial, at the cost of subordinated individuals, which to a varying degree will suffer from malnutrition.

INTRODUCTION

When talking about factors regulating animal populations we are accustomed to use concepts such as food shortage, diseases, predation and other environmental factors. It is not until recently that physiological and behavioural factors have been taken into consideration when explaining what regulates populations. In this context we might think of the importance of stress and territoriality. Under special circumstances other behavioural factors could be important as well.

In this paper I want to present some evidences that dominance relationships in roe deer (*Capreolus capreolus*) and reindeer (*Rangifer tarandus*) might be an important regulating factor on the population under severe environmental conditions.

GENERAL CONSIDERATIONS

Roe deer are often subject to severe environmental stress in Scandinavia where the species is living at the edge of its range. Availability of forage is usually limited by snow depth, which also hampers mobility of the animals. As a result many roe deer die from malnutrition during the winter period. The extent of annual mortality is difficult to estimate, but the relation between different years can be obtained by comparing the number of roe deer carcases which are submitted to the National Veterinary Institute in Stockholm for examination (Borg, 1970). A total of 2, 827 roe deer were submitted to the Institute for examination between 1948 and 1969. Of these 759 (26. 8%) were submitted in 1966. The high loss of roe deer during 1966 was due to an extremely severe winter in most parts of Sweden. Starvation had contributed to the deaths of about 70% of the roe deer examined in 1966, while in most normal years starvation is associated with the deaths of about 50% of the deer examined.

The annual natural mortality in reindeer is even more difficult to estimate. All the reindeer in Sweden are more or less domesticated, slaughter is selective and shortage of food is compensated for by extensive supplementary feeding. Factors like these and others make it difficult to estimate the natural reduction of the population.

Roe deer are also fed supplemental feed rations during the winter. The extent of supplemental feeding varies depending upon the severity of the winter. Thus, during the winter of 1965-66 extensive relief feeding was carried out. The relief food is most often hay or some special wildlife feed stuffs available on the market, or both. Feeding is usually concentrated at certain sites with a rack for hay and a tray for the wildlife feed. Even though feeding of this kind was very extensive during the winter of

1965-66, the Swedish roe deer population was considerably reduced.

During the winter of 1965-66 a surprisingly high number of dead roe deer were found close to the feeding stations (Borg, personal communication). The mortality that occurred even though food was available could be interpreted as being due to a rapid change from natural to artificial food, which gave the rumen microbial organisms too little time to adapt to the new food. In that situation the roe deer could not utilize the food consumed. As many of the animals had their rumens filled with spruce needles and had not eaten any of the artificial food, another possible explanation might be found in the social relationships among the roe deer at a feeding site. This possibility raised the following questions:

1. Are the members in the relatively stable winter groups of roe deer socially organized according to a hierarchical system?
2. If there is a ranking order, is it correlated with the animal's utilization of the food?
3. If there is a ranking order, are high ranked individuals likely to be better adapted to stand severe environmental conditions than low ranked individuals?
4. If (2) and (3) are true, does it mean that it is the 'wrong' animals which are benefitted? Or in other words, do animals with the best natural chance for survival get even better chances, because of winter feeding, whereas animals with poorer natural chances for survival have these chances reduced even further by winter feeding?
5. How should feeding stations by equipped to be beneficial to animals of different social positions?

The situation in reindeer is somewhat different, mainly because they are supposed to be better adapted to stand severe winter conditions than are roe deer. On the other hand, reindeer are living in denser concentrations, are mainly dependent upon digging in snow for the food they obtain. Reindeer are known to be hierarchically organized when artificially fed (Espmark, 1964), and preliminary observations indicate that such an organization is manifested also in natural situations.

When a reindeer herd stops at a fresh winter feeding area, the animals start to dig craters in the snow in which grazing can take place. Digging is most frequent upon arrival at the area and slows down as most of the area becomes covered with craters. From that time onward there is a tendency to extend the existing craters. A well grazed area after a time often looks like a system of complicated labyrinths. In such an area there is a pronounced competition for food. High ranked animals do not tolerate low ranked animals to graze in a crater but chase or threaten them away and take over the crater. High ranked animals also tend to spend more time grazing than do animals of lower social order. The result of this competition will be that the low ranked animals are forced to use already grazed areas or they have to wait for their turn until the more dominant animals are satisfied. The ultimate result might be that dominant reindeer are more likely to survive a hard winter than are low ranked reindeer, which probably will suffer a great deal from malnutrition. It is thus assumed that dominance relationship in reindeer might be a contributing factor in regulating the number of animals under extremely severe winter conditions.

THE ROE DEER STUDY

Turning to roe deer, I want to present some observations made on the behaviour of a roe deer group at a feeding station during the winter of 1970-71. The study was made at the Öster-Malma Laboratory, where the animals were kept within an enclosure of about 30 acres. The group included six individually marked animals (Table 1). The juveniles were born within the enclosure and the adults had been placed there as fawns (Nos. 1 and 2) or as sub-adult (No. 6). There were no filial relationships between the adults. Feeding was begun in the middle of November, but the observations did not begin for 2 months. Thus, the animals were quite familiar with the feeding place by that time. The food consisted of hay rich in clover that was placed in a rack, and a special feed for roe deer with the commercial name of Capré. The special feed was

TABLE 1. AGE, SEX AND FAMILY RELATIONSHIPS OF THE SIX ROE DEER STUDIED

Roe deer Number	Sex	Year Born	Parents	
			Female	Male
1	♂	1967		
2	♀	1967		
3	♂	1970	2	1
4	♂	1970	6	1
5	♀	1970	2	1
6	♀	1966		

placed in roofed trays about 6 m from the rack. The trays were 60 cm in length and 20 cm in width. This made it possible for two animals to stand side by side to eat. Thus, four roe deer could feed simultaneously at one tray. The observations were made from a 5 m high tower about 75 m from the feeding site.

Observations were begun on January 12 and were made on 4 days each week until February 5. The equipment at the feeding site during that period was the rack and tray A (Fig. 1). On February 6 tray B was placed at the feeding site and the second set of observations (Period 2) were not begun until February 16 and were made on 4 days each week until February 26. During the break, the roe deer became accustomed to the new situation. All observations were made during the forenoon and were continuous for 3-4 hours each time. In total, the observations covered 133 hours—84 hours during the first period and 49 during the second.

The roe deer had unrestricted access to hay, which was renewed once a week. The special feed was given when the observations were begun—generally twice each day. The animals did not have free access to the special feed: the daily amount offered was about 0. 5 kg per animal. Because of this restriction, the animals took much of their food from the natural vegetation, which was readily available because of the extremely mild winter (the snow depth never exceeded 4 cm during the observations and the mean temperature was –1 . 5°C). The special feed was restricted in order to enhance the competition between the feeding animals making it easier to study the hierarchical situation.

The special feed was much preferred to hay. Thus, the special feed was eaten during 17 percent of the time the animals stayed on the feeding site while the coresponding figure for hay was 5 percent. Due to this preference, agonistic reactions within the group were numerous, especially during the first observation period. The outcome

Fig. 1. The feeding station during the second observation period.

sub dom	1	2	3	4	5	6
1		124	69	39	72	24
2			3	37	1	32
3				26	4	13
4					6	2
5				2		10
6			2		7	

Fig. 2. The rank order in the roe deer group. The figures stand for victories (across) and losses (down).

of these agonistic reactions was used to determine the dominance order (Fig. 2). The dominance order was almost linear, the exceptions being a few incidents between Nos. 5 and 4, 6 and 3 and 6 and 5. All of these deviations from the linear order fell within the first observation period. During the second period, the dominance order was stable and linear.

The data suggests that sex and age are correlated with the roe deer's possessive social rank. Thus, the only adult buck dominated all other animals, including the older adult doe (No. 6) and the juvenile males (Nos. 3 and 4) dominated the juvenile doe (No. 5). An exception to the trend of older animals being dominant over younger ones was No. 6, the oldest animal in the group, which was subordinate to all the others (except in the incidents indicated in Fig. 2), even to her juvenile son (No. 4). A possible explanation for this exception was that this doe was taken care of when about 7 months old after being found seriously wounded in a hind leg by a fox (*Vulpes vulpes*). After another 3 months, she was released in the enclosure. Although she was rapidly recovering, she was still seriously hampered in her locomotion and was rejected by the other roe deer. Although she eventually fully recovered, it was assumed that her low social status remained as a result of conspecific treatment during the period of recovery.

In all, 473 agonistic encounters between the roe deer were observed at the feeding place. The encounters were most frequent during the first observation period, when the animals had access to only one tray containing the special feed. The frequency of aggressive encounters dropped significantly after the placing of another tray at the feeding site (Fig. 3). The difference in agonistic behaviour between the two observation periods is also shown in Fig. 4, which also indicates the difference in the number of attacks received by the various deer. Doe No. 2 was the animal most often attacked during the first period: all the attacks were by the adult buck. In the second period, No. 4 received more attacks than any other animal in the group.

As indicated in Fig. 2, there was a great difference in tolerance between the pairs of animals. This difference is also indicated in Fig. 5, which shows the frequency of

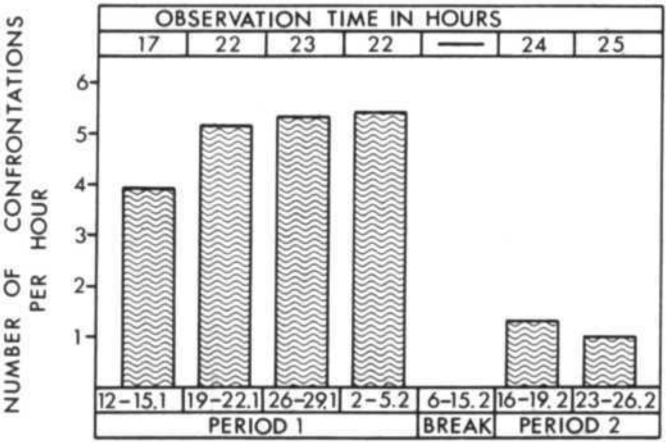

Fig. 3. Frequency of aggressive reactions during the two observation periods.

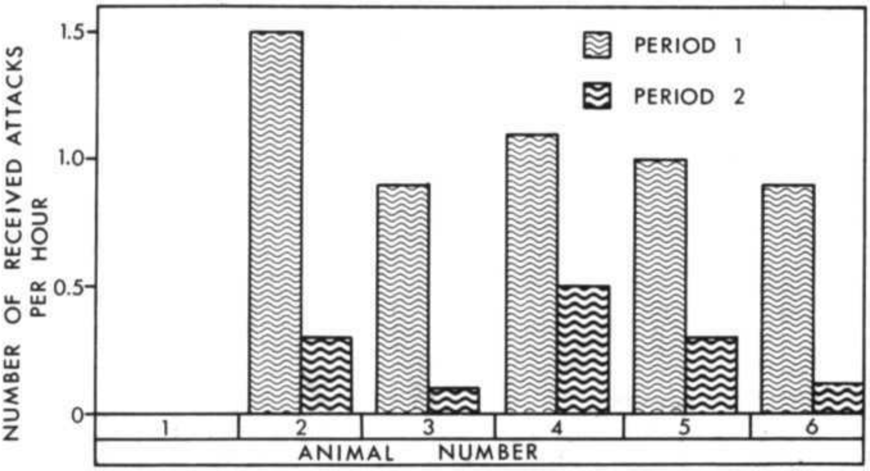

Fig. 4. Frequency of attacks received by each roe deer during the two observation periods.

simultaneous stays at the A-tray by each respective pair. The most frequent pairs were made up of the combinations of adult buck—juvenile buck (1-3 and 1-4), mother-offspring (2-3, 2-5 and 6-4) and of juveniles belonging to the same family (3-5). Fig. 5 also shows that simultaneous feeding was less frequent with reduced competition for food during the second period when two trays were available than in the first period when only one food tray was available. Doe No. 6 only sporadically stayed at the feeding tray with roe deer other than her male offspring.

The aggressions were classified into four principally different types: threat, chase, butting and striking with the front hooves. Due to variations in the intensities of the aggressions, one type often changed into another. The frequency of the different types and their intermediates are shown in Fig. 6. Brief descriptions of the four main types of aggressive behaviour follow.

Threat was seen in all animals and was the most frequent aggressive behaviour. It was observed in two different forms. A dominant animal threatened by tossing its

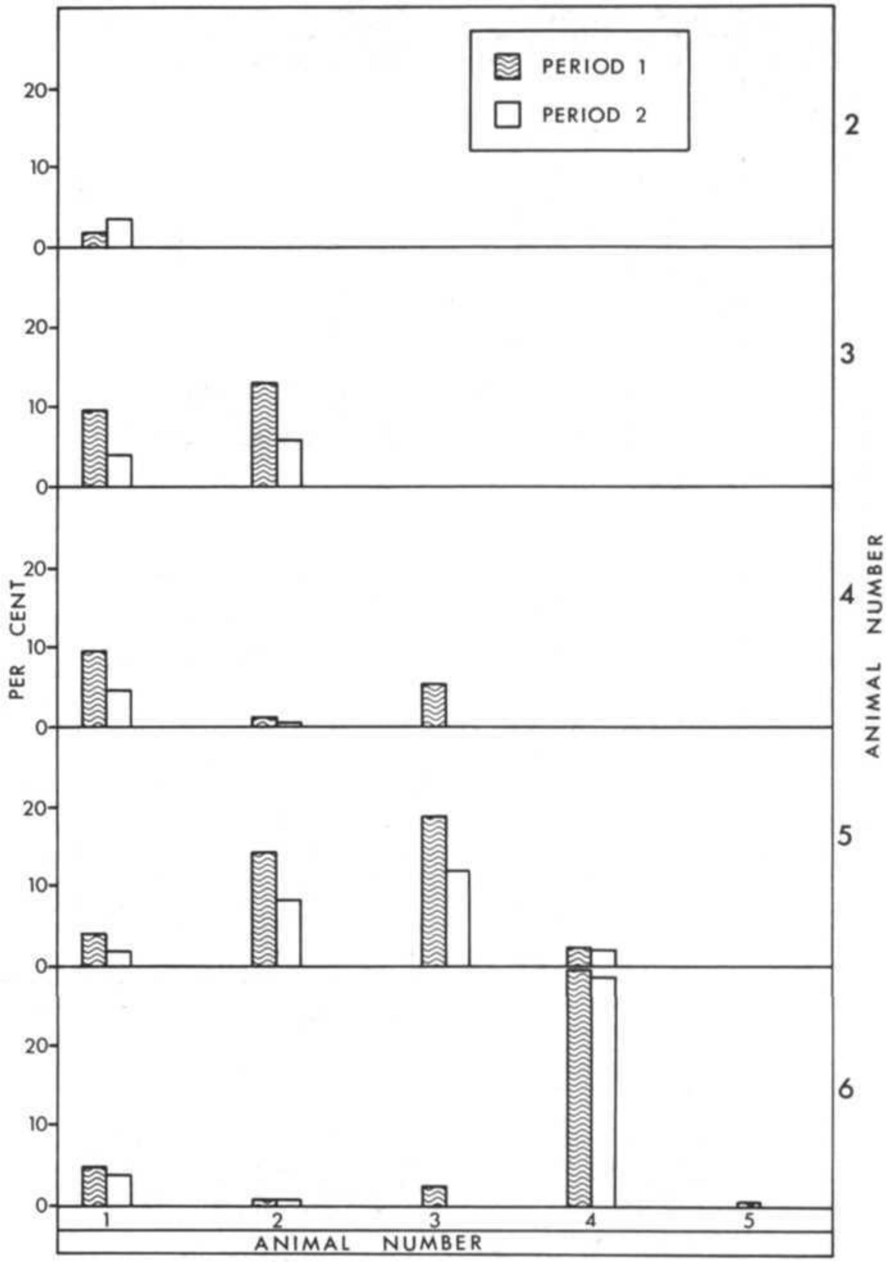

Fig. 5. Frequency of simultaneous periods spent at A-tray by each pair. Expressed as the percentage of total feeding time.

head towards an animal of lower social order. This threat form occurred when two roe deer were standing close to each other at a tray. The other form which might be called head-high threat, occurred when a dominant animal approached a subordinate one. The threatening animal moved slowly with a stiff gait, the neck was held almost vertical, the nose was drawn backwards, the ears were slightly laid back, and the eyes were slightly narrowed.

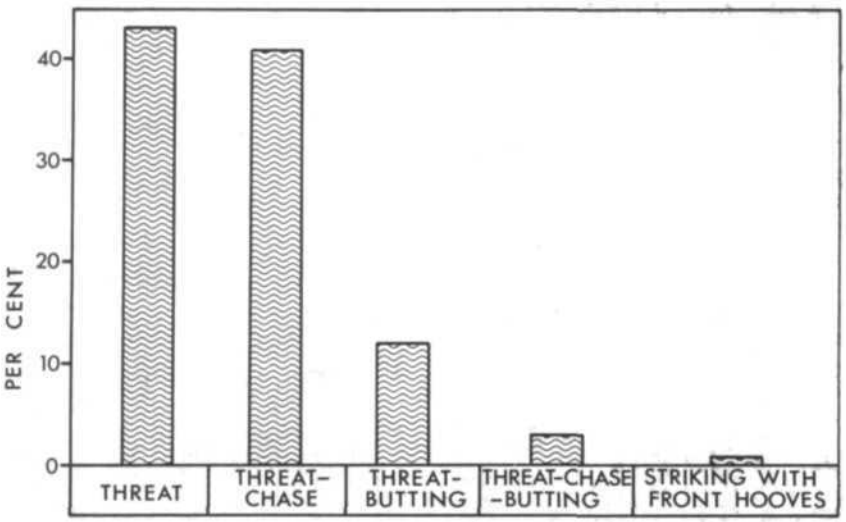

Fig. 6. Frequency of different types of aggression expressed as a percentage of total number of observations.

Threat was not always sufficient to release withdrawal in the threatened animal. With a higher level of aggression the threat would turn into a *chase* of over 10 to 15 m. The chasing animal held its neck somewhat above the horizontal plane, the nose was drawn backwards, the ears were laid back, and the eyes were narrowed. Threat with subsequent chase was observed in all roe deer and made up 41 percent of all agonistic encounters observed.

Butting occurred in 15 percent of all observations and was observed in both sexes. In most incidents butting was preceded by threat and the attacked animal was always hit on its flank or neck. Butting was also seen in connection with the chase. Eight observations were made of head-on fights between bucks. The intensity of these fights was apparently much lower than when the attacks were directed against other parts of the body, and it was sometimes difficult to see whether the head-on fights were manifestations of real aggression or of play. In all incidents, the fight started very carefully, the opponents slowly pressing their foreheads together. A gradual increase in severity of the fight followed, and the dominant roe deer directed its attacks against the neck and flanks of the opponent, who ultimately fled.

Striking with front hooves was observed only in three cases (Nos. 1 and 2). The attacks were preceded by the threat, but when this did not release withdrawal in the threatened animal, the dominant roe deer rushed at the subordinate ane and slapped it repeatedly on its flank with a front hoof.

The relationship between social status of the roe deer and the time they spent eating was tested with rank correlation (Dixon and Massey, 1969). No correlation was found when comparing social status with the total feeding time (Fig. 7).. However, when looking separately at the consumption of hay and the special feed it appears that high ranked animals spent significantly more time eating the special feed than did animals of lower ranking order ($r = 0.772$; $0.05 < p < 0.025$). On the other hand, low ranked animals tended to spend more time eating hay than did high ranked animals although this connection was not statistically significant ($r = 0.714$; $p < 0.05$). This could indicate, however, that low consumption of the special feed was compensated for by an increased intake of hay, and that hay was considered as survival food when compared with the special feed. There was also a tendency for low ranked animals, No. 6 in particular, to visit the feeding place at times when other deer were absent.

When at the feeding site, the feeding activity of the animals varied considerably. No. 6, for instance, was feeding almost 40 per cent of the time she spent at the feeding site during the second observation period, whereas No. 3 spent less than 20 per cent of his time feeding while he was at the feeding site (Fig. 8). When comparing the two animals as to their total feeding time, however, No. 3 spent more time eating than No. 6 (Fig. 7).

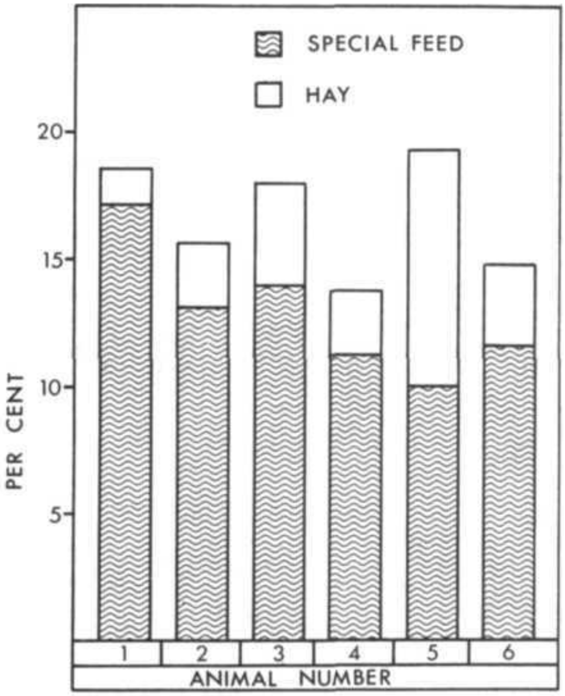

Fig. 7. Feeding frequency expressed as a percentage of the total feeding time of the roe deer group.

Fig. 8 also indicates the effect upon feeding activity of the change made at the feeding site at the end of the first observation period. On the average, the time spent feeding on the special feed increased from 15. 5 per cent in the first period (when only one tray was available) to 20. 0 per cent in the second period when the deer had access to two trays. The relative amount of time spent feeding on hay was about the same during both periods (an average of 5. 1 and 4. 8 per cent of the total time spent feeding, respectively).

CONCLUSIONS

Before any similar data can be presented for the reindeer, extensive observations will have to be done on individually marked animals of known age, sex and filial relationships. The study on roe deer presented in this paper is only preliminary and generalizations should be made with caution. This is due to the small number of animals observed and also to the restricted environmental conditions of the deer. In order to obtain conclusions based on more numerous observations and more representative material, further study of roe deer under natural conditions is proceeding, From the present data, however, it can be stated that roe deer in a winter group are socially organized according to a hierarchical system. It is also evident that the utilization of attractive artificial food is greater in high ranked animals than in animals of lower social order. This condition had apparently no dangerous effect on the low ranked roe deer in the present study. In interpreting this, however, the

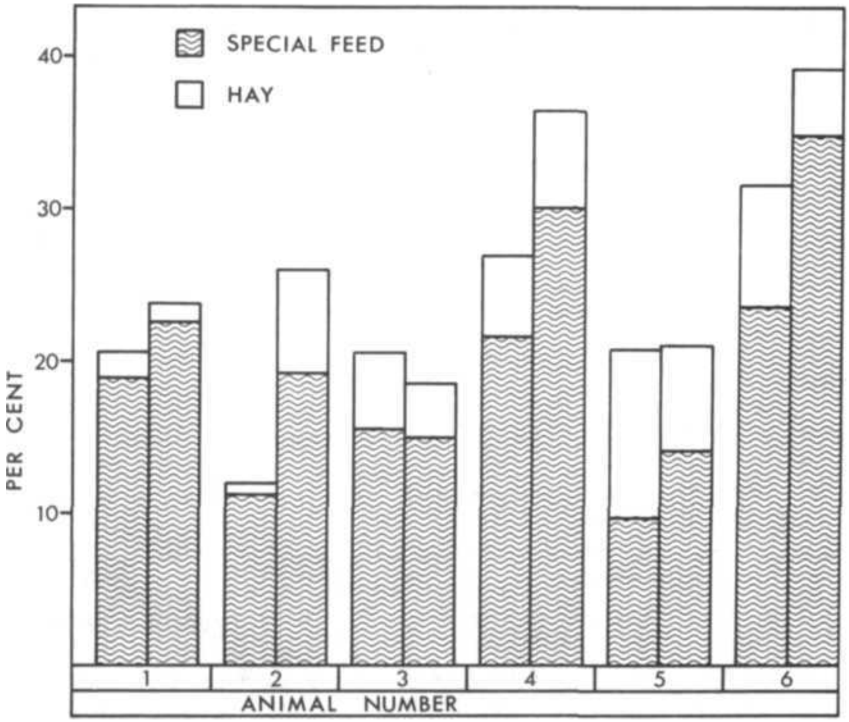

Fig. 8. Feeding activity of the roe deer expressed as a percentage of the time the deer stayed at the feeding station, the differences between the two observation periods being indicated for each animal.

extremely mild winter, which made it easy for the animals to find natural food, should be kept in mind. Furthermore, the animals in this study had easy access to artificially supplemented food when compared with most roe deer fed in the wild. It is thus expected that the relationship between social order and utilization of supplementary food will be even more evident in roe deer living in the wild under severe winter conditions.

When roe deer are accustomed to a feeding place, they spend a considerable part of their time there. The roe deer in this study spent more than two-thirds of the observation time at the feeding site. This means that animals of low ranking order are attractd to the feeding site but that they have relatively few possibilities for obtaining food. Under unfavourable conditions, this could result in starvation, inanition and death in these animals.

Supplemental feeding of roe deer in winter is primarily meant for those animals which are expected to suffer most from lack of natural food. If the assumption is right that the lowest ranked animals are in the deprived group, the connection between social order and utilization of artificial food indicated in this study, strengthens the assumption that the relief is given to wrong animals.

This is likely to happen when the feeding stations are so sparse that a group has to rely mainly upon one station and when food is given in restricted amounts in a single device at the feeding site. The study indicates that the number of aggressive encounters between roe deer is reduced and the feeding time increased when the animals have access to more food facilities at the same feeding site. Further experiments will show whether this is an effective method to extend the relief to more roe deer without using more food, that is, to obtain a more adequate distribution of the food among animals of different social orders.

It is evident from Borg's report (1966) that roe deer in the age group 1-7 years are better adapted to withstand hard winter conditions than are young (< 1 year) and old (< 7 years) animals. Of the roe deer suffering from inanition, 48. 8 per cent were juveniles, 37. 2 per cent were adults, and 14. 0 per cent were old animals. In comparing these figures with the age composition found in a natural roe deer population (Andersen, 1953; von Essen, 1958), it appears that juveniles and old animals are more likely to be victims of starvation than are adult animals. Further observations will show whether these exposed categories are socially subordinate as to food competition and whether this condition could have an influence upon the high mortality rate.

ACKNOWLEDGEMENT

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Paper No 45

The Relationship of Caribou Migration Behaviour to Pipeline Construction

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ABSTRACT

An investigation of the impact of a proposed buried gas pipeline across the migration routes of the Porcupine caribou herd of the Yukon Territory is being conducted by a consortium of oil and gas companies sponsoring the proposed pipeline. It was noted that the caribou have been quick to use seismic line clearings for travel routes, probably because they present unrestricted view and compacted snow conditions. It is anticipated that they would similarly use a pipeline right-of-way.

INTRODUCTION

Two years ago the Trans-Alaska Pipeline Systems (TAPS) proposed to build an elevated, 48-inch pipeline from Prudhoe Bay to Valdez on the Gulf of Alaska to carry oil from the Arctic Coast on its overland journey, en route to west coast American ports. The proposal quickly met heavy opposition from conservation groups in Alaska and the lower forty-eight states. Canada officially added its voice to the opposition pointing out the risk of oil spillage from tankers along its Pacific coast. It soon became evident that the TAPS officials had not paid adequate attention to the possible damage that a heated oil pipeline might inflict on the Alaskan environment. The conservation forces were able to obtain a court injunction and the issue of a permit for the construction of the pipeline has been postponed until the United States government authorities have been satisfied that adequate steps would be taken to minimize damage to the environment.

The Alaskan pipeline controversy did not go unnoticed or unheeded in Canada. A group of Canadian Oil Companies joined to build the Mackenzie Valley Test Facility at Inuvik in early 1970, to examine the effects of buried and elevated oil pipelines on the Arctic environment. The Department of Indian Affairs and Northern Development, that holds the responsibility for the Northwest and Yukon Territories affairs, commenced to prepare a set of land use regulations, and in September, 1970, the federal government issued a series of guidelines to companies interested in the construction of northern pipelines. One of these guidelines was that they were expected to undertake environmental research and be prepared to submit reports on their findings.

Amid the furore over the effects of transporting hot oil in pipelines over Arctic lands underlaid by permafrost, scant attention has been paid to the problem of carrying the natural gas associated with the Arctic oil reserves. The reserves of natural gas at Prudhoe Bay, Alaska have been estimated at 26 trillion cubic feet. This resource will find a ready market in the United States and Canada by 1975. Three groups of oil and gas transmission companies are currently conducting feasibility studies to transport this natural gas to various southern markets.

The Northwest Project Study Group is a consortium of six firms: three oil producers with holdings at Prudhoe Bay, Alaska: Atlantic Richfield Co., Humble Oil and Refinery Co. and Standard Oil Co. (Ohio); and three gas transmission firms: Trans Canada Pipelines Ltd., Michigan-Wisconsin Pipeline Co. and Natural Gas Pipeline Co. of America. The ultimate goal of this group is to construct a pipeline 2, 500 miles long from Prudhoe Bay, to Emerson, Manitoba; up to forty-eight inches in diameter, with a capacity of 3. 5 billion cu. feet of gas per day. The cost is estimated today at three billion dollars, which would make this project one of the most costly ever undertaken by private industry.

Williams Brothers (Canada) Limited of Calgary is conducting the initial feasibility study which itself will cost in excess of twelve million dollars. Various aspects of the feasibility study include: engineering and design, terrain and route studies, potential gas reserves along the proposed pipeline route, economic feasibility and financial support, sociological and economic studies of possible impact on northern communities and residents, and environmental and wilflife studies.

Included in the feasibility study has been the construction of the $3. 5 million Arctic Test Facility at Sans Sault on the Mackenzie River, north of Norman Wells. At this site studies can be carried out on fully instrumented sections of buried and elevated gas pipeline in order to indicate reactions under different environmental conditions.

The environmental and wildlife studies included in the overall feasibility study have a budget of $2. 5 million and in themselves constitute the most comprehensive study of wildlife and vegetation ever financed by private industry in northern Canada. The objectives of these studies are: (1) to define possible areas of conflict between construction and operation phases of a gas pipeline and the wildlife resources and to establish procedures to avoid or minimize such conflict; (2) to find means to suitably restore vegetation cover over a buried pipeline in order to avoid thermal erosion and arrest surficial erosion; and (3) to provide baseline information on the status of the biota before pipeline construction that would serve as a basis for future resource planning and management by government authorities.

Five field parties were in the field during 1971, one each studying: fishes, birds, big game, furbearers and vegetation. The field studies commenced in April, 1971, and will continue through the 1972 field season. A total of thirteen biologists and their technical assistants were involved in these field programmes. Much useful material has been gathered with respect to fish populations, avifauna, furbearers and vegetation cover during the first year, but I propose to limit my remarks to the caribou research program during the remainder of this paper.

The caribou, big game and furbearer studies are being conducted by Renewable Resources Consulting Services of Edmonton. The caribou research team is led by Elmer De Bock, assisted by John Russell and Glen Semenchuk. I serve in the role of consultant in mammalogy, and have had the pleasure of joining them during different periods of the field study. Much of the following information has come from their observations and I am pleased to acknowledge their contributions to this report.

THE CARIBOU PROBLEM

From the very beginning of public interest in the possible environmental effects of northern pipelines, grave concern has been expressed over the risks to the survival of the wild native caribou inhabiting northern Alaska and Canada along the proposed pipeline routes. As a caribou researcher I shared some of this apprehension and was very pleased for the opportunity to join a research team studying the problem before a pipeline was actually approved.

The natural gas pipeline route proposed by the Northwest Project Study group passes eastward from Prudhoe Bay, on the Arctic coast of Alaska, across northern Yukon Territory and up the Mackenzie Valley to the Alberta boundary, west of Great Slave Lake. This route traverses the home range of the Porcupine (International) herd of barren-ground caribou (*Rangifer tarandus granti* J. A. Allen.) as well as the range of scattered herds of woodland caribou (*Rangifer tarandus caribou* Richardson) in the Mackenzie Valley. The Porcupine herd is probably the least known of all the major herds of barren-ground caribou in North America. Far more attention has been paid to the herds east of the Mackenzie Valley in Canada, and to the herds in western and central Alaska. The only previous noteworthy studies are those of Munro (1954) and Skoog (1968). Otherwise information on the numbers and distribution of this herd has been gleaned from scattered individual aerial surveys and reports (Kevan, 1970). In view of its possible hybrid origin between *R. t. groenlandicus* and

R. t. caribou (Banfield, 1961), there was even some question whether the migration behaviour patterns were similar to other herds of barren-ground caribou.

The Porcupine herd was known to winter over a large area of northern Yukon and the north-eastern corner of Alaska and to migrate northward in spring to the Yukon coast and then turn westward to fawn in The Arctic National Wildlife Refuge of Alaska. They usually retraced their path eastward in July to the Yukon coast, occasionally passing down the east slope of the Richardson Mountains immediately west of the Mackenzie Delta in autumn to their little known winter ranges. Two possible gas pipeline routes traverse this vast domain: the northern route lies along the Arctic Coast of Alaska and the Yukon Territory, turning southward around the northern shoulder of the Richardson Mountains, along the east side of the Mackenzie Valley and then southward again. The southern route would cross the Brooks Range south east of Prudhoe Bay and skirt the southern boundary of the Arctic National Wildlife Refuge to the Yukon Boundary, then across the Yukon Territory north of the Porcupine River, crossing the Richardson Mountains in the vicinity of Fort Macpherson and then ascend the Mackenzie Valley southward.

The objectives of the caribou investigations are: to delineate the winter ranges, migration routes, fawning and summer ranges of the Porcupine herd over a two year period, to evaluate the possible effect of pipeline construction and operation upon native caribou hunting, to study caribou behaviour patterns that might be affected by pipeline construction and operation, to determine the seasonal occupancy by caribou of the areas traversed by the two possible routes, and to determine present population level, sex and age segregation and annual increment. The study has been conducted by means of over 600 hours of aerial survey in a light fixed-wing aircraft as well as by jet-helicopter which permitted landing to observe ground conditions. Two-man field camps have also been established among the migrating bands and maintained for periods of a week or more.

Fig. 1. Concentration of caribou on alpine tundra prior to spring migration. (Photo: Renewable Resources Consulting Services, Edmonton).

The results may be summarized as follows. The Canadian portion of the International Porcupine herd was estimated to include about 70,000 animals in the summer of 1971. This is about twice the number previously estimated by Canadian wildlife biologists, but lends credence to American estimates that have placed the grand total as high as 140, 000 animals. The 1971 winter range was located in the Porcupine Highlands, northern slopes of the Ogilvie Mountains and the Trevor Range. The spring migration (Fig. 1) was delayed by deep snow conditions but commenced about April 22, and was in full swing by May 15. Two routes were followed northward: most of the herd travelled directly north crossing the flooded Porcupine River and continued across the Old Crow flats, while the rest migrated north along the western flanks of the Richardson Mountains. Both groups turned westward crossing the British Moutains into Alaska by about June 5. Fawning took place in the Wildlife Refuge but a few fawns were born in the northern Yukon as far east as the Blow River. The herd returned in massed numbers in early July to the southern rim of the Old Crow flats, and then retraced their paths westward again towards the end of the month.

The ground counts of sex and age composition suggested a growing herd, that had a successful reproductive season during 1970, and suffered light calf mortality during the winter of 1970-71. The ratio of yearlings to females plus unclassified animals during the spring migration was 50. 7 per cent, or an adjusted 24 per cent of the total herd. Predation by wolves and grizzly bears appeared to be at normal levels. Native hunters from Old Crow, Yukon Territory and Aklavik, N.W.T.. harvested approximately 400 animals during the spring migration. A rough estimate would place the annual harvest of this herd at approximately 2, 500 animals including hunters from Fort Macpherson, Unuvik and Arctic Village, Alaska.

As far as the immediate problem of caribou and gas pipeline is concerned probably the observations on migration behaviour are of most interest. The Porcupine herd was found to exhibit all the social behavioural patterns recognized earlier in eastern barren-ground caribou herds. These included the traditional cervine matriarchial society (Darling, 1937), with adult cows leading the migration northward in spring while the adult bulls dallied behind on the winter range and followed other routes later. There was the same pattern of migrating in single file (Fig. 2), the refusal to cross old burns or valleys buried in deep snow. Indeed the depth and density of snow on the terrain appeared to be a major factor in delineating winter ranges and migration routes (Pruitt, 1959).

The caribou appeared to follow traditional routes as indicated by deeply rutted trails. They crossed the swollen Porcupine River at the tips of northward pointing peninsulas.

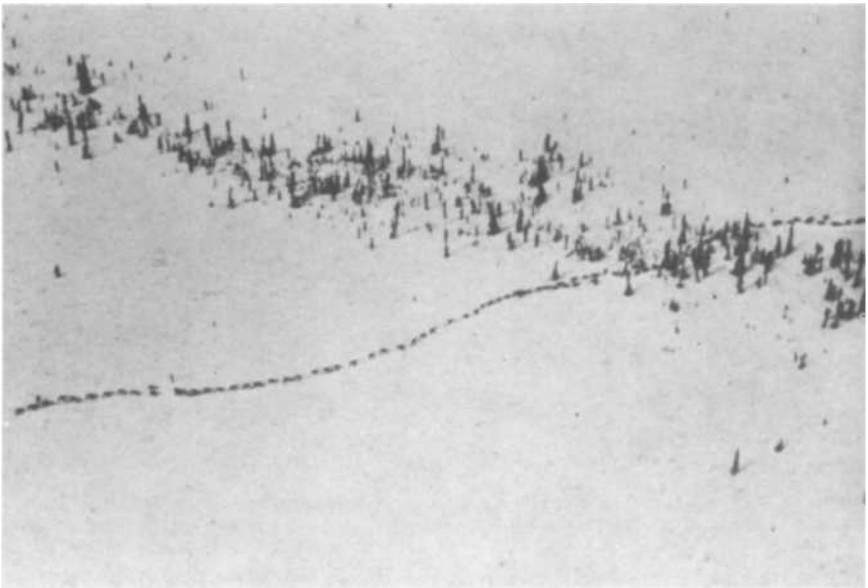

Fig. 2. Caribou migrating single file across a muskeg covered by deep spring snow. (Photo: Renewable Resources Consulting Services, Edmonton).

The village of Old Crow is strategically placed on the north bank of the river opposite one of these points, as are many northern settlements in Canada. During migration the caribou exhibited the usual lack of caution in passing through villages or camp sites that lay in their path. One special feature of their migration was their choice of route in mountainous terrain where they regularly climbed over the steepest mountain slopes perhaps in response to the shallow snow depth, or to utilize terrain offering escape from their predators.

The Porcupine caribou also exhibited the behavioural pattern of congregating into dense herds for a week or two prior to migration (see Fig. 1). These periods of congregation and movement were followed by dispersal over the ground and a loss of momentum. Such congregations occurred prior to the spring migration of pregnant cows and young northward and again in early July after fawning when the young were led back to summer ranges in the northern Yukon where the bands tended to disperse again. There was a final congregation at the rutting period in September and October prior to the migration to winter ranges in the Ogilvie Mountains. This extensive annual migration pattern of the caribou is of importance in locating a pipeline which might be crossed four times per year by tightly packed columns of caribou following traditional routes.

During my earlier studies on caribou east of the Mackenzie Valley I noted (Banfield, 1954) that migrating caribou appeared to choose routes offering the easiest walking conditions such as frozen lakes in winter and gravel eskers at any season. The area occupied by the Porcupine herd is largely unglaciated and therefore lacks the eskers so prominent on the glaciated Precambrian highlands to the east. Much of the winter range in the Porcupine Highlands, however, has recently been traversed by a network of seismic lines and winter roads as a result of oil exploration. It is not surprising therefore to observe how readily the caribou have taken to following seismic lines during their travels (Figs. 3 and 4). When a band of migrating caribou reaches a cleared seismic line or winter road, they often travel along it for some distance, particularly if it leads in the direction of their migration. If it leads off at a tangent to their intended route, they will eventually turn off and resume their normal migration. Such a reaction to cleared lines has aroused some concern, because of certain increased hazards to the caribou. It has been noted that wolves also tend to

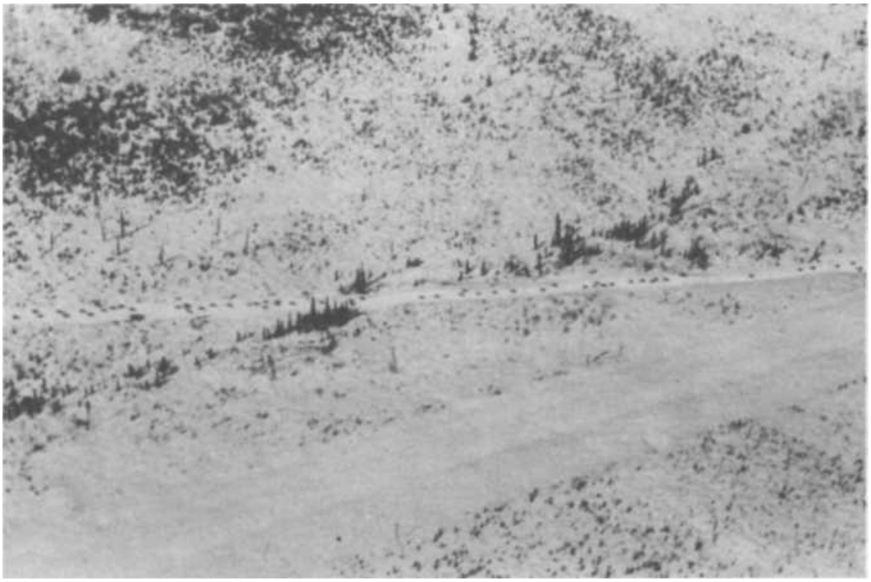

Fig. 3. Caribou migrating along a cleared seismic line. Note animals moving abreast rather than in file. (Photo: Renewable Resources Consulting Services, Edmonton).

Fig. 4. A seismic line cleared the previous winter through the boreal forest. (Photo: A. W.F. Banfield).

hunt along the cleared lines and have an increased advantage over their prey. The caribou attempt to escape by running along the packed snow on the cleared line. As the wolves close in, the caribou plunge into the deeper snow of the woods where they are soon overtaken. We have also speculated on the risks of the pregnant females following the seismic lines for too great a distance and being led away from, or delayed in reaching their traditional fawning grounds; and on the possibility that the migrations might be diverted from normal routes, causing the native hunters to miss their accustomed source of food.

Our particular interest in the caribous' adoption of seismic lines for migration routes lies in the fact that the right of way for a buried gas pipeline covered by a re-established sod will closely resemble the seismic lines. It will therefore introduce all of the above hazards. In addition the passage of migrating files of caribou will have a damaging effect on the pipeline if their hooves cut ruts in the sod allowing the thermal and surficial erosion that the vegetation mat was expected to prevent. For these reasons we plan to conduct experiments on existing seismic lines by placing several snow fence barriers across the lines hoping to discourage their usage.

Gravel berms have been suggested and tested experimentally as insulating covers for elevated pipelines, or pipelines laid on the ground. Knowing the caribou's preference for using eskers as highways, one can predict that caribou traffic would lead to mechanical erosion of the gravel cover.

Another engineering feature of gas pipelines that merits investigation are the compressor stations that would be situated at approximately forty-five mile intervals | along the line. The gas turbines are extremely noisy as well as the gas flowing through pipe elbows under pressure. The noise level at a compressor intake is in the vicinity of 115 decibels. However, the buildings to house the compressors can be insulated with sound-reducing material and the pipes similarly wrapped. It is expected that the sound emission can be reduced to 75 db. or lower, 400 feet from the site. The effects of this level of noise on caribou is not known at present. We hope to simulate it by amplified tape recordings of actual compressor stations at field sites in order to observe caribou reactions. Evidence gathered at compressor stations in southern Alberta leads us to expect that large mammals will not be seriously disturbed by this continuous noise.

Most caribou herds have become accustomed to fixed-wing aircraft flying overhead. As long as the aircraft fly at about 1000 feet or more the caribou are not disturbed and do not change their direction of travel or even rise from their beds. However it has been observed quite generally that they are frightened by helicopters flying at the same heights. The newer jet helicopters seem to be particularly disturbing to caribou, often causing them to change their direction of travel.

Considerable concern is felt over the possible effects of increased air traffic during the construction phase of the pipeline. Helicopter traffic over the fawning grounds might well cause mortality among the new born fawns. We hope to quantify our observations on aircraft disturbance in the future.

Thus recent developments in Alaska and Canada have led to close co-operation between industry, government officials and game biologists in examining northern environmental problems associated with proposed pipe-line construction. When I mentioned to the Executive Vice President of Williams Brothers my grave fears about the environmental effects resulting from a disturbance of the permafrost layer, he replied, 'the very same problems that worry an ecologist scare the hell out of a pipeline engineer.' It is these risks of environmental degradation as a result of thermal and surficial erosion that has led the engineers to plan on trenching, laying the pipe, backfilling and insulating during the winter months so that the permafrost will not be disturbed. They plan on the pipeline being encased in frozen ground through the Arctic sector of the pipeline. The gas flowing through the pipe would also be chilled to a temperature approximating the surrounding permafrost to provide stability to the regime.

Such a winter construction program along the proposed route would have little effect on the caribou population if they occupied winter ranges in proximity to the 1970-71 winter ranges. The Porcupine herd, however, has in the past wintered on the Old Crow flats, near the southern alternative route.

In conclusion I would say that at the present point in our investigations, it appears that the construction of a buried natural gas pipeline as proposed does not in itself constitute a grave risk to the survival of the migratory International Porcupine herd of caribou. If it was associated with an elevated oil pipeline, a road and a communications line, the total effect would be more of a hazard to caribou. There are several other problems evident but it is likely that suitable solutions can be found (Figs. 5

Fig. 5. Winter road across the Porcupine highlands.

Fig. 6. Rich grass sward resulting from climax vegetation disturbance on the winter road.

and 6). The decision whether to build a pipeline or not, and where, will not be based solely on the effects on the caribou populations, but rather on a full consideration of many environmental factors. It is encouraging, however, to see industry, government and conservation groups working together to plan the harvest of petroleum resources without causing irreparable damage to the fragile Arctic and Subarctic terrestrial ecosystems.

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Paper No. 46

Reaction of Caribou to Various Types of Simulated Pipelines at Prudhoe Bay, Alaska

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ABSTRACT

Two pipeline simulations with passage provisions for caribou movements have been constructed by Alyeska Pipeline Service Company and BP Alaska, Inc., at Prudhoe Bay, Alaska. Research objectives of the study are outlined. Summaries are given of the movements of 1, 707 recorded caribou encounters at both sites. A 20-minute 16 mm film has been prepared to illustrate some response differences of individuals and groups of caribou to the pipelines. A brief outline is also given of a research proposal to study the reactions of semi-domesticated reindeer to simulated pipelines on Seward Peninsula, Alaska.

INTRODUCTION

The discovery of large oil deposits on Alaska's North Slope in 1968 by Atlantic-Richfield and Humble Oil and Refining Companies has initiated much interest in the impact of man's continued encroachment on the Arctic ecosystem. Moreover, the proposal to transport the large reserves by a 48-inch (120 cm) pipeline 800 miles (1287. 5 km) from Prudhoe Bay to the ice-free port of Valdez to the south has seeded much controversy between industry and conservationists. One issue receiving much debate is whether or not sections of the pipeline which are above ground could prove to be insurmountable barriers to caribou during their traditional migrations.

In order to gain an insight into the reactions of caribou to pipelines and associated crossing facilities, a study was begun this summer to observe the reactions of caribou on their summer range to man-made obstructions. Co-sponsored by Alyeska Pipeline Service Company, BP Alaska, Inc., and the U.S. Bureau of Sport Fisheries and Wildlife, two simulated pipelines were constructed at Prudhoe Bay.

THE FIRST SIMULATED PIPELINE

With 4 foot snowfencing, Alyeska constructed an optical barrier to simulate a 48-inch pipeline. Approximately 10, 200 feet (3. 2 km) in length, the snowfencing was elevated 20 inches (50. 8 cm) above ground surface on 10 foot (3.1 km) spruce poles of 4-6 inch (c. 12. 7 cm) diameters spaced 25 feet (7. 6 cm) apart. Burlap was stapled along the total length of the fence on the windward side to reduce the possibility of wind movement but more importantly to present as complete an optical barrier to caribou as possible.

Two gravel ramps of 100 foot (30. 5 m) and 75 foot (22. 9 m) lengths, 8 foot (2. 4 m) heights, and four underpasses served as passage provisions for caribou. Three of the underpasses, each 100 feet in length, were raised above ground approximately 7 feet 8 inches (2. 3 m). The fourth underpass was 150 feet long with a ground clearance of approximately five feet (1.5m). In an attempt to simulate the three dimensional configuration of an elevated pipeline, it was decided to erect all underpasses with a double span of snow fencing placed 4 feet (1. 2 m) apart on 8 inch (20. 3 cm) spruce poles at 25 foot (7. 6 m) centers. A tower, 14 feet (4. 3 m) in height was erected 45 yards (41. 2 m) fromthe structure to facilitate our observations and photography of caribou behavior (Fig. 1).

Fig. 1. A small band of caribou feed near the snowfence-burlap barrier constructed to simulate the proposed 48-inch pipeline. Note the gravel ramp and the underpass provided to facilitate caribou movements across the structure.

THE SECOND SIMULATED PIPELINE

BP Alaska, Inc., on the other hand, using 20 foot (6. 1 m) joints of 24 inch (60. 9 cm) galvanzied culverting constructed a 3, 600 foot (1097. 3 m) pipeline. Of the total length, 3, 000 feet (916 m) was raised 30 inches (76. 2 cm) above ground anchored to waterfilled oil drums spaced 20 feet (6. 1 m) apart. In order to simulate the gathering and feeder lines considered for use in the Prudhoe Bay oilfields, the remaining 600 feet (182. 8 m) was raised on pilings to give ground clearances of 8 (2. 4 m), 6 (1. 8 m), and 4 (1. 2 m) feet. Within this section of pipe, an expansion loop 20 × 40 feet (6. 1 m × 12. 2 m) in size was constructed and canted eastwards to provide ground clearances of 6 (1. 8 m) and 8 (2.4 m) feet above the surface of the gravel road and tundra respectively. This length of elevated pipeline provided what was assumed to be the ground clearances necessary to permit caribou passage. At the northern terminus a cable was stretched for a distance of 900 yards (0. 8 km) atop oil drums spaced at intervals of 30 feet (9. 1 m). Strips of fluorescent 'dayglo' flagging were fastened to the cable at 5 foot (1. 5 m) intervals along the total length. Intended to act as a lead, the cable-drum barrier was expected to channel caribou against the elevated pipeline. A tower was erected also to facilitate observation of caribou responses to the barrier (Figs. 2 and 3).

RESEARCH OBJECTIVES

Field data and observational records were centered on three general themes:

(a) Behavior of individual caribou and caribou groups in the vicinity of man-made obstructions.

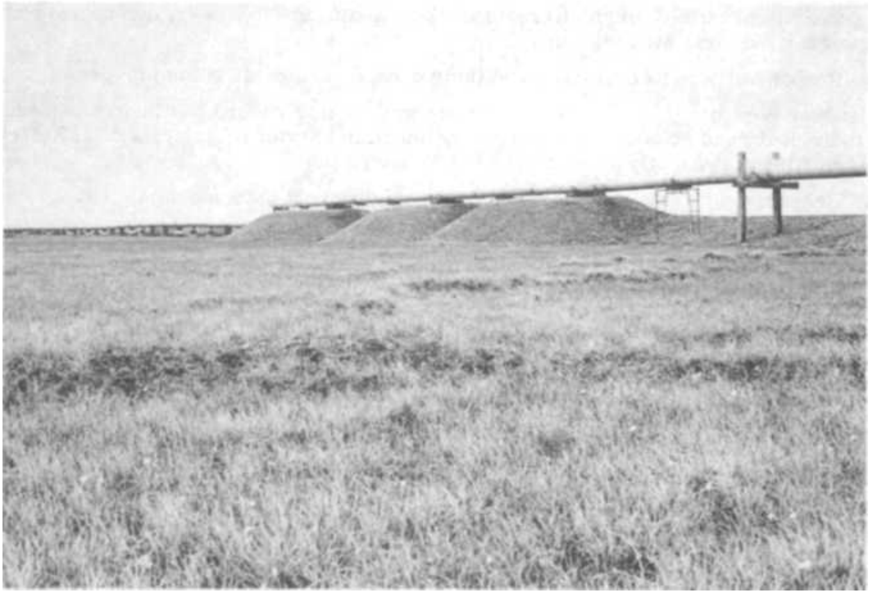

Fig. 2. Looking south along the 24-inch culverting constructed to simulate the transit-feeder pipelines proposed for use at Prudhoe Bay. Gravel embankments and wooden piling supports give an 8 and 5-foot clearance, respectively, in the underpasses, considered sufficient for passage of caribou beneath the obstruction.

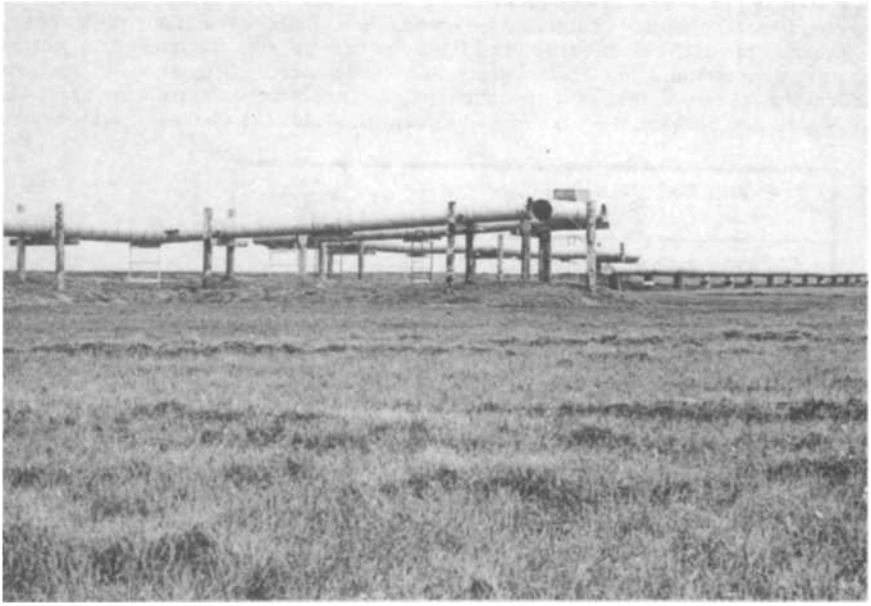

Fig. 3. Looking north along the simulated transit-feeder pipeline. The expansion loop provided a maximum clearance of 8 feet, believed sufficient for easy passage of caribou across the pipeline. The observation tower and its ladder can be seen behind the open ended section of culverting.

(b) Reactions of caribou when presented with deflection or choice situations that is, when in proximity to an alternate method of passage (ramp vs. underpass) over or under the simulated pipeline.

(c) Responses of maternal cows and their calves when confronting pipelines.

Whenever possible, 16 mm cinematography was used to record continuous sequences of individuals and groups encountering the pipeline barriers. Analysis of 3200 feet of 16 mm film is presently being conducted to determine:

(a) Response differences of caribou groups of different size and composition to simulated pipelines.

(b) Response differences of caribou groups of similar size and composition to simulated pipelines.

(c) Individual response differences of cows, calves, yearlings and bulls to pipelines.

(d) Response differences of groups and individuals when encountering deflection or choice situations (ramps vs. underpasses).

RESULTS

During the observation period, June 8 to August 8, a total of 1, 707 caribou encounters was recorded at both sites by direct observations (1521) and track counts (186). Of these, 605 observations were made at the BP feeder line simulation and 916 recorded at Alyeska's 48-inch 'pipeline'.

Once encountering either simulation, caribou were observed to follow similar movement patterns. At Alyeska's site in 1, 102 encounters; 136 (12. 4%) used ramps; 60 (5. 4%) walked through underpasses; 7 animals (0. 6%), 3 calves, 2 yearlings, 2 unknowns, crawled beneath the fence (raised 18 to 20 inches above ground) and 899 (81. 6%) were diverted in their course of movements (Table 1). Likewise, at the BP site, in 605 observed encounters, 101 (16. 7%) returned to the east; a total of 495 animals (81. 8%) were diverted in their movements along the pipe to its terminals; and 9 caribou (1. 5%) crawled beneath the pipe (Table 2). However, when computed on basis of the numbers of animals approaching the structures from the east or west the movement patterns become more meaningful. At the burlap-snowfence barrier (Fig. 4) of 301 'eastern' encounters approximately equal proportions of animals used the passage provisions (42. 5%) as had coursed the barrier to its terminals (43. 2%) whereas 13. 6% returned

TYPE AND DIRECTION OF MOVEMENT	*NUMBER OF ANIMALS*	*PERCENT*
I. Diverted movements:		
(a) from west to north	*73*	*6.6*
(b) from west to south	*80*	*7.3*
(c) from east to north	*58*	*5.4*
(d) from east to south	*72*	*6.5*
II. Reversed movements:		
(a) to east	*41*	*3.7*
(b) to west	*575*	*52.2*
III. Using passage provisions:		
(a) ramps	*136*	*12.3*
(b) underpasses	*60*	*5.4*
(c) under fence	*7*	*0.6*
Total	*1,102*	*100.0*

TABLE 1. MOVEMENTS OF 1, 102 CARIBOU OBSERVED AT ALYESKA'S SIMULATED 48 INCH PIPELINE

TYPE AND DIRECTION OF MOVEMENT	NUMBER OF ANIMALS	PERCENT
I. Diverted movements:		
(a) from west to north	32	5.3
(b) from west to south	15	2.5
(c) from east to north	20	3.3
Id) from east to south	428	707
II. Reversed movements:		
(a) to east	101	16.7
(b) to west		
III. "Crawlers"	9	1.5
Total	605	100.0

TABLE 2. MOVEMENTS OF 605 CARIBOU OBSERVED AT BRITISH PETROLEUM'S SIMULATED FEEDER-TRANSIT PIPELINE

to the east. Of the 801 'western' encounters, only 8. 4% had used the ramps and underpasses whereas 19. 0% had coursed the barrier to its terminals and 575 animals (71. 8%) returned to the west. At BP's feeder-transit pipe simulation, the movement patterns of caribou, although similar, differed proportionally from those described at Alyeska's site (Fig. 5). The greater proportion of caribou encountering the structure from the east and west were diverted in their course of movements to the ends of the structure. Of the smaller proportions, some were reversed from their original direction of travel to the east (18. 2%) and only 9 animals (1. 5%) crawled beneath the pipe.

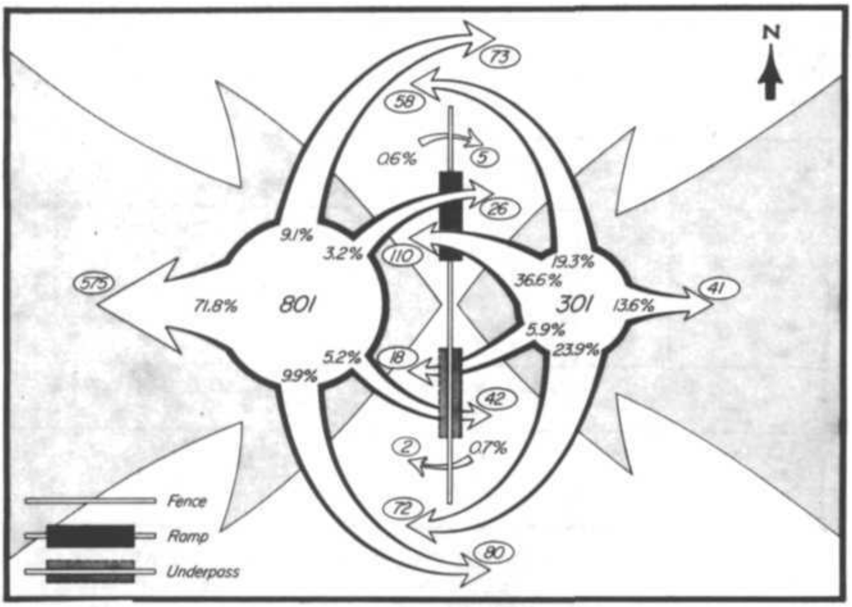

Fig. 4. Movements of 1, 102 caribou encountering Alyeska's simulated pipeline.

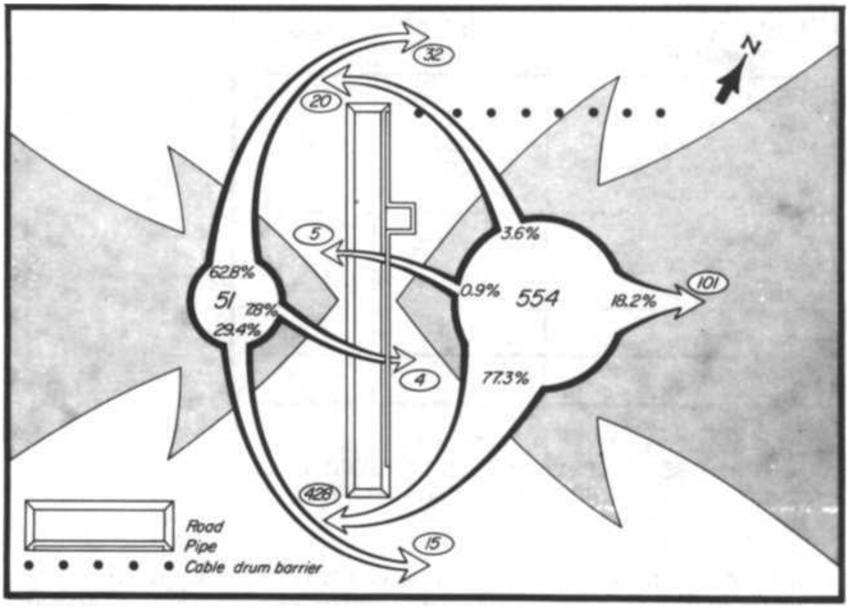

Fig. 5. Movements of 605 caribou observed at British Petroleum's simulated feeder-transit pipeline.

The frequency of use of passage provisions at Alyeska's snowfence barrier was seen to differ with respect to age and sex classes, and group size. It was found that a greater proportion of caribou using ramps were cows, calves and yearlings than was the case for underpasses (Table 3). Also, groups smaller than 11-15 animals in size made greater use of ramps and underpasses than groups of larger size even though a large proportion (48%) of these smaller groups were diverted along the course of the barrier. Generally, groups of smaller size were more inclined to investigate any passage provision encountered than was the case for groups of size larger than 6-10 animals (Table 4). Nevertheless, they used ramps and underpasses less frequently than individual caribou (Table 5a). When considered as individuals however, 83% of

AGE AND SEX CLASSES	*COMPOSITION OF ANIMALS USING*			*NUMBER OF ANIMALS DIVERTED*	*TOTAL*
	RAMPS	*UNDERPASSES*	*UNDER FENCE*		
Cows	*12(37.5)*	*4 (12.1)*	—	*308(36.4)*	*324(35.4)*
Colves	*7(21.9)*	*2(6.1)*	*3(60.0)*	*167(19 7)*	*179(19.5)*
Yearlings	*8(25.0)*	*6(18.2)*	*2(40.0)*	*191(22.6)*	*207(22.6)*
Bulls	*5(15.6)*	*21(63.6)*	—	*180(21.3)*	*206(22.5)*
Subtotal	*32(3.5)*	*33(3.6)*	*5(0.5)*	*846(92.4)*	*916*
NUMBER AND PROPORTION OF ANIMALS USING PASSAGE PROVISIONS FROM TRACK COUNTS - COMPOSITION UNKNOWN					
No tracks	*104(55.9)*	*27(14.5)*	*2(1.1)*	*53(285)*	*186*
Total	*136(12.4)*	*60 (54)*	*7(0.6)*	*899(81.6)*	*1,102*

TABLE 3. COMPOSITION OF 916 CARIBOU OBSERVED AT ALYESKA'S SIMULATED PIPELINE AND OF 70 ANIMALS USING ALL PASSAGE PROVISIONS.
FREQUENCY OF USE OF PROVISIONS IN 1, 102 RECORDED INDIVIDUAL ENCOUNTERS IS SHOWN

all animals that had encountered the fence were diverted from their original course; the smaller portion moving to its terminals and the larger portion returning from whence they came (Table 5b).

GROUP SIZE	*NUMBER*	*NUMBER AND PROPORTION OF GROUPS USING*		*NUMBER OF GROUPS DIVERTED*
		RAMPS	*UNDERPASSES*	
1	*27*	*7 (25.9)*	*12 (44.4)*	*8 (29.7)*
2–5	*29*	*3(10.3)*	*9 (31.0)*	*17(58.7)*
6–10	*13*	*3(23.1)*	*2 (15.4)*	*8 (61.5)*
11–15	*6*	*0(0.0)*	*0 (0.0)*	*6 (100.0)*
16–20	*2*	*0(0.0)*	*0 (0.0)*	*2 (100.0)*
21–25	*4*	*0(0.0)*	*0 (0.0)*	*4 (100.0)*
26–30	*4*	*1(25.0)*	*0 (0.0)*	*3 (75.0)*
31–35	*1*	*0(0.0)*	*0 (0.0)*	*1 (100.0)*
36–40	*1*	*0(0.0)*	*0 (0.0)*	*1 (100.0)*
41–45	—	—	—	—
46–50	*1*	*1(100.0)*	*0 (0.0)*	*0 (0.0)*
51–415	*2*	*0(0.0)*	*0 (0.0)*	*2 (100.0)*
Total	*90*	*15(16.7)*	*23(25.6)*	*52(57.7)*

TABLE 4. FREQUENCY OF CARIBOU GROUPS OF DIFFERENT SIZE AND COMPOSITION USING ALL PASSAGE PROVISIONS AT ALYESKA'S SIMULATED PIPELINE.

GROUP SIZE	*NUMBER*	*NUMBER AND PROPORTION OF GROUPS USING*			*NUMBER OF GROUPS DIVERTED*
		RAMPS	*UNDERPASSES*	*UNDER FENCE*	
Individual(1)	*27*	*7 (25.9)*	*12(44.4)*	*0*	*8(29.7)*
Various (2-415)	*63*	*8(12.7)*	*11(17.5)*	*0*	*44(69.8)*

TABLE 5A. A COMPARISON OF THE FREQUENCY OF USE OF PASSAGE PROVISIONS BY CARIBOU GROUPS (OF DIFFERENT SIZE AND COMPOSITION) AND INDIVIDUALS.

GROUP SIZE	*NUMBER*	*NUMBER AND PROPORTION OF INDIVIDUALS IN 63 GROUPS USING*			*NUMBER OF INDIVIDUALS DIVERTED*
		RAMPS	*UNDERPASSES*	*UNDER FENCE*	
	1,075	*129(12.0)*	*48(4.5)*	*7(0.6)*	*891(82.9)*

TABLE 5B.

DISCUSSION

The present data are mostly inconclusive at this early stage of the study. However, they do lend supporting evidence to show that responses of caribou to man-made obstructions differ among groups and individuals as related to sex, age-class, size and composition of the groups. In most cases, caribou paralleled both barriers for varying distances before returning to their points of origin or seeking access to the other side around the terminals. Use of passage provisions by individuals and groups of caribou was infrequent, but it would be premature to make conclusions at this time on whether this can be expected to hold true. To make this study more complete then, additional information is needed on the ability of caribou to learn to use ramps and pass beneath over-head obstacles. Furthermore, our studies concern only the behavioral responses of caribou at post-calving time and knowledge is lacking on the seasonal response differences of this species to pipelines. In any case, detailed analysis of the behavior of caribou upon encountering the obstructions should be of value in improving the design of passage facilities and further assessing the likely impact of above ground pipelines on caribou movements.

In the summer of 1972, our field studies will be resumed. Our main objectives will be followed as before, but others will be added. First, the responses of individuals and groups on subsequent encounters will be emphasized. Hopefully, individual animals will be anesthetized and tagged and groups marked by aerial application of dyes for later identification. In this way, some indication will be given of the numbers of animals that return and attempt to overcome the pipeline. Needless to say, the recognition of animals will provide an opportunity to study the ability of caribou to learn to overcome man-made obstructions. Also, response differences of individuals and groups with subsequent encounters should become evident. Secondly, more information is needed to establish a relationship betweeen wind, insects and use of passage provisions by caribou. Next season, insect populations will be sampled on both sides of each barrier. Activity records and use of ramps and underpasses under different wind and insect conditions will be compared to gain an insight on this relationship.

Questions concerning the responses of caribou to pipeline barriers during migrations, pre-calving, calving and rut periods still remain open. Limited to post-calving activities, our present study is inadequately designed and logistically impossible to provide the answers to these questions. Therefore, the U.S. Bureau of Sport Fisheries and Wildlife, U.S. Bureau of Land Management, U.S. Bureau of Indian Affairs and the Alaska Department of Fish and Game have jointly agreed to support a related study of the responses of semi-domesticated reindeer to a simulated pipeline on Seward Peninsula. The main objectives will be similar to those already outlined, but other advantages are offered. With BIA's model reindeer herd we will be able to gain more insight into the response differences of this species to simulated pipelines at pre-calving and rutting times. Seasonal migrations will be simulated. At these times, reindeer will be herded towards the pipeline and observations of their response when under migrational stimuli recorded. Other areas of interest to be considered also in this study can be briefly stated:

(a) Responses of habituated individuals on subsequent encounters,

(b) Responses of reindeer to snowcover phenomena adjacent to the pipe, and

(c) Age and sex-related response differences of individuals.

Moreover, since the Seward study lends itself to some control, hopefully we will be able to further appraise ramp designs and ground clearances required to facilitate easy passage of caribou across the Alyeska pipeline.

With these two studies, we hope to be in a better position to answer some of the many questions being raised on the impact of elevated large diameter pipelines on caribou behavior. This knowledge should benefit both Canada and Alaska at this time especially when oil apparently is the key to the north.

Paper No. 47

Fraying Behaviour and Management of Roe Deer

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ABSTRACT

A study of fraying behaviour in Scottish roe deer *(Capreolus capreolus*) revealed that bucks removed the bark from about 85% of the affected trees by mock fighting and the remainder by rubbing for olfactory marking. Frayed trees were located where bucks were most frequently seen and not necessarily around the borders of territories. Measurements indicated that the effects on individual trees were similar to those reported for continental Europe.

Damage to a plantation was not as great as casual inspection suggested. About one quarter of the trees frayed in 1964 appeared likely to die but only 3-6% of the trees in the plantation had been killed by fraying during the previous 3 years. This loss about equalled that from browsing by roe deer and was less than that from frosting. Results of a shooting experiment suggested that fraying could be reduced most effectively by shooting non-territorial bucks, especially yearlings; indiscriminate shooting would be inefficient and might actually increase fraying.

INTRODUCTION

Many Cervids scrape their antlers against young trees and remove bark from the stems. In roe deer (*Capreolus capreolus*) this behaviour is called fraying. Although the effects of fraying on young conifers in plantations have been well known for many years, they have not been well documented; nor have the behaviour patterns responsible for fraying been scientifically investigated. Explanations by various authors have been based mainly on speculation and have shown little agreement. For example, Schumacher (1936) found scent glands in the foreheads of roe bucks and suggested roe might be marking territories. Tegner (1951) held that bucks were removing velvet from antlers. von Raesfeld (1960) ascribed fraying damage to mock fighting. Hennig (1962a) believed that all these behaviour patterns were involved in fraying. The effects of fraying on plantations in Britain are considered sufficiently serious for the British Forestry Commission to hire 'trappers' to shoot roe deer in many forests.

This paper presents the results of a 1964 study of fraying behaviour in roe deer, including field observations of roe behaviour, counts and measurements of frayed trees and a shooting experiment. These were aimed at answering the questions (1) what behaviour patterns are involved in fraying, (2) how extensive is the damage to plantations, and (3) how can fraying be reduced?

THE STUDY AREA

The main study area was located in southwest Scotland at Castle O'er Forest, a Forestry Commission plantation about 30 km north-east of Dumfries. The elevation was 200-300 m above sea level. The mean daily temperature was 8°C and the annual rainfall about 1200 mm (Clim. Atlas. Br. Is.). Frequent cloud cover and fog reduced sunshine to about 1120 hours annually. The mixed brown forest soils and peaty podsols supported a grassy moor dominated by *Molinia caerulea* and *Nardus stricta.*

During the 1950's Sitka spruce (*Picea sitchensis*) and Norway spruce (*Picea abies*) were planted on about 1850 ha of this moor. These trees were 4-5 m high in 1964. Because of frost damage, some 0.8 ha were replanted during 1960-3 with Scots pine

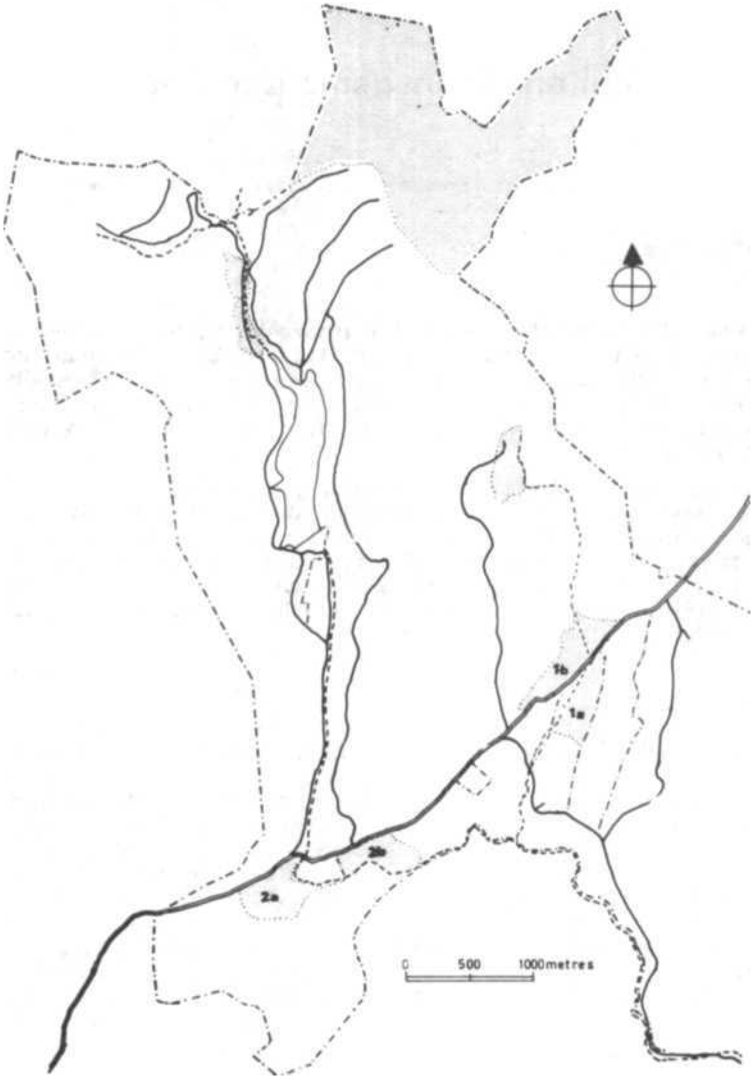

Fig. 1. Castle O'er study area showing the large newly-planted area and six other areas in the forest re-planted after frost damage, all particularly vulnerable to fraying by roe deer. The numbers refer to the shooting experiment treatments. (1) to shoot resident territorial bucks and any which replaced them, but leave other bucks alone. (2) to shoot all bucks *except* territorial bucks.

(*Pinus sylvestris*), lodgepole pine (*Pinus contorta*) and a few Douglas fir (*Pseudotsuga menziesii*) (Fig. 1). The replacements, at about 2 m spacing, were particularly susceptible to fraying by roe deer in 1964 because the older trees provided good escape cover and adjacent grassy areas contained attractive food. 'High seats' or elevated platforms 3-5 m above the ground, had been constructed at each vulnerable spot to assist in shooting the offending roe deer (Fig. 2).

I also observed behaviour of roe deer at two other study areas, one in northeast Scotland and one in southwest England, during 3 years.

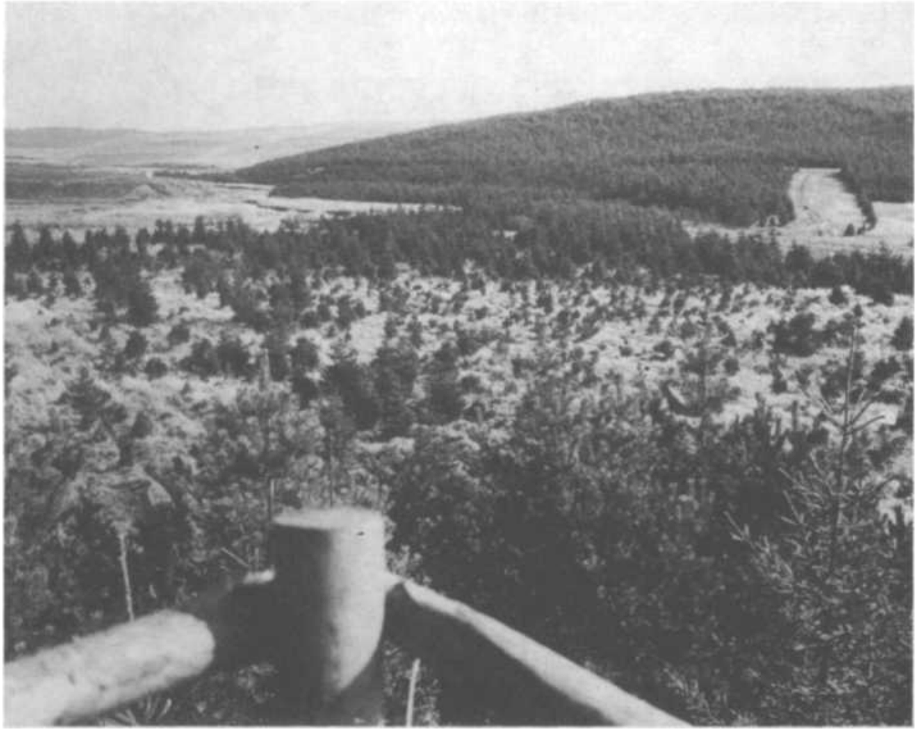

Fig. 2. View from the high seat in treatment area 2a, showing the good visibility where trees are small and the poor visibility and good escape cover for deer where trees are older. Moorland used for sheep pasture surrounds the forest.

METHODS

The observations of roe deer on the vulnerable replanted areas of Castle O'er Forest were made with the aid of the resident trapper and two other trappers from neighbouring forests, all employed by the Forestry Commission primarily to control numbers of roe deer. We used binoculars and telescopes to watch roe deer from high seats, and occasionally from vehicles or on foot, taking care not to disturb the deer more than necessary. Most observations were near dawn and dusk when roe deer are most active (Bubenik, 1960). No deer were marked. We identified individual bucks by the shapes of their antlers, a reasonably reliable method (Cumming, 1966). Individual does could not be identified. All observations were recorded in notebooks.

I followed Turcek (1962) in measuring with a metal tape the heights of frayed trees and the upper and lower limits of fraying. The diameter of each stem was measured with calipers at the center of the frayed area and the percentage circumference of the stem from which bark had been removed was estimated by eye. The locations of individual trees were not marked, but the areas of major fraying were recorded on a map.

I counted all newly frayed trees on four areas in April, May, July and August and marked them with metal tags (Fig. 3). Tagged trees were not included in subsequent counts unless they had been frayed again. Fresh fraying could be recognized easily from the white wood and liquid sap. To find the continuing effects from fraying in previous years, I counted the frayed trees on a systematic sample of plots 30 × 2 m, similar to those of Passmore and Hepburn (1955). On two areas (1a, 2a), counts of trees in every third row provided estimates of the total numbers of trees and their sizes. I counted trees browsed by roe deer and trees damaged by frost on areas la, lb and 2a for comparison.

Fig. 3. The tag used to mark trees frayed by roe bucks was small and placed high in the tree. There was little chance of its frightening the bucks and preventing them from fraying the tree again.

The trappers did all the shooting, but entirely under my direction. Most resident bucks were well known from many observations. When resident bucks were shot, new bucks were identified at least three times over a period of at least a week before they too were shot. All deer were shot from high seats using .222 and .270 rifles with telescopic sights. None ran farther than about 100 m after being shot.

The shooting experiment compared two treatments: (1) territorial bucks were shot and other bucks were left, (2) territorial bucks were left but all other bucks were shot. Each treatment was carried out on two areas.

RESULTS

Field Observations of Roe Behaviour

All fraying occurred during May-August, that is during the period prior to and including the rut, which is from mid-July to mid-August. From 1896 observations of roe behaviour during 3 years, I identified 3, or possibly 4, behaviour patterns which might have resulted in fraying.

(1) Bucks removed velvet from their antlers, presumably by rubbing them against trees. I did not actually see wild roe removing velvet, but the latest date when I saw an adult buck with velvet was the first week of April. The latest date for a yearling buck (i.e. a buck approximately 1 year old) was the second week of July,

Fig. 4. Tame roe buck mock fighting a pole placed in its pen; in lunging at the tree, the buck circled round it thus removing the bark from the entire circumference. Eighty five per cent of the fraying damage in Castle O'er forest was attributed to this behaviour.

Fig. 5. Wild roe buck rubbing side of face against trunk of mature pine in the study area in N.E.Scotland. Such rubbing was also done on plants, possible causing fraying damage. Since bucks often scraped the ground and sometimes sniffed the objects rubbed on, this was interpreted as marking behaviour.

but most yearlings had cleaned their antlers by the end of June. A tame buck removed its velvet during a 24 hour period and Hennig (1962a) reported similar short time periods for wild bucks. The longest period during which some velvet clung to antlers of wild bucks was about one week.

(2) In mock fighting, a buck of any age attacked a small tree vigorously with its antlers, head lowered and antlers pointed forward, circling and lunging at the tree so that bark was stripped from a large section of the stem (Fig. 4). I watched mock fighting on 10 occasions on the different study areas, all between the first of May and the end of the mating season in the third week of August.

(3) On fifty occasions bucks rubbed their foreheads, sides of their faces and chins against plants varying in size from herbs to large trees (Fig. 5). They scraped the ground with their front feet on half of these occasions. This was apparently olfactory marking since the bucks were observed smelling the objects being rubbed on nine occasions. This behaviour also occurred during May-August. It differed from mock fighting in that the head was held higher with the antlers pointed upward and there was little lunging or circling.

(4) A behaviour pattern observed only once but also reported by Hennig (1962a) involved striking the antlers sideways against small trees. This may have been only a variation of mock fighting.

TABLE 1. MEASUREMENTS OF FRAYED TREES AT CASTLE O'ER COMPARED WITH THOSE OF TURCEK (1962)

	Castle O'er	Turcek (1962)
	Native conifers mainly *Pinus sylvestris*	Native conifers mainly *Larix decidua* and *Pinus sylvestris*
Number of trees measured	221	
Height of trees (cm):		
Mean	84	
range	30-197	
Lower limit of fraying (cm):		
mean	25	26
range	2-68	10-62
Upper limit of fraying (cm):		
mean	44	61
range	13-88	40-120
Length of fraying (cm):		
mean	19	40
range	1-48	10-90
Diameter at mid-point (cm):		
mean	17	16
range	5-46	5-56
Estimated %age mortality	24*	75†

* Estimated from number of trees with 75% or more of bark removed.
† Method of estimating is not specified.

Note: This table shows that trees of the same diameter were frayed at Castle O'er and on the Continent, but height and length of fraying were greater on the Continent and estimated mortality was higher.

Counts and Measurements of Trees

Ninety-two per cent of the 279 counted frayed trees were pines, though they composed only 17% of the trees on the vulnerable areas." All frayed trees were under 2 m high and 68% were under 1 m high. By comparison, only 57% of all trees on the vulnerable areas and 42% of all pines were under 1 m.

Fig. 6. Frayed tree plainly visible from a distance, because the bark had been removed to expose the white wood. This tended to give an impression that more tees were frayed than was actually the case.

Fraying usually removed bark from a continuous vertical area of the stem extending from about 25 cm above the ground for some 40 cm (Table 1). The strip of bare white wood remaining was visible over long distances (Fig. 6). The mean percentage circumference of the stem from which the bark was removed varied on different parts of Castle O'er Forest from 35-56%. Some trees were girdled. Many were pushed back and forth so violently that stems were loosened in the ground, probably causing root damage. Yet the trees were sufficiently resilient so that few stems were broken off. The orientation of the frayed patches was not recorded, but there was no obvious relation to either compass direction or the locations of territorial bucks. I examined 3 trees immediately after a buck attacked them in a mock fight and found bark removed from a continuous section of each stem (Fig. 7). But 15 per cent of the frayed trees showed only slight scratches on opposite sides of the stems (Fig. 8). These marks were so distinctly different that I suspected they resulted from a different behaviour pattern.

Only 3 tagged trees were frayed twice in 1964. By contrast, 31 trees frayed in previous years but still living were frayed again during 1964 (Fig. 9), and 3 trees killed in earlier years by fraying were frayed again in 1964 (Table 2). There was no evidence that bucks frayed trees around the boundaries of their territories (Fig. 10). They appeared to fray most trees in the places where the bucks were most frequently seen. Although in one instance, this resulted in heavy fraying along the common boundary of two adjacent territories, fraying was equally severe elsewhere in the same territories.

Fig. 7. Fraying encompassed much of the circumference of 85% of the trees affected, probably as the result of mock fighting.

Fig. 8. The remaining 15% of the trees were only narrowly frayed on opposite sides of the stem, suggesting that this might have resulted from bucks rubbing their foreheads up and down the stems.

TABLE 2. COUNTS DURING MARCH-APRIL, 1964 OF TREES FRAYED AND BROWSED ON AREA 2A

Total living trees	356
	%
Browsed before 1963	26
Killed by browsing before 1963	1
Browsed 1963	13
Killed by browsing, 1963	2
Frayed before 1963	11
Frayed 1963	6
Killed by fraying, 1963 and before	3
Frosted	26

By August, the foliage had turned yellow on trees with 75% or more of the circumference stripped of bark, and these appeared likely to die. Only 24% of the frayed trees were so affected, much less than Turcek's (1962) estimate of 75% mortality among frayed trees in continental Europe.

Up to 100 pines per ha showed evidence of being frayed prior to 1964 (Table 3). This amounted to 17% of all pines. Only a maximum of 7% of Sitka spruce in any one area were frayed and 0.5% of Norway spruce. Counts revealed that trees dead or dying

Fig. 9. Some trees were deformed by fraying in previous years and frayed again in 1964, but few were frayed twice in one year. The calipers used to measure stem diameter are shown.

from past fraying amounted to 6% of all trees on one area and 3% on another. The remaining frayed trees were somewhat deformed but were recovering (Fig. 9).

Browsing prior to 1964 had affected 230 pines/ha or 38%, along with 11% Norway spruce and 7% Sitka spruce (Fig. 11). Browsing did not appear to affect trees seriously unless the tips of the trees had been removed or so many twigs eaten that the tree died. On one area tips had been browsed from 17% of the pines, 6% of the Norway spruce and 7% of the Sitka spruce. On a second area, 3% of the pines had been killed by browsing. About half of all visible effects from previous fraying and browsing resulted from roe activity in 1963. Presumably earlier effects were slowly being overgrown. The counts of trees affected by frost revealed that about 26% of the pines were stunted and mis-shapen.

Shooting Experiment

Between 7 March and 11 August 1964, we recorded 69 observations of roe deer on the 4 vulnerable areas where the shooting experiments were carried out; in addition, the trappers made many more casual sightings and we also observed roe on surrounding areas. Each of the vulnerable areas were occupied by only 1 territorial buck, with 1 or 2 does and, in some cases, 1 or 2 yearlings. When territorial bucks were shot they were quickly replaced, but when yearling bucks were shot they were not replaced (for a complete description and discussion see Cumming, 1966).

Substantially fewer (20-50% less) trees were frayed on the two areas where non-territorial bucks were shot (treatment 2) than on the 2 areas where territorial bucks were shot (treatment 1) (Table 4). Least fraying occurred on the area where 2 yearling bucks were shot (and never replaced) before fraying began. These results are too few for statistical analysis, but they suggest that the removals created marked differences in the extent of fraying. Paradoxically the percentage of trees frayed on area 2a, where non-territorial bucks were shot (2.5% of all trees, 4% of pines) was

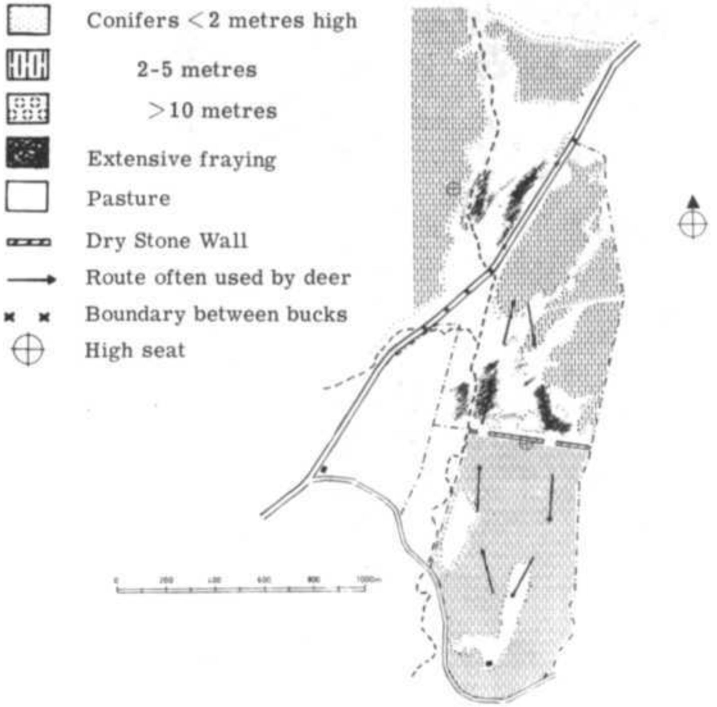

Fig. 10. Treatment areas la and lb (north and south of main road, showing where most fraying occurred. Note that it was no more frequent where the two territorial bucks met than at other places where they were often seen, e.g. along the stream. The 'boundary' does not imply a rigidly defended line.

greater than on area la where territorial bucks were shot (1.0% of all trees, 2% of pines). This appeared to be because area la had about 5 times as many vulnerable trees (Table 5) on twice as great an area but only twice as many trees were frayed. That is, the number of trees frayed was not related to the number available. It might appear related to area, but this was not the case when compared with area lb which was much smaller than either but had the most trees frayed.

Removing individual bucks merely changed the rate of decrease in numbers of newly frayed trees, which, with one exception, were fewer on every area for each count from May to August. The greatest decrease in the number of newly frayed trees (81%) occurred in an area where a yearling buck was shot and not replaced. The next greatest decrease (69%) was in an area which was to have been kept free of territorial bucks, but could not be, because the first replacing buck seldom ventured from the nearby larger trees into the vulnerable area where it could be seen. Thus, it may not have been there often enough to fray many trees. The third and fourth greatest decreases in numbers of newly frayed trees (57%, 42%) occurred for successive counts on a place where no additional bucks were shot because yearling bucks, shot early in the spring, were not replaced. The least decreases (28%, 25%, 23%) occurred on the two places where territorial bucks were shot. The only increase in the incidence of new fraying occurred at a time and place where no deer were shot; but this was the same place where the subsequent shooting of a yearling buck resulted in an 81% reduction in fraying, and this buck may have been present earlier but not seen.

I could not find exactly how many trees each buck frayed because the dates of counting trees and removing bucks did not coincide. But the counts occurring between re-

Fig. 11. Frosting (left) and browsing (right) affected more trees than fraying, but the browsing of only the sides of a tree, as in this case, did not seem to reduce its growth rate.

moval dates provide approximations. On this basis, 7 adult bucks, frayed about 49, 35, 27, 61, 59, 56, and 22 trees respectively. These numbers are remarkably constant since the first 4 bucks were present only about 1 month, the 5th about 2 months and the last 2 bucks over 5 months each. Thus, 5 bucks each present for 1-2 months frayed 231 trees or 46 each, and 2 bucks present over 5 months frayed 78 trees or 39 each.

DISCUSSION AND CONCLUSIONS

Mock fighting and rubbing appeared to be the behaviour patterns most frequently involved in fraying. Both were commonly observed on the study area throughout the May-August period when fraying damage occurred. In contrast, adult bucks cleaned their antlers in March before any trees were found frayed. Yearling bucks cleaned their antlers during the period when trees were being frayed but the process lasted such a short time for each animal, probably only about 24 hours, that any contribution to fraying must have been small. Similarly, striking antlers sideways against trees was not important for it was never observed on the study area and only once elsewhere.

The relative importance of mock fighting and rubbing was difficult to assess because there were not enough field observations to permit measuring their frequencies by direct enumeration. The observation that 85% of the trees bore marks similar to 3 trees which I examined immediately after seeing a buck attack them provides reasonable ground for suggesting that mock fighting was involved in 85% of all fraying damage. I was not able to examine a tree immediately after seeing a buck rub on it to find whether the other kind of marks which I observed were due to rubbing. Yet the mainly up-and-down motion of the buck's head in this behaviour, with little or no circling by the animal, suggests that parallel marks on opposing sides of the stem might be expected. If this was the case, 15% of the trees were damaged as a result

TABLE 3. COUNTS DURING MARCH-APRIL, 1964 OF TREES FRAYED AND BROWSED BY ROE IN PREVIOUS YEARS, AT CASTLE O'ER

	Treatment areas								
	Area 1a—77 plots, 0.47 ha Territorial bucks shot			Area 1a-8 plots, 0.05 ha Territorial bucks shot			Area 2a—38 plots, 0.23 ha Non-territorial bucks shot		
	Pinus sylvestris	Picea abies	Picea sitchensis	Pinus sylvestris	Picea abies	Picea sitchensis	Pinus sylvestria	Picea abies	Picea sitchensis
Total living trees in sample	282	609	115	24	54	14	46	313*	272*
Living trees/ha	600	1290	245	480	1080	280	200	1360	1180
Frayed trees/ha	100	6	2			20	13	4	26
Percentage of total trees frayed	17%	0.5%	1%			7%	7%	0.3%	2%
Browsed trees/ha	230	43	6	120	120	20	52	4	
Percentage of total trees browsed	38%.	7%	5%	25%	11%	7%	26%	0. 3%	
Number of trees with tips removed/ha	51	4	2	80	60	20			
Percentage of total trees with tip removed	9%	0.3%	1%	17%	6%	7%			

* Including trees outside the actual treatment area

TABLE 4. COUNTS OF FRAYED TREES AT CASTLE O'ER, 1964 IN CONJUNCTION WITH THE SHOOTING EXPERIMENT

	Treatments (1) Territorial bucks shot				(2) Non-territorial bucks shot			
	1a		1b		2a		2b	
	No. of frayed trees	% reduction	No. of frayed trees	% reduction	No. of frayed trees	% reduction	No. of frayed trees	% reduction
							(10 Mar- 2 yearling bucks shot)	
22-23 April	0		0		0		0	
20 May	49		61		25		12	
	(26 May- adult buck shot)		(29 May- adult buck shot)					
10 July	35 (21 July- adult buck shot)	28	45 (Replacement buck too retiring to be shot)	25	26 (7 July- yearling buck shot)	–4	7	42
11 August	27	23	14	69	5	81	3	57
Totals	111		120		56		22	

Note: This table shows:

(a) fraying in all areas decreased from May to August.
(b) greatest reduction in fraying occurred where a yearling buck was shot and least where adult bucks were shot.
(c) each replacement buck in treatment 1 frayed about as many trees as bucks resident throughout May-Aug in treatment 2.
(d) more trees were frayed in treatment 1 where adult bucks were shot, than in treatment 2 where other bucks were shot.

TABLE 5. COUNTS OF TOTAL NUMBERS OF TREES ON TREATMENT AREAS

	Treatment la (territorial bucks shot)					
	Species					
	Pinus sylvestris	*Pinus contorta*	*Picea abies*	*Picea sitchensis*	*Pseudotsuga menziesii*	Total
No. of trees	2507	85	7399	1263	9	11253
Height (m)	%	%	%	%	%	%
1	42	22	63	55	100	57
1-2	36	78	29	27		31
2-3	11		7	14		8
3-4	7		1	3		2
4+	4			1		1
Trees of all heights	22	1	66	11	0.1	

	Treatment 2a (non-territorial bucks shot)				
	Species				
	Pinus sylvestris	*Picea abies*	*Picea sitchensis*	*Pseudotsuga menziesii*	Total
No. of trees	1745	385	92	55	2277
Height (m)	%	%	%	%	%
1	43	65	89	100	50
1-2	39	19	11		34
2-3	16	11			14
3-4	2	5			3
4+					
Trees of all heights	77	17	4	1	

of rubbing behaviour alone. Additional rubbing may have occurred on frayed or unfrayed trees without leaving any visible marks, but this was not considered fraying.

Mock fighting seemed similar to the 'mock battle' in moose (*Alces alces*) mentioned by Altmann (1959) and analogous to the 'sham-fighting' in *Odocoileus* described by Cowan and Geist (1961). It also seemed similar to 'Schlagen' described for red deer (*Cervus elaphus*) by Schloeth (1968), but not the 'thrashing' described by Struhsaker (1967) studying wapiti (*Cervus canadensis*). The latter resembled rubbing behaviour in roe deer instead. Mock fighting in roe deer differed from 'bush-thrashing' in caribou (*Rangifer tarandus*) as described by Lent (1965) though the functions may have been similar.

Mock fighting in roe deer was considered a displacement activity by Hennig (1962a) and Braestrup (1956), but Kurt (1964) was probably more precise in calling it redirected activity. This term was defined by Ficken & Dillger (1960) as behaviour in which an act initiated by a normal stimulus is directed to a substitute object upon the unavailability of the original source. In one clear instance, a buck exchanged loud aggressive barks with a territorial neighbour, then turned and lunged at a small tree nearby. However, bucks were also seen mock fighting when there were no other deer near them and no apparent external stimulus. There may, or course, have been olfactory stimuli which I could not detect.

The idea that most fraying results from mock fighting fits with the observation that bucks frayed the most trees where they were most frequently seen, rather than around the borders of territories. Presumably an external or internal stimulus would cause the animal to attack any suitable object nearby. Since there was no evidence of bucks patrolling boundaries, but only pathways within territories, there was no reason for bucks to fray near the edges of territories any more than near frequently travelled routes within them. This interpretation would also explain why the trees were frayed only once. There would be no incentive to fray the same tree again if the buck was fighting it rather than marking it; it fact, there might be reason to avoid previously frayed trees if their resilience was lessened by the first fraying, as it certainly was when the trees were loosened or broken. The idea that most fraying was due to mock fighting would also explain why there was no apparent orientation of frayed marks. If the buck was fighting the tree rather than marking it, there would be no reason why he should fight it on any particular side. In addition, the circling of the buck would tend to obscure any orientation there might have been. It is still possible that bucks might have marked trees around the boundaries of their territories by rubbing behaviour without showing any visible signs, but they were never observed either marking or patrolling any distinct boundaries (Cumming, 1966).

These observations differ from those reported by some other authors, Hennig (1962b) for example, possibly because of the relatively low density of roe deer at Castle O'er compared with those in Germany. At Castle O'er roe were probably no more numerous than in north-east Scotland where I estimated their density to be about 7 deer/100 ha; whereas roe deer in Germany would probably be at densities more like those on my study area in south-west England where I estimated densities of about 30 deer/100 ha. Yet even in the latter study area I saw no evidence of fraying or marking around territory boundaries. Perhaps the apparent fraying and patrolling along territory boundaries in Germany was due to local landscape features channelling the movements of bucks along a few easily travelled routes around the edges of isolated woods. Observations of this behaviour would give the impression that bucks were patrolling and marking boundaries, though, in fact, they may have been only patrolling and fraying along major travel routes around the edges of woods and these routes happened at times to coincide with the boundaries of territories.

Why roe prefer to fray pines is not clear. There were no obvious differences between species in tree heights or stem diameters. Perhaps, the relatively long section of stem without branches in pines facilitates fraying and the resilience of the stem may be suitable for mock fighting. Turcek (1962) found pines similarly favoured in Europe, but also found several other species heavily frayed including some hardwoods. Perhaps these other species had similar clear, resilient stems. Certainly the spruces on the study area did not have such stems.

Measurements of frayed trees at Castle O'er and on the Continent suggest that fraying behaviour remains similar for roe deer in widely different areas. The greater heights to which fraying extended in Turcek's study can be explained by the larger size of roe on the Continent (Huxley, 1931, Barclay, 1933). Presumably lower limits of fraying remain about the same regardless of the size of the animal, for they are even similar for red deer (Schloeth, 1968).

Fewer trees were frayed in the plantation than casual observation suggested. The white wood of the frayed trees is visible at great distances as shown in Fig. 6, and the number of white marks seen in a casual walk through a plantation gives an impression of many more frayed trees than actually occur. Still the fraying damage was significant. About ¼ of the trees frayed during 1964 were likely to die. The loss in terms of dead or dying trees has accumulated to 3-6% of the trees in the vulnerable areas as a result of fraying during the previous 3 years. Some additional loss would occur from stunting and disfiguring. Yet past browsing affected trees about equally with past fraying; and, in the low areas where these observations were made, frost affected them even more. About one quarter of the trees were stunted by frost to the extent that it seemed doubtful whether they would ever grow to useable size.

Results of the shooting experiment, though meagre, suggested that the best way to reduce fraying in a plantation would be to shoot non-territorial bucks and leave territorial bucks as much as possible to themselves. The results further suggested that the shooting should start in March before fraying begins. Compared with selective removal, indiscriminate shooting of deer would be inefficient. If the deer shot happened to be territorial bucks, more fraying might result than if no deer were shot. These conclusions support the ideas of Gibson and MacArthur (1965).

It would have been desirable to set up control areas for the experiment in which (1) no deer were shot and (2) all deer were shot; but this proved impossible under field conditions. The area where no deer were shot for 3 months provided a situation close to one of these controls, and less fraying occurred than where territorial bucks were shot. It would also have been desirable to shoot does to find whether their removal would affect fraying, but a regulation against shooting does after March prevented this.

If there is any validity in the suggestion that each resident buck frays about the same number of trees whether it is present 1 month or 4 months, this would explain why more fraying resulted from shooting resident bucks than from shooting no bucks. If fraying is mainly due to a redirected activity, mock fighting, it may be that young bucks with relatively low social status engage in fraying more frequently than older bucks because they fear to challenge the older more dominant animals. There may also be an element of play in which young bucks prepare for future real fights. In addition, it is possible that younger bucks are more aggressive, for Rowell (1966) found subordinate wild baboons (*papio anubis*) more aggressive than dominant baboons. These speculations might explain why more fraying occurred when yearling bucks were allowed to remain than when older bucks were left. In any case, since territorial bucks were always replaced but non-territorial bucks were seldom replaced, the best policy to reduce fraying would seem to be to shoot the latter.

The idea that fraying behaviour is due mainly to mock fighting permits speculation on other possible ways of reducing fraying. It is possible that competition for territories results in more mock fighting on the part of all bucks concerned. If this is true, it would be best to leave one territorial buck on each territory and remove all competition, that is, all other bucks. It might also be possible to make some changes in tree planting procedures. Since bucks usually circle in mock fighting, trees planted closer together so that circling would not be possible might provide some protection. This suggestion also takes account of the observation that the number of trees frayed on two areas was not related to the number available. Additional reductions in percentages of frayed trees might be obtained by planting larger areas, since the number of frayed trees seemed to depend on the number of bucks rather than the size of the area. Of course, it would be best not to plant adjacent to stands of larger trees which would provide good escape cover for the deer. Combining all these measures should make possible a reduction in fraying damage to levels which can be tolerated and still leave trophy bucks for sport hunting.

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Paper No. 48

Ungulate Behaviour and Management, with Special Reference to Husbandry of Wild Ungulates on South African Ranches

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ABSTRACT

Nineteen species of wild ungulates, out of a total fauna of 44, are now important in terms of numbers, distribution, or both, on farmed land in South Africa. They have attained this status for a variety of reasons. Factors such as cultural attitudes, legislation, the (real or imaginary) dangerous or harmful attributes of larger forms or of those acting as vectors of disease in domestic livestock, and other economic considerations have been important in determining which species were eliminated and which were not. The paper attempts to show the role played by the behavioural patterns of the successful surviving species in enabling them to adapt to the environment provided by land used for agricultrual and pastoral farming.

The small, solitary species inhabit more or less dense cover in which they are dispersed by their territorial or home range behaviour. They are difficult to eliminate, even when deliberate extermination is attempted, and appear to compete little with domestic livestock. Their sedentary habit assists in making them proof against disturbance by man. Fences, unless they be of netting, are no barrier to the smaller species, while bushbuck are not contained by fences of standard height.

Of the semi-gregarious forms, klipspringer, mountain reedbuck and vaal rhebok occupy hills and mountains where the terrain gives security. Reedbuck shelter in tall grass and reeds. Fences do not hinder free movement while spacing behaviour usually tends to limit density to a level at which competition with domestic animals for food is of little practical consequence. Kudu are wary, difficult to hunt in the dense vegetation they prefer and are able to move freely over fences. Competition with cattle for food appears to be important only in some regions, as for example the Eastern Cape Province and perhaps in South West Africa. The small groups in which kudu occur preclude congregations which might lead to serious competition.

By occupying thick cover, and by extreme wariness, together with a high reproductive rate, bushbuck resist extermination in the face of constant persecution for damage to crops. Warthog tend to be dispersed by low sociability and home range behaviour but may compete with livestock for food to some degree.

The seven social species are behaviourally most closely akin to domestic ungulates, with many of the attributes considered favourable for domestication. Except for eland, they probably all compete, at least to an extent, with domestic livestock for food, although critical studies of the competition have yet to be carried out.

Gemsbok, eland, blue wildebeest and hartebeest are important mainly on large holdings where extensive pastoral farming is practised. Springbok, blesbok and impala are the three dominant farm species, springbok mainly in the arid western part of the country, blesbok in the central and eastern grassland regions, and impala in the northern and north-eastern savannah. Both springbok and blesbok are easily controlled by fencing and all three species are now of some economic importance.

The future of farm ungulates is related to changing patterns of land use and to economic factors. There is a trend to apply sophisticated grazing management in smaller paddocks and the role in these conditions of wild ungulates, which cannot easily be moved to rest the food plants, requires close scrutiny. Their economic value is not determined only by their utility as meat producers, however. Recreational hunting

and game viewing on private land has already become a source of revenue for some farmers. Its value is likely to assume increasing importance in the future and rational management on scientific lines will become increasingly necessary.

INTRODUCTION

South Africa, in this paper taken to comprise the Republic of South Africa and the Territory of South West Africa, had a varied and abundant ungulate mammal fauna in historic times. The orders Proboscidea, Perissodactyla and Artiodactyla were represented by 44 species (Table 1). Development of the country, following its settlement by Europeans in 1652, led to a marked reduction in the numbers and restriction of the range of most species (see, e.g., Van der Merwe, 1962; Sidney, 1965). Two, the quagga *Equus quagga* and the blaauwbok *Hippotragus leucophaeus,* became extinct.

TABLE 1. COMPOSITION OF LARGER UNGULATE FAUNA OF SOUTH AFRICA IN HISTORIC TIMES

Order	Family	Sub-family	No. of Species
Proboscidea	Elephantidae		1
Perissodactyla	Rhinocerotidae		2
	Equidae		3
Artiodactyla	Suidae		2
	Hippopotamidae		1
	Giraffidae		1
	Bovidae	Bovinae	6
		Cephalophinae	3
		Hippotraginae	15
		Antilopinae	10
			44

Some forms, particularly the largest ones, are now entirely or virtually confined to parks and reserves. These include the elephant *Loxodonta africana;* two species of rhinoceros, *Diceros bicornis* and *Ceratotherium simum;* the hippopotamus *H. amphibius;* the Cape race of the mountain zebra *Equus z.zebra;* the giraffe *Giraffa camelopardalis*; the roan antelope *H. equinus,* and others.

A number are rare and survive only over small portions of their original ranges. Reviews of ungulate status and distribution have been published for the Transvaal by Kettlitz (1962), for Natal by Vincent (1962), for the Orange Free State by Van Ee (1962), for a part of the Cape Province by Bigalke and Bateman (1962), and for South West Africa by Bigalke (1958) and Van der Spuy (1962).

The species of particular interest in the context of this paper, are those which are relatively widespread and abundant on privately owned farm and ranch land at the present time. Private land makes up approximately 69% of the area of the Republic of South Africa (472, 359 sq. miles = 122, 104, 200 ha) and 47% of South West Africa (total area 318, 261 sq. miles = 82, 429, 600 ha). It is for the most part used primarily for crop or live-stock production, although the economic value of wildlife on farms has increased in importance in recent years (Riney and Kettlitz, 1964). The surviving wild mammals are, by and large, those which are adapted to the conditions created by the primary form of land use. The species are listed in Table 2.

The range of several of the commoner farm species has been enlarged and the populations increased by secondary redistribution. This has taken place mainly during

TABLE 2. LARGER UNGULATES OF LOCAL OR GENERAL IMPORTANCE ON FARMED LAND IN SOUTH AFRICA

Family		Species	Main Localities
Suidae	Bushpig	*Polamochoerus porcus*	EC,N,T
	Warthog	*Phacochoerus aethiopicus*	N,T,SWA
Bovidae			
Bovinae	Bushbuck	*Tragelaphus scriptus*	EC,N,T
	Kudu	*Tragelaphus strepsiceros*	EC,NC,T,SWA
	Eland	*Taurotragus oryx*	SWA
Cephalophinae	Blue Duiker	*Cephalophus monticola*	EC,N
	Grey Duiker	*Sylvicapra grimmia*	General
Hippotraginae	Vaal Rhebok	*Pelea capreolus*	C,T
	Reedbuck	*Redunca arundinum*	N
	Mountain Reedbuck	*Redunca fulvorufula*	C
	Gemsbok	*Oryx gazella*	SWA
	Blesbok	*Damaliscus dorcas phillipsi*	T,C
	Hartebeest	*Alcelaphus buselaphus*	SWA
	Blue Wildebeest	*Connochaetes taurinus*	T, some N
Antilopinae	Springbok	*Antidorcas marsupialis*	General except N
	Klipspringer	*Oreotragus oreotragus*	C,T
	Steenbok	*Raphicerus campestris*	General
	Grysbok	*Raphicerus melanotis*	C
	Impala	*Aepyceros melampus*	Mainly T, some N

C = Cape Province; EC = Eastern Cape; NC = Northern Cape; N = Natal; O = Orange Free State; T = Transvaal; SWA = South West Africa.

the last 15 years. Translocation was initiated by enthusiastic farmers and also by some of the conservation authorities which attempted to provide interested landowners with nucleus populations for restocking. All these conservation authorities are now to some extent involved in the capture and translocation of game. In addition many farmers are active in capturing and distributing the commoner species.

SOCIAL BEHAVIOUR

The ungulates listed in Table 2 may be simply classified into three categories according to the size of the groups in which they are normally found (Table 3). The allocation of species to these categories is in some cases somewhat arbitrary. Nonetheless the classes represent increasingly complex types of social organisation which profoundly affect the management of the animals.

(a) Species occurring singly or in pairs

Five species are usually described in older, general works as being essentially solitary. Recent studies of some of these provide quantitative information on group sizes and give some idea of the nature of their intra-specific behaviour. Elder and Elder (1970) report on 167 sightings of bushbuck; lone animals made up 72% of the observations, lone males (55) being seen slightly more often than lone females (50). Only 10 sightings were of groups larger than two and the largest consisted of 5 animals. Verheyen (1955) reports that both males and adult females occupy territories of 2-3 acres, usually pear-shaped, with access to communally used 'neutral' ground.

TABLE 3. SOUTH AFRICAN FARM UNGULATES CLASSIFIED ACCORDING TO SOCIABILITY

Solitary or pairs	Semi-gregarious	Gregarious
Bushbuck	Klipspringer	Eland
Blue duiker	Vaal rhebok	Gemsbok
Grey duiker	Mountain reedbuck	Blesbok
Steenbok	Reedbuck	Hartebeest
Grysbok	Kudu	Blue Wildebeest
	Bushpig	Springbok
	Warthog	Impala

Von Gadow (unpublished) observed 59 blue duiker, of which 78% (46) were single, 17% (10) in pairs and 5% (3) in a group of three. He found dung heaps in the field and suggests that they may indicate behaviour of a territorial nature. In the closely related and possibly conspecific (Ansell, 1968) *Philantomba* (=*Cephalophus*) *maxwelli,* Rahm (1960) has described preorbital gland marking in captive animals. Aeschliman (1963), working with animals of the same species in captivity, describes territorial behaviour involving preorbital gland marking and the utilisation of dung heaps. In captivity, an adult male marked 79 times in 4 hours, an adult mature female 21 times and two younger mature females 8 and 9 times respectively.

Wilson and Clarke (1962) write of the grey duiker—'(it) is generally spoken of as a solitary animal and although this was found on the whole to be true, pairs were also frequently recorded, almost half as many times as single animals'. Bigger groupings were found to be very rare and only five groups of three were noted. These authors also describe aggressive behaviour between males and between females, when placed in the same enclosure. They consider it to be 'strongly suggestive of an animal with a territorial system'. Personal observations (Bigalke, unpubl.) confirm aggression between adult males brought together in a pen, usually resulting in the death of one individual. Shortridge (1934) noted that males in the field 'appear to fight much among themselves'. Preorbital gland marking by a male and a female in captivity has recently been established (Greig and Bigalke, unpubl.) and the existence of dung heaps noted. This latter observation confirms the remark by Shortridge (1934) that duiker 'are in the habit of returning to the same open spots to deposit their droppings, although large massed accumulations.... are not formed'. Wilson (1966) found grey duiker to occupy a very small home range.

No quantitative data is available on the groupings of steenbok and grysbok. Lamprey (1963) gives qualitative confirmation of earlier observations (e.g. Shortridge, 1934) that steenbok are solitary although sometimes seen in pairs. Stevenson Hamilton's (1913) observation that Sharpe's grysbok, *Raphicerus sharpei,* which is closely related to the grysbok *R. melanotis,* is 'very solitary in habit, and, even when a pair are put out of the same patch of bush, they seem generally to have been lying in different parts of it', has been confirmed for both this species and the Cape grysbok by a number of later observers (e.g. Shortridge). All three species of *Raphicerus* use dung heaps (Stevenson Hamilton, 1913; Shortridge, 1934; pers. obs.) and have well developed preorbital glands, suggesting that they display territorial behaviour.

(b) Semi-gregarious species

Klipspringer, sometimes considered to be solitary, are probably best placed in this group. Wilson and Child (1965) give an analysis of 168 groups of klipspringer, totalling 313 animals. The average group size was calculated to be just under two animals, with a range of 1 to 6. Singletons constituted 22.1%, pairs 47. 2% and threes 15. 3% of the sample. Massed accumulations of dung are characteristic of areas inhabited by klipspringer (Shortridge, 1934; pers. obs.) and deposits of preorbital gland secretions have been found near the dung heaps (Walther, 1966; Tinley, 1969). Territorial behaviour thus probably exists.

Reedbuck live in pairs of male and female or female and young, or in family groups of male, female and young (Jungius, 1969). The mean size of 34 groups in Natal was 1. 8, with a range of 1 to 3 (Rowe-Rowe, *in litt.*). Jungius has shown that territories are occupied jointly by a male and a female, although they may not always remain together within these areas. The female rears her young in the territory. It is not known whether the pair bond is permanent or is only important during the mating season. Territories are maintained by the males through a combination of advertising behaviour (display of chinspot, whistling) and the diffuse deposition of dung and urine, and probably also of small quantities of gland secretions, throughtout the territory. Two territories were found to extend over areas of 48 ha and 60 ha respectively in summer. In winter, a shortage of water caused reedbuck to concentrate around available sources and to exert pressure on the two territory holders in question. As a result the extent of each territory was reduced to 35 ha. Temporary congregations of reedbuck, e.g. on good grazing grounds, are often encountered (Jungius, 1969).

Little is yet known of the social behaviour of the mountain reedbuck *Redunca fulvorufula.* Observations by early naturalists, brought together in Shortridge (1934), all show that it is found in small groups. For example, Selous (quoted in Shortridge) stated that herds usually number from three or four to fifteen animals with only one adult male and, sometimes, a few immature males. Records collected by officers of the Natal Parks Board in the Drakensberg show that the mean size of 540 groups is 3. 67, with a range of 1-21 (Rowe-Rowe, *in litt.*). Personal observations confirm that only a single adult male is usually present in the herds, and it would seem that these are small and possibly permanent harem groups. Selous (*loc. cit.*) also notes the occurrence of solitary males, while Shortridge suggests the existence of a territorial system, writing 'the rams are very pugnacious, and, it is said to be impossible to keep two males together in one enclosure without one eventually killing the other'.

The vaal rhebok or ribbok *Pelea capreolus,* has a similar form of social organisation. The mean size of 514 groups seen in Natal is 3.1 and the range 1-9 (Rowe-Rowe, *in litt.*). The herds have one adult male and solitary males occur (Shortridge, 1934; pers, obs.).

Information available on the size and composition of kudu herds has been summarised by Wilson (1970). Some authors have recorded herds of up to 30, but these are apparently exceptional. The biggest group encountered in the course of his study by Wilson numbered 15, while Simpson (1968) found herd size to vary from a maximum of 7 in the dry season to 12 in the winter. Herds tended to be larger in December-January, possibly as a result of females aggregating before calving, and in July, when the rut takes place, than at other times of year (Simpson, 1968). Wilson (1970) found the mean size of 35 herds in Rhodesia to be 5. In a tsetse-fly control area in Zambia, where 185 groups totalling 768 animals were seen, he counted 33 single animals and found the average herd size to be 3. 9 (Wilson, 1965). Males occur singly and in small herds (up to 16—Wilson), females in herds with or without juveniles and sometimes accompanied by one or more males. There is a suggestion that males are only in temporary association with groups of females and young (Wilson, 1970).

In the warthog, the social unit is a small group, often composed of two or more mature females with their half grown young, sometimes accompanied by an adult male. Females go off on their own when about to give birth to a litter and this habit probably prevents the formation of large groups. Each group has its own home range including sleeping holes, resting, feeding, drinking and wallowing places. Ranges overlap with those of other groups; there is no territorial defence and animals may move to a new area if seasonal vegetational changes make this necessary (Ewer, 1968, quoting Frädrich, 1965). Mating by the male accompanying a family group and aggression towards a solitary male in the vicinity is described by Simpson (1964).

Bushpig behaviour has not been studied in detail. The sounders have been described by various authors as containing from 4-20 pigs (Sowls and Phelps, 1968) and are said to include a dominant adult male (Astley Maberley, 1963).

(c) Gregarious species

The system of social organisation in the hartebeest (Backhaus, 1959), blesbok (Du Plessis, 1968), blue wildebeest (Estes, 1968; Watson, 1969), springbok (Bigalke, 1970) and impala (Leuthold, 1970; Jarman, 1970) is similar to that of many other gregarious bovids. Populations are organised into three main classes: herds of females and young, variously called breeding herds, harem herds or nursery herds; herds of adult and sub-adult males, sometimes accompanied by sub-adult females and often called bachelor herds; and solitary adult males.

Backhaus (1959) records herds of hartebeest (*Alcelaphus buselaphus lelwel*) in the Garamba Park numbering 4-15 animals. They are mother-young groups accompanied, apparently permanently, by one adult male, and occupy fixed territories. He also saw male herds but no solitary males. Gosling (1969) has found solitary male Coke's hartebeest (*A. b. cokei*) defending territories of 0.4 km^2 in the Nairobi Park. Solitary males do occur in *A. b. caama* observed in the Northern Cape Province, South Africa (pers. obs.). Of 40 sightings of *A. b. caama* from the air (pers. obs.) 10 were of solitary animals. The remainder were made up as follows:

groups of	2-5	6-10	11-20
number	17	8	5

The largest herd of the same sub-species seen by Eloff (1959b) in the Kalahari Gemsbok Park numbered 35, but he also records an assemblage of 200 seen in the adjacent part of Bechuanaland (now Botswana). Eloff (1959a) also notes that hartebeest, together with eland and springbok, took part in several large scale movements beyond the boundaries of the Park, apparently in search of fresh grazing.

Solitary male blesbok are found throughout the year but the number increases markedly during the rut in March and April (Du Plessis, 1968), when some of them defend harems (or territories within which the harems are herded?) of females, accompanied by six-month-old lambs. Du Plessis did not consider the solitary males to be territorial. However David (1970) has since described well-developed territorial behaviour in solitary male bontebok (*D.d. dorcas*), a closely related sub-species. He also found some evidence of harem herds living on male territories throughout the year. Du Plessis encountered large, mixed aggregations of blesbok during the winter months following the rut, as well as after the onset of the rains, when they congreated on the burnt grassland. For example, on one occasion in November, the entire population studied was distributed in only four herds (numbering 590,299, 72 and 17 respectively) on green burns.

In sedentary blue wildebeest, Estes (1968) found a permanently established territorial network. Approximately 25-50% of the adult males occupied territories which were closely spaced, on average a distance of 130-160 yards apart. Territorial activity was much lower during the dry season (June-October) than after the onset of the Short rains (November-December) and reached a peak during the rut in May and June. Females and young occurred in separate, small nursery herds with an average size of approximately 10 animals, of which 6 were adult females. They occupied small home ranges of 1 sq. mile or less. Bachelor herds were separated. In nomadic wildebeest there were large, mobile aggregations of 100-1000 females and young with attached bachelor herds. Males established temporary territories or 'pseudo-territories' (Watson, 1969) when the aggregations remained stationary. The mean size of 'pseudo-herds' held by bulls in their 'pseudo-territories' in the Serengeti region is 28. 4 (Watson, 1969). About half of these animals may be adult cows.

In the springbok (Bigalke, 1970 and in press), solitary territorial males are encountered throughout the year but there is evidence for an increase in their number during the rut in April and May. At this time, harem herds of up to 35 females and lambs are tended, although larger groups with several rutting males are also occasionally seen. In the succeeding months of the dry season, mixed herds of up to several hundred predominate. Females and newly born lambs form separate groups, the lambs resting together in sub-groups in the vicinity of the females. Large, mixed aggregations of up to several thousand animals occur during the rainy season. Non-territorial males associate in fairly loosely knit bachelor herds throughout the year.

Adult male impala have also been shown to be territorial (Leuthold, 1970; Jarman, 1970) and remain within areas of 0. 2-0. 9 sq. km in the Nairobi National Park. Other males run in male herds, most of which number from 2-15, or in the rarely encountered mixed groups of both sexes and all ages. Herds of females and young are basically independent of the territorial males but may stay with the same male for long periods. The size of these groups was generally smaller—up to 25 in most cases—in a region with fairly dense vegetation, than in a more open environment when herds of over 35 were common (Leuthold, 1970).

All animals are fairly sedentary under the stable and favourable environmental conditions of the Nairobi Park, home ranges of individual males and females measuring 2-6 sq. km (Leuthold, 1970). In the more arid Serengeti Park, Jarman (1970) found sedentary behaviour of a similar kind during the dry season, but in the rainy season, animals moved to areas of green flush and formed feeding concentrations of large, diffuse herds of both sexes and all ages. Territoriality was then at a minimum. Seasonal changes of range in response to food are also reported by Lamprey (1963). Leuthold (1970) emphasizes the flexibility of the social organisation which enables the species to meet the exigencies of the various habitats throughout its wide range.

The eland has quite a different pattern of social behaviour. Large mixed herds of 100-150 or more occur during the summer (Lemon, 1964:Martin, 1968), probably associated with rutting and with a good food supply. In winter, smaller herds of 10-50 predominate (Lemon). Martin records groups as small as 3-5 in April. Small male parties and solitary males occur in the valleys of the Natal Drakensberg during winter while the rest of the population is dispersed in small groups at higher altitudes (pers. obs.). Large herds contain several adult males (Lemon; pers.obs.) and a social hierarchy appears to exist, reducing intraspecific aggression and ensuring the cohesion of the groups. A rank hierarchy was well developed in a semi-domestic herd (pers. obs.). No evidence exists for territorial behaviour of any kind.

The social behaviour of gemsbok has not been studied in detail. Shortridge (1934) gives the usual size of groups as 3-12 and occasionally up to 25, although larger, presumably temporary, feeding aggregations, are on record. Solitary males occur.

INFLUENCE OF SOCIAL BEHAVIOUR AND HABITAT REQUIREMENTS ON POPULATION DENSITY

The density at which ungulates normally occur and can be maintained, is basically dependent on the productivity of the vegetation. The availability of water and of cover are further important factors while social behaviour influences the manner in which the resources of the environment are shared amongst members of the population.

(a) Solitary species

Social behaviour is of greatest importance as a determinant of density in solitary species. According to Ewer (1968) 'In solitary species the predominant function of territory is the primary one—spacing out of individuals and ensuring an adequate area for the rearing of each family'. The secondary, male competitive function is simply integrated with the primary one by means of a contest which decides who shall be allowed to enter the female's territory and mate with her.

Densities are influenced by spacing behaviour. This can be said in spite of the fact that the precise nature of the behaviour is not yet known in many cases. Whether either, or both, sexes occupy territories 'where each individual is exclusively dominant over all others of the same sex at a particular site or area, but not elsewhere' (Watson and Moss, 1970, referring to the definition by Tinbergen, 1957), or whether they inhabit home ranges, the species are spaced out.

There is little information on the sizes of territories or home ranges inhabited. Bushbuck have been found to occur at densities of approximately 2. 8 per square mile in Rhodesia (Dasmann and Mossman, 1962), 1. 3 per square mile in the Rwindi-Rutshuru area of the Congo (Hubert, 1947), and 0. 6 per square mile in the Nairobi Park (Foster and Coe, 1968). An average of 6. 4 bushbuck per square mile per annum was shot in the Umfolozi area of Zululand for 7½ years, without apparently reducing the population significantly (Mentis, 1970). These density figures are probably not indicative of territory size, since bushbuck habitat is usually of local occurrence in savannah. Verheyen (1955) suggests that bushbuck in the Albert Park, Congo (now Zaire), spend most of their time in territories of only 2-3 hectares.

Bourliere (1963, quoted in Owen, 1966) gives a figure of 0. 8 *Cephalophus maxwelli* (closely related to or conspecific with *C. monticola*) per square mile in a forest in Ghana.

Dasmann and Mossman (1962) calculated the densities of grey duiker in four different areas in Rhodesia to be 0. 3, 1. 0, 1. 6 and 5. 5 per square mile respectively. In at least one case their figure was subsequently found to be too low. Wilson and Roth (1967) report a density of 2 to 3 per square mile instead of 1. 6 per square mile on one ranch where Dasmann and Mossman worked. Child and Wilson (1964) saw an average of 1. 5 per mile along 60 miles of road where visibility was approximately 100 yards on either side. The density would seem to have been of the order of 13 animals per square mile. This higher figure approaches that suggested by tsetse control figures from the Umfolozi reserve area in Natal. Mentis (1970) records that the average duiker offtake was 5. 9 per sq. mile over 7½ years and as in the case of the bushbuck offtake did not appear to reduce the population significantly. If the offtake for sustained yield is about one third of the total population, as Wilson and Roth (1967) imply, then the Umfolozi population may have been as dense as 18 animals per square mile. At 2-3 per square mile, the average territory size would be 86-129 hectares, at 18 per square mile, only 14 hectares.

Eloff (1959a) encountered steenbok at from 1 per 2.4 miles to 1 per 7.6 miles along roads and tracks in the Kalahari Gemsbok Park. He presents separate counts for each four-mile segment of the distance covered. In 22 such segments in which steenbok were seen, 10 had 1 each, 7 had 2, 2 had 3, 1 had 4 and 2 had 5 steenbok. Lamprey (1963) mentions a density of 1 per 10 square miles in the Tarangire reserve. Much higher densities, of the order of 1 animal per 5 ha, are suggested by observations in fynbos on the west coast of the south-western Cape Province (Cape Nature Conservation Department, unpubl.). Dasmann and Mossman (1962) encountered Sharpe's grysbok at a density of 0. 3 per square mile in Rhodesia, but grysbok in the Western Cape Province appear to be much more closely spaced (pers. obs.).

Clearly social behaviour is not the only spacing factor. Food, water and cover must all be expected to influence the sizes of territories or home ranges occupied. There is however no published information on the relative importance of these factors in determining population density.

Water is of little or no importance in the case of steenbok (Eloff, 1959a) and grey duiker (Wilson, 1966) and possibly also grysbok. In South Africa, blue duiker and bushbuck inhabit vegetation which is confined to moist areas so that it is difficult, and of no great importance, to separate the influence of cover and water on their distribution and density.

The solitary habit is closely associated with the occupation of closed environments where it is difficult for animals to maintain contact with one another. Adequate cover is necessary for all five species, only the steenbok tolerating somewhat more open conditions than the others. There is no information on whether variations in the density of cover as such influence carrying capacity.

All five species are essentially browsers (Wilson and Child, 1964; Wilson, 1966; Lamprey, 1963; Dorst and Dandelot, 1970) and thus utilise plants with a nutritive value which remains fairly consistently high throughout the year, in contrast to the grass on which grazers depend. Seasonal changes in the availability of food do not therefore appear to exercise much influence on their distribution. The animals tend to be sedentary and seasonal shifts of populations are unknown. Thus Wilson (1966) and Wilson and Roth (1967) found only minor changes in the activity and feeding behaviour of grey duiker from wet to dry season. The animals were markedly sedentary in the rainy season but quite mobile in the dry season when they fed on a greater range of plant species. However even the dry season movements were still local. There are no data to show how territory size is related to food supply, although the large differences in the density of e.g. grey duiker in different areas mentioned above, suggest that a correlation is to be expected.

(b) Semi-gregarious species

In klipspringer, the density limiting effect of the small social groups is reinforced by specialised habitat requirements. As is well known, the species inhabits rocky hills and mountains. The animals are mainly browsers and are not water dependent (Wilson and Child, 1965). Reedbuck, also occurring in small groups, have equally specialised but different habitat requirements. For example, in the Kruger National Park (Pienaar, 1963; Jungius, 1969) they are common in open and semi-open parts of the long-grass savannah woodland and treee savannah; elsewhere they are confined to the islands of suitable habitat provided by the long-grass and reed communities of vleis, dambo-like depressions and rivers. Reedbuck are mainly grass eaters and are water dependent (Field, 1970).

Density figures must be treated with reserve because of the restricted habitat occupied. Dasmann and Mossman (1962) give a figure of 0. 2 klipspringer per square mile. Bourlière (1955) records reedbuck occurring at a density of approximately 4. 5 per square mile in the Congo while Foster and Coe (1968), working in the Nariobi Park found 0. 24 per square mile. The two reedbuck territories measured by Jungius (1969) and found to extend over 48 and 60 hectares in summer, reduced to 35 hectares in winter, have already been mentioned.

Mountain reedbuck and vaal rhebok are also rather specialised in their habitat requirements since they are essentially animals of hilly and mountainous country. Cover is of some importance for mountain reedbuck and both species appear to be, at least in many parts of their range, water dependent (Shortridge, 1934). Little is known of their food preferences, Dorst and Dandelot (1970) describing the mountain reedbuck as a grazer which also browses on leaves and twigs and the vaal rhebok as a grazer only. The social behaviour suggests that the harem herds may occupy fixed home ranges or territories so that some behavioural limitation of density occurs.

Kudu do not appear to show territorial or home range behaviour. Simpson and Cowie (1967) and Simpson (1968) have reported marked seasonal differences in distribution on a ranch in Rhodesia. During the wet season the animals were widely dispersed and distribution appeared to be random. Food, cover and water are then widely available. In the cold season, more animals occupied habitats at intermediate altitudes and in the dry season the majority were concentrated in low lying riverine and *Acacia* thickets. The seasonal change in range was more clearly defined in females than in males, perhaps because of the increased physiological demands of pregnancy. Concentration in the riverine *Acacia* thickets in the dry season was thought to be mainly related to the availability of both food and cover, the leafy vegetation providing browse and shelter. The presence of water may have been a contributory factor since, although not dependent on water, kudu drink regularly when it is available. These findings suggest that environmental factors may have more influence than social behaviour on the spacing of kudu.

We have already noted that warthog family groups occupy home ranges and that these overlap with the ranges of other groups. Warthog feed mainly on short grass (Lamprey, 1963) but take some non-graminaceous plants and roots. They move readily if the food supply requires it. Warthog are dependent on free water and usually wallow when visiting water holes. The preferred habitat is open woodland but quite dense closed woodland may also be tolerated (Lamprey, 1963).

Bushpig inhabit dense cover in moist regions and feed on a variety of monocotyledonous and dicotyledonous plants as well as roots, fruits and carrion (Sowls and Phelps, 1968). They are serious pests of agricultural crops in many areas. Whether or not they are dependent on free water has not been discovered and we do not know if seasonal movements take place.

(c) Implications for management

1. *Control of numbers*

Where spacing behaviour is one of the factors determining population densities, over-utilisation of the habitat does not seem to occur. It is a matter of experience that the numbers of the solitary antelope discussed, as well as those of klipspringer, reedbuck and vaal rhebok among the semi-gregarious forms, have not required control in South

African parks and reserves. Mountain reedbuck numbers were however judged to be excessively high and control measures were instituted in the Mountain Zebra National Park, near Cradock, several years ago. Similarly, warthog have had to be heavily controlled in some Natal reserves. Complaints of over-browsing by kudu are heard from farmers in the Eastern Cape Province from time to time, but kudu have not yet been controlled in any parks and reserves, possibly because habitat utilisation is kept at a low level by seasonal movements of the kind mentioned above.

The mechanism of density limitation in solitary species has not been described. It is likely to be akin to that known to operate in roe deer. Watson and Moss (1970), summarising the findings of several workers who have studied this territorial species, write that dominant roe deer expel subordinate individuals into less favourable habitats where they suffer a higher mortality rate. When a population was fenced, reproductive performance, body weight and antler size decreased. The fenced deer had apparently reached a higher population level than would have been the case if emigration followed by predation had occurred. 'Obviously, food is important, but behaviour and predation may also limit deer populations in a natural situation'.

In fenced reserves where predators are absent and emigration is impossible, death of 'excess' animals may be expected among solitary species and control measures may be advisable to maintain the animals in good condition. Introductions of solitary species into populated regions are not likely to increase the population density.

2. *Cropping*

Some, and perhaps all, solitary species can tolerate quite heavy cropping. Presumably removal at the optimal rate, once this has been determined, takes the place of expulsion and subsequent losses to predators in maintaining a stable population. Examples of the effect of exploitation are available for grey duiker and bushbuck.

During the course of tsetse control operations in Eastern Zambia, 422 grey duiker were shot in an area of 200 square miles in two years. The population was not apparently significantly reduced. Shooting seemed merely to remove the annual increment, estimated to be of the order of 1-2 duiker per square mile (Wilson and Roth, 1967).

As previously noted, Mentis (1970), discussing the tsetse control campaign in the Umfolozi reserve and surrounding land, reports that grey duiker and bushbuck populations were not much affected by 7½ years of shooting. In an area of 462. 8 square miles, 20, 461 duiker were shot, an average of 2, 728 per annum of 5. 9 per square mile per annum. The bushbuck kill was 22, 232, averaging 2, 964 per annum or 6. 4 per square mile per annum. At the end of the campaign, both species were reported to be 'very numerous'. Du Toit (1954) assessed the degree of eradication achieved and wrote 'game observers reported large numbers of the smaller species of antelope and evidence of the presence of considerable numbers of the nocturnal bushpig, when to the casual observer, all game appears to have been eliminated. In fact, a balance appeared to have been struck whereby natural increase in the thicket-inhabiting species balanced the rate at which they were being destroyed'.

While the rate of cropping sustained is a function of the reproductive capacity, the behavioural response is of particular interest here. Wilson and Roth (1967) found that the duiker responded to continuous hunting by a gradual shift in the period of maximum activity, from the early morning and noon hours to the late afternoon and early evening. This diminished hunter success. Despite heavy hunting pressure and other major distrubances associated with tsetse control operations, the duiker population did not emigrate from the area. This sedentary behavioural trait seems, from casual observation, to be common to all the solitary species and many of the semi-gregarious forms discussed here. There are numerous examples of these animals surviving at the outskirts of quite large South African towns, while the fact that they are important farm species shows the adaptation to agricultural activity and disturbance. The sedentary trait is an important attribute fitting these species for survival and exploitation in inhabited regions.

The dense cover preferred is an important element in this ability to survive. Management must ensure that cover is provided. Their habitat, coupled with the dispersal of the animals, makes cropping by conventional hunting difficult however. The 422 grey duikers mentioned above were shot by 26 hunters stationed in the 200 square mile area, a density of one hunter to 5-6 square miles (Wilson and Roth, 1967) and an average annual bag of only 8 duiker per hunter. By and large, the behavioural attributes of the solitary and semi-gregarious species make them better suited to sport hunting than to exploitation for meat production.

(d) Gregarious species

Group formation is associated with the occupation of open habitats, where grass is an important source of food, fluctuating seasonally in quantity and more particularly in quality. Seasonal movements activated by changes in food supply, and in some cases by the availability of water, are often necessary for survival. Territoriality is more important as 'an agent of male selection' (Ewer, 1968) in social species with a harem, system than as a factor leading to spacing out. However Ewer has emphasised that social organisation is fluid in gregarious forms, not 'something the species has got in the same way as it has got characteristic anatomical and behavioural attributes' but an adaptable response to environmental conditions.

The densities of the gregarious ungulates dealt with here are, in general, more directly governed by the productivity of the environment and by behavioural responses to food and water, than by the presence of cover or by spacing behaviour and the sedentary habit.

1. *Food and habitat*

Blesbok are grazers of open grassland (Du Plessis, 1968); hartebeest and wildebeest are mainly grazing species of grassland and open woodland (Lamprey, 1963; Leistner, 1967). Gemsbok are essentially grass feeders which also dig for roots and tubers and do a fair amount of browsing (Leistner, 1967); they occupy open or lightly wooded country. Eland are mainly browsers (Van Zyl, 1965; Leistner, 1967; Kerr *et al.*, 1970) which live in plains country, savannah and montane grassland. Impala are by preference primarily grass-eaters, although able to utilize a wide variety of other plants (Stewart, 1971); they inhabit open woodland. Springbok are mixed feeders (Van Zyl, 1965; Skinner *et al.*,, 1971; Bigalke, in press), which seem to use grasses mainly in the rainy season and shrubs in the dry season. They prefer open plains and sparse savannah.

2. *Water*

Blesbok and wildebeest are water dependent and hartebeest are generally also considered to be so (Eloff, 1959a; Lamprey, 1963;pers.obs.) although Shortridge (1934) described them as occupants of waterless areas in South West Africa. Springbok (Bigalke, in press) and impala drink where water is available but even then impala drink relatively little and infrequently (Young, 1970). Both species have the capacity to survive in the absence of free water (Shortridge, Lamprey, *op. cit.*). Gemsbok also drink, but their very low requirements enable them to live independently of surface water. Survival of eland in waterless areas is achieved not by low requirements but by selecting succulent food, resting in the shade, forming dry faeces and by possessing a narrow thermal neutral zone (Taylor, 1969).

3. *Density*

Social behaviour may have an important influence on spacing in some gregarious species under certain conditions. Thus the harem herds of hartebeest which Backhaus (1959) observed in the Garamba Park appeared to remain in their territories throughout the year. One territory which he measured had an area of 3 sq. km. It must be presumed that food and water supplies were adequate all year round. In contrast, Eloff (1959a) found that hartebeest in the Kalahari Gemsbok Park were seasonally mobile and there were occasional large scale shifts of the population, the animals apparently moving to regions where local rain storms had produced fresh green grass. The observations of David (1970) and Du Plessis (1968) show comparable differences between bontebok and blesbok in different areas. In the Bontebok National Park some territorial bontebok males maintain their territories throughout the year and appeared always to be associated with the same harems. This sedentary behaviour may be associated with the relative constancy of environmental conditions. The park is situated in a region where rain falls throughout the year with a maximum in spring (Grobler and Marais, 1967). There are no drastic or spectacular seasonal changes in the vegetation comparable in magnitude with those near Pretoria where Du Plessis worked. He studied blesbok in a 'sour' grassveld region where the pasture is of very poor quality in the winter. After burning, there is a flush of succulent grass when the summer rains start. The blesbok were only dispersed in harem herds during the rut. In early winter they moved about in large, mixed herds, changing to smaller groups in late winter. When the rains started they congregated on the burns.

Wildebeest provide the most striking example of the different roles which social behaviour may play in spacing gregarious animals under different environmental conditions, Sedentary wildebeest in the Ngorongoro Crater have permanent grazing and water. As we have already seen, 25-50% of the males occupy territories while females and juveniles are found in small groups which move about restricted home ranges.

Bachelor herds occupy peripheral unfavourable habitat. Migratory wildebeest in drier environments move about in large mixed aggregations, following grazing and water and not spaced by social pressures (Estes, 1968). Only when migration comes to a halt do males take up temporary territories.

Large mobile assemblages of springbok (Bigalke, 1961 and in press) and impala (Jarman, 1970) congregate on green flush produced by localised rain showers, and the spacing effect of social behaviour is only clearly apparent during the rut.

Gemsbok are seasonally mobile (Eloff, 1969a; Bigalke 1961) and gather on patches of fresh pasture, but very large herds comparable with those of wildebeest, for example, have not been recorded. This may be partly the result of smaller populations, but seems also to be related to less highly developed sociability.

Eland are nomadic (Eloff, 1959a, Bigalke 1961) and this behavioural trait is probably very important in such an ecologically tolerant animal. We have already noted that herds tend to be larger in summer and smaller in winter when dispersal is probably an important means of obtaining enough food.

Implications for management

The influence of the large, gregarious and mainly grazing species on the vegetation is, clearly, much more marked than that of small, solitary and semi-gregarious forms, dispersed by their pattern of social behaviour and in many cases, limited by specialised habitat requirements.

We have shown that green flush attracts large congregations. In arid regions where rainfall is often local, these assemblages of animals may crop the grasses of small areas very heavily at the time when the growing plants are most susceptible to damage. Only where good food, and water, is abundant throughout the range, do social interactions tend to have a spacing effect which serves to spread the pressure on the food plants. In most cases the spacing effect of intra-specific intolerance is usually only marked during the rut. Too many animals, even if they are dispersed and sedentary, can also lead to overgrazing. The distribution of water affects dispersal mainly in the dry season, when the animals have only dry food.

Management of these gregarious ungulates on farms involves careful control of numbers in the first instance. Too many animals set undesirable patterns of plant succession in train, leading to deterioration of the range and to phenomena such as the encroachment of woody plants in grassland. The animals are difficult to move at will, so that the systems of grazing control which can be applied with domestic animals, cannot be used.

Fencing farms into paddocks makes it easier to manage some species (see below). Where paddocks are large and climate and vegetation permit the use of fire, block burning is a useful method of attracting concentrations of animals to different areas in rotation. Manipulation of water points can also assist in moving animals, but this is usually only successful in the dry season.

Social species living in herds in relatively open country can be more easily and economically cropped in large numbers than solitary and semi-gregarious forms. However constant hunting quite soon leads to behavioural adaptations and techniques must be varied. Shooting from hides at water-holes or with the aid of strong lights at night, are methods which may be successfully employed in many cases.

CONTROLLING THE COMPOSITION OF POPULATIONS

Where natural populations are managed merely to keep the numbers within the carrying capacity of the vegetation, control should have the aim of maintaining natural age and sex ratios. Our main interest is however in populations which are managed for trophy hunting and those cropped for maximal production.

In the first case, it is necessary to know what proportion of mature males can be shot without disrupting the social organisation to the extent that reproduction is affected. When cropping, the sex and age composition of the kill which will produce the highest sustained yield must be known. These are not purely behavioural questions. The answers depend on whether a species is polygamous or monogamous, and also on the age at which males and females become sexually mature, and whether sexually mature males are also behaviourally adequate for successful mating. In many cases the basic information required to provide the answers is not yet available.

(a) Solitary species

It is generally assumed that solitary species are monogamous and the fact that the sex ratio in natural populations often approaches unity supports this view. Wilson and Roth (1967) found a unit sex ratio in 422 grey duiker shot in Zambia. There were almost equal numbers of each sex among 324 steenbok shot in Zululand (Mentis, 1970). However Wilson and Kerr (1969) counted 67 males and 35 females in 102 steenbok foetuses and Van Bruggen (1964) saw 47 males, 10 females and 10 unsexed animals in the Kruger National Park. In Sharpe's grysbok, Dasmann and Mossman (1962) report a proportion of 100 females: 81 males, but the sample was not large. Elder and Elder (1970) recorded virtually equal numbers of male and female bushbuck in 167 sightings. However Mentis (1970) reports that 59.9% of 2, 535 bushbuck shot in Zululand were females and Wilson and Child (1964) found a ratio of about 80 males: 100 females among adult bushbuck (shot) although the overall sex ratio of all age groups approached equality.

If it is assumed that dominant individuals of both sexes occupy territories, resulting in the presence of a 'floating reserve' of subordinate animals which are normally lost by emigration or fall prey to predators, disease or starvation, then the removal of territory holders would be expected to 'make room' for subordinates. If adult males are shot, they should be replaced by younger animals. Since the small antelope appear to be quick maturing, reproduction should not be affected by a shortage of fertile males. Assuming monogamy, unselective cropping of both sexes should theoretically produce the highest yield.

Unselective hunting has in fact been shown to stimulate increase in a population of grey duiker (Child and Wilson, 1964) and it is probably safe to assume that this is the best management technique for solitary species. It is in any event the only practicable one, for it is exceedingly difficult to select one sex or the other when hunting small antelope in thick cover.

There is some evidence suggesting polygamous mating in bushbuck. We have already noted the preponderance of females reported by some authors. Verheyen (1955) describes both male and female bushbuck as territorial, but he observed as many as 10 animals together on a communal grazing ground. A particularly fine male had only to appear to be immediately joined by one or other of a pair of females. He would then return to his territory with the female. Mating was not observed however. This observation and the unequal sex ratio suggest the unusual combination of polygamy with territoriality of both sexes. If further work shows this to be the case, cropping for the greatest yield should be planned to take both males and females in the proportion in which they occur. Selective removal of dominant males as trophies, which is easy in this sexually dimorphous species, may simply permit sexually mature but normally subordinate, non-terriorial males to take over the mating functions of the animals which have been shot. However the age of sexual maturity in male bushbuck is not known and until it is, little more than speculation is possible. A 'buck law' has been in operation for bushbuck in the Cape Province and Natal for many years and populations seem little affected by hunting on this basis.

(b) Semi-gregarious species

Wilson and Child (1965) found a sex ratio close to unity in klipspringer, counting 44 males and 52 females. In a reedbuck kill of 840 animals shot in Zululand, the ratio was not significantly different from unity (Mentis, 1970). The same author reports unit ratios for mountain reedbuck (n = 31) and bushpig (n = 179) and a slight excess of females (52.4%; ratio significantly different from unity) among 4, 681 warthog, all shot in Zululand.

Simpson (1968) records 61 males: 100 females in kudu (n = 289), which is in agreement with the figure of 64: 100 (n = 305) from Zululand (Mentis, 1970). Dasmann and Mossman (1962) found a ratio of 46 : 100. Only Wilson (1965) shows more males than females (119 : 100) in the sample collected by shooting, although on his sight records he obtained a ratio of 42 males per 100 females. Simpson (1968) considers that Wilson's non-conforming kill figures are the result of a higher hunting mortality in males, or a lower visibility in sight counts. In any event, kudu have a sex ratio not significantly different from unity at birth, and male mortality thereafter is higher than that of females (Simpson, 1968; Dasmann and Mossman, 1962).

Management techniques for klipspringer and reedbuck are affected by their specialised habitat requirements. Where they are sparsely distributed in isolated islands of suitable country, selective removal of males may be undesirable because the chances of replacement from the 'floating reserve' are slight. Where good habitat is widespread and the animals common, and assuming monogamy, which seems to be the case, it should be possible to manage them like solitary species. Removal of dominant males for trophies should not depress reproduction, since they would be replaced by younger males which probably mature quite quickly. It must however be noted that the age of sexual maturity has not been determined for either species. Unselective cropping at a rate determined by population dynamics of the species might be expected to be as suitable as for solitary species. The only evidence available concerns the effect of tsetse control hunting in Eastern Zambia (Wilson and Child, 1965). Klipspringer proved difficult to eliminate, probably because of their specialised habitat and high reproductive potential. Indeed the authors suggest that hunting may have stimulated an increase in the population studied.

In the polygamous mountain reedbuck and vaal rhebok male herds may be expected to provide replacements for mature males shot from harem herds. Unless cropping of males is very heavy, a shortage seems unlikely to develop since these fairly small antelope, by analogy with others of comparable size, probably become sexually mature by the age of about two years. The question of how many apparently excess males, which do not seem necessary for reproduction in polygamous species, should in fact be kept, will be discussed under the heading of 'gregarious species' below.

Child *et al.* (1968) have discussed the implications of the apparently monogamous mating behaviour of warthog, and of delayed attainment of sexual maturity in males, for the management of the species. In a dry area of Rhodesia, they found that females matured as yearlings, but males a year later. The sex ratio was unity, so that there were more sexually mature females than males among animals of 24 months or older. In one sample collected there were 122 sexually mature males, and of 173 mature females, only 124 had bred. Thus the number of females breeding in any season would appear to depend on the number of mature males. Selective hunting of males will therefore depress reproduction. A maximum sustained yield can only be obtained by harvesting correct proportions of males and females, taking into account the existence of a pool of sexually mature females which do not take part in reproduction.

Too little is known of the social behaviour and sex structure of bushpig populations to comment on management.

The mating behaviour of the kudu has not been described[1]. They rut in winter, with maximal development of the testes in June (Skinner, 1971). Simpson (1968) found a peak in herd size in July and associated this with the rut. Wilson (1970) encountered one or more bulls with herds of cows and calves on 10 occasions during May. Kudu

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[1] But see Walther 1964. *Z.J. Tierpsychol.* 21: 393-467.-eds.

are certainly polygamous but males probably do not mate with large numbers of females. The mean July herd size recorded by Simpson was only about 3. 5 (over 20 herds) and the maximum 12. Selective shooting of adult males carrying trophy heads is unlikely to disrupt reproduction since fully developed horns with 2½ twists probably take 6-6½ years to develop (Simpson, 1968). At the age of two yours horns only have one twist. The age of male sexual maturity is not known but since females may mate at about 17 months (Simpson), males, even if they mature later, must be expected to be sexually mature long before their horns attain desirable trophy size.

Exclusive cropping of horned males of all ages must be expected to lead to a shortage, particularly since, as we have noted, the male mortality rate is higher than that of females. Cropping must therefore take both sexes, but it is not possible to suggest an optimal ratio from available information.

(c) Gregarious species

We have seen that competition among males of most of the gregarious species for access to females, results in the formation of harem herds. Comparison of the size of the harem herds with sex ratios found in wild populations, makes it clear that relatively few male hartebeest, blesbok, wildebeest, springbok and impala succeed in mating.

The number of hartebeest cows in harem herds varies from 2-14, according to Backhaus (1959), and this author quotes D'Elzius (1957) who found the population to contain slightly more cows than bulls. Among 3, 457 adult hartebeest, males and females were almost equally represented (Foster and Kearney, 1967). Du Plessis (1968) counted 2-25 blesbok females in harems and calculated a mean of 7. 6 in one year, and 10. 4 in the next. Since there are no longer any wild blesbok, the sex ratio in natural populations is unknown, but an adult ratio of about 1 male : 2. 6 females is reported by du Plessis.

Bigalke (1970) found the mean size of springbok herds during the rut to be 18. 7. Impala harems are similar according to Leuthold (1970); in one area, 54% of the harem herds contained 6-25 animals while in another where the vegetation was less dense, they were somewhat larger, 69% of the groups varying in size between 26 and more than 35. These authors found an adult male: female ratio of roughly 1 : 2 in both species.

Only for wildebeest has the proportion of the male population which copulates been estimated. Estes (1968) found the year-round average size of nursery herds in Ngorongoro to be 10, including 6 adult females. With a sex ratio of 40 males: 50 females, he calculated that adult, territory-holding bulls constituted some 7-14% of the total population and perhaps 25-50% of the adult males. He writes: 'up to 50 per cent if not more of the adult males may be relegated to bachelor herds at any time, not because they are unfit, but simply because they are supernumerary'. Only some of the territorial individuals were successful in mating. The proportion of reproductively active males may be still smaller in other populations, since several authors have reported a preponderance of males:-52 males: 42 females in Serengeti (Talbot and Talbot, 1963) and about 58 males: 42 females in the Nairobi Park (Foster and Kearney, 1967) and in Zululand (Mentis, 1970). Talbot thought that only 8% of his animals, and 16% of the adult males, were lone (i.e. territorial and reproductive) bulls.

The few data available for eland show an adult sex ratio of 14-16% males in Malawi (Martin, 1968) and about 25% males in Natal (Natal Parks Board, unpublished). Foster and Kearney (1967) report 69. 8% males in a sample of 172 adults from the Nairobi Park but this figure is so different from the others that it must be treated with suspicion. The only information on gemsbok sex ratios known to me is a figure of 35 males: 65 females among 302 animals counted in the Etosha Park (Bigalke, unpubl.). The proportions of male eland and of gemsbok which play an active part in mating has not been determined.

The removal of adult males by trophy hunting is unlikely to depress reproduction. The males of all species for which data are available, attain sexual maturity and are physiologically capable of mating, long before they become sufficiently dominant to have access to females. Dominance by older males leads to an 'inhibition of effective puberty' (Sadleir, 1969) or 'psychological castration' (Altmann, 1960) and removal of these older animals must be expected to give younger ones the chance of mating, normally denied them.

Rowe-Rowe and Bigalke (in press) observed successful mating by a male blesbok only about 19 months old. Blesbok of this age are easily distinguishable in the field and are never seen in harem herds. It is of interest that this animal did not appear to be able to mate during the usual rutting season, when he was about 27 months old, but managed to do so later with the result that the young of his three adult female partners were born about three months later than usual.

Skinner *et al.,* (1971), found spermatozoa for the first time in testes of springbok aged 48 weeks. They state that 'Sexual maturity is rapidly achieved after 50 weeks of age'. Impala males are capable of fertilization from the age of about 13 months and an animal of 17-18 months mated successfully (Kerr, 1965). In neither species do males of these ages participate in the rut.

Wildebeest bulls appear to be physically capable of reproduction as two-year-olds, yet few become territorial before the end of their third year (Estes, 1968). The few animals seen to participate in the rut at 28-29 months were subjected to intense psychological, and physical, pressures. Estes writes: 'of half a dozen that were kept under observation, not one withstood the battering of his neighbours for more than a few hours before abandoning his place'. A male eland of 18 months mated successfully with a female of the same age, but other males of this age played no part in mating in a semi-domestic herd where adult males were present (pers. obs.).

The most important question from the point of view of management is: what proportion of males to females is needed for optimal reproduction? The non-copulating segment of the male population seems so obviously unnecessary that there is a strong tendency to dispense with it. There is a suggestion that a normal 'wild' sex ratio may even depress the conception rate under conditions of semi-confinement, because the males interact so vigorously. When the apparently excess males were shot in a herd of black wildebeest (*C. gnou*) on a reserve, the calf crop increased markedly (Van Zyl, pers. comm.). Even in a wild population—of kob (*Adenota kob*)—Leuthold (1966) has suggested that reproduction may be more efficient at low densities where males defend territories of 100-200 m diameter, than at high densities where their territories or leks are only up to 30 m in diameter and male interactions are very frequent.

On the other hand, the presence of supernumerary males ensures selection for the most vigorous animals. It is difficult to imagine any other practicable way of maintaining the genetic quality of managed populations. The role of male stimulation in synchronising oestrus is well known in domestic artiodactyls and other mammals (Sadleir, 1969) and is likely also to be important in the species under discussion. These, at least outside the tropics, have short and distinct lambing seasons, as Bigalke (1970) has shown for springbok, Fairall (1971) for impala, and Du Plessis (1968) for blesbok; remarkable synchronisation within the tropics for wildebeest in the Serengeti has been recorded by Watson (1969), who states that 80% of the calves are born within a three-week period. Oestrus is therefore well synchronised and the 'excitement' provided by male interactions may play a significant part in achieving this. The role of odours has not been studied at all, but it can also be expected to be important. Sadleir's (1969) comment is relevant 'it would seem more than likely that future research will demonstrate that odours act as pheromones and can influence the reproduction of wild animals at high densities in exactly the same way as occurs in the laboratory'.

For the purposes of practical management, the best solution possible in the present state of knowledge is probably to strike a compromise between the normal sex ratios of wild populations and the male: female ratio observed in harem herds during the rut.

REACTIONS TO CONFINEMENT

So far, we have attempted to describe the behavioural attributes of our species as observed in wild and more or less undisturbed populations. Management on farms and ranches, most of them fenced, is concerned with the behavioural reactions to confinement. This is clearly a relative term, but for the purposes of this paper, confinement in areas so small that the animals require artificial feeding will not be considered. Behaviour under these circumstances is the province of the zoo biologist. It is also clear that the size of enclosed areas *per se* is of little interest; it is size in relation to the productivity of food plants and the presence of cover and water that is important. In general, farms tend to be larger and more extensively managed in areas of low productivity, and smaller, with smaller and more intensively managed paddocks in highly productive regions. Game populations are greatest and of most importance on the large, extensive pastoral holdings where they range over fairly big areas in a more or less natural state and are not closely confined. The techniques of managing them more effectively under such conditions are not yet well understood.

1. Reaction to fences

Farm fences in South Africa are usually 4 ft.-4 ft. 6 in. high. In sheep farming regions, most are made of netting wire and are commonly called 'jackal-proof fences. Cattle ranches are enclosed with fairly simple fences of plain or barbed wire. The effectiveness of these barriers in holding wild ungulates is related to the size, behaviour and locomotory abilities of the animals. However, as Hediger (1950) has pointed out, 'excitement weakens all a barriers' and enclosures which are normally adequate, may fail to hold excited and disturbed animals, or those strongly motivated by hunger or thirst. The size of the enclosure also affects the adequacy of the fence, and Kettlitz (1962), urges a policy of 'the smaller the enclosure the stronger the fence'.

The small solitary antelopes do not jump fences and are contained by netting, but slip easily between strands of plain or barbed wire. Bushbuck jump well however and according to Astley Maberley (1963) can clear fences less than 7 ft. high.

Of the semi-gregarious forms, the kudu, a tragelaphine like the bushbuck, is a prodigious jumper and an 8 ft. fence is necessary to keep them out of croplands. Reedbuck, mountain reedbuck and vaal rhebok jump fences of standard height. Nothing appears to have been recorded of the response of the klipspringer. Warthog burrow and can only be contained by netting with the lower end buried.

Blesbok are easily confined by simple fences but crawl beneath or between the lowest strands if these are too far apart. (Kettlitz, 1962). Hartebeest also use regular creeps but do occasionally jump over (pers.obs.). Springbok crawl through or under wire strands but very rarely jump fences unless hard pressed, in spite of their spectacular leaping abilites. Walther (1968) has drawn attention to the fact that none of the gazelles are behaviourally equipped to overcome vertical obstacles—in complete contrast to the tragelaphine bovids. Impala jump normal fences with ease and need a 7 ft. barrier to hold them, although they can clear 8 ft. when pressed (Kettlitz, 1962). Gemsbok creep through or under stranded fences but do not, as far as I am aware, jump over them. Eland, like kudu, are spectacular jumpers in spite of their large size and are capable of jumping 6-7 ft. fences (Skinner, 1967), although a 6 ft. 6 in. barrier successfully contained a semi-domestic herd in Natal (pers.obs.).

Animals which have become accustomed to a fence, tend to accept it as an insuperable barrier. Even when it is removed, farmers often find it difficult and usually impossible to drive springbok, blesbok (pers.obs.) and impala (Kettlitz, 1962) across the line of a known fence. This behaviour thwarts efforts to drive animals from one paddock to another in order to apply rotational grazing systems, and adds to the practical difficulties of efficient game management.

2. Social behaviour in confinement

Ewer (1968) considers an increase in aggressiveness to be a normal feature of captive behaviour among mammals. Under farm conditions, it would seem to be the lack of space for victims of aggression to escape, rather than an increase in aggression as such, that poses problems in small paddocks.

We have already suggested that the weaned young of solitary territorial species may be expected to be killed, or to die from harassment and lack of a place to live, if they cannot disperse because of the presence of fences. There is not yet any clear evidence to support this view. We do not know to what extent territories may be compressible and behaviour capable of modification by confined conditions. That some modification is possible is suggested by casual observation of captive grey duiker (Greig and Bigalke, unpublished). Females, like males, tend to occur singly and are probably territorial, or at least occupy individual home ranges in the wild. In a group consisting of an adult male and three females living in a small zoo paddock, the largest female A is clearly dominant over the other two females B and C. She marks with her preorbital glands almost as frequently as the male. Female C, probably the youngest, is often virtually confined to a kennel by the aggressive behaviour of A. It is interesting that A tolerates B, who is probably her daughter; perhaps sociability is well enough developed to permit establishment of a ranking order of two, but not of three. Much more work is needed to find the greatest densities at which solitary species can be maintained.

The social species are all, except perhaps the gemsbok, seasonal breeders in South Africa. Male aggressiveness reaches a peak during the rut and in species with territorial males and a harem system, rivals are often vigorously pursued. Aggression of dominant males towards yearlings has also been reported in blesbok (Rowe-Rowe and Bigalke, in press) and wildebeest (Estes, 1968), at the time when the next crop of young are born. This rather surprising behaviour may be related to excitement induced by the smell of parturient females. In any event, yearlings are chased with tremendous vigour.

In small paddocks, blesbok males frequently kill other males and even females and lambs (Kettlitz, 1967). It is clear that behavioural responses of this kind influence the density at which social species can be maintained, but no exact information is available on the densities and sex ratios necessary to maintain normal behaviour.

The hierarchical system within eland herds seems to be similar to that of the Bovini which Ewer (1968) discusses. The fact that it successfully reduces aggression, makes eland easy to keep and has certainly been an important, and perhaps hitherto unrecognised, reason for the success of domestication experiments such as those described by Treus and Kravchenko (1968) and Pesselt (1963).

3. Response to herding

When social species are hunted or captured, they are often driven to the guns or catching pens. Horsemen, motor vehicles or aircrfat may be used. Herding from the air does not generally seem to be very successful in the case of springbok and blesbok in open country, but experienced horsemen can move the animals quite efficiently. A helicopter has been shown to be highly suited to driving wildebeest, impala, kudu, warthog and other species (Oelofse, 1970).

Animal catchers and hunters believe that a study of the routes which the animals usually follow when they are alarmed, is a prerequisite if they are to be successfully driven to a pen or on to a line of guns. When arranging drive hunts of springbok and blesbok, farmers often position the guns in a fixed place and drive in a standard pattern. This suggests the existence of favoured routes with which the animals are familiar. Well-worn paths are indeed a familiar feature of all areas where wild ungulates are found and Hediger (1950) in particular has emphasised the fact that animals tend to move between 'biologically significant points connected in a characteristic manner by means of definite tracks or beats'.

4. Temperament

While it is difficult to discuss an attribute as vague and ill-defined as temperament, there is little doubt that the species under discussion differ considerably in this regard. The differences have significant implications for handling and management. It is a matter of experience, and well known to farmers who work with them, that blesbok are docile, and easy to capture and transport (Kettlitz, 1967; Visagie, 1968). Impala and springbok are nervous and difficult to catch and transport, often resulting in high losses (Kettlitz, 1962) unless they are treated with skill and care. Eland have a reputation for docility (Bigalke and Neitz, 1954) and have been successfully domesticated in several trials (Posselt, 1963; Treus and Kravchenko, 1968). Gemsbok and vaal rhebok have a reputation for aggressiveness (Shortridge, 1934) and gemsbok may be captured with ease by using trained dogs to bay them. The animals are so intent on the dogs that they pay no attention to the approach of people (pers.obs.).

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Paper No. 49

Implications of Social Behavior in the Management of Uganda Kob

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ABSTRACT

Uganda kob are the predominant ungulate among nine species in the Toro Game Reserve, where about 18,000 kob live in a geographically isolated area. The population is subdivided into social units oriented around permanently located territorial breeding grounds. Between the tight clusters of territories at the breeding grounds, widely spaced single territories contribute further to the social structure of the total population. Observations of tagged individuals showed that about half of the mature males remained within 500 m of the home territorial breeding ground over 90-100% of the time, whereas only 14% of the females were found within 500 m of the home lek 90-100% of the time. Both males and females returned to the home TG for mating.

The reproductive cycle in the female kob is about 280 days. Annual natality was at a rate of 1. 35 young per breeding female, or about 10, 500 for the population of 18, 000. Juvenile mortality, based on nonlactating females <160 days pregnant, was about 47%. Despite the high productivity, it is doubtful that the annual rate of exploitation by legal cropping can exceed about 1,000, given the rate of mortality imposed by lions and leopards and the potential perturbations to the social system likely to occur at higher rates of harvest. To preserve genetic viability and the social organization of the population requires a pattern of harvest that protects territorial males, concentrates on young males in bachelor herds, and distributes the offtake among the separate subunits of the population.

Under a regime of cropping that has taken the kob's social system into account, the population level and the permanent territorial breeding grounds in the Reserve appear to have remained remarkably stable over the past decade.

INTRODUCTION

Sustained harvesting of a population of wild animals for recreation or commerce often is strictly a 'numbers game,' based on a model that takes into account natality, juvenile mortality, mean annual adult mortality rate, longevity, pattern of reproduction, population fluctuations, and similar numerical parameters. The model can be improved by adding the dynamics of the population in relationship to the animal's impact on its food supply, changes in vegetation, predator-prey relationships, and other ecological components; and by including genetic changes induced by exploitation. A model capable of the fine-tuning needed in more precise management in the future, as ecosystems become increasingly modified, should also take into account the social organization of a population and the role of social behavior in numerical regulation.

The objective in this paper is to show the importance of including knowledge of social behavior in managing a population of ungulates. In the Toro Game Reserve in the Semliki Plains of western Uganda about 18, 000 kob antelope *Adenota kob thomasi* (Sclater, 1896), are organized into about 13 sub-units of 1,000 to 1, 5000 individuals, each sub-unit being oriented around a permanently located, conventional territorial breeding ground (TG). The TGs are conceptually identical to the leks of the prairie chicken (*Tympanuchus cupido*), sharp-tailed grouse (*Pedioecetes phasianellus*), sage grouse (*Centrocercus urophasianus*), black grouse (*Lyrurus tetrix*), Gould's manakin (*Manacus vitellinus*), and many other birds, an excellent discussion of which is given by Wynne-Edwards (1962). The overall effect of the kob's social structure is to spread the population out over about 400 km^2 of habitat. Exploitation of this population for the market by the Uganda Game Department over the past decade has taken into consideration the animal' s behavior and social organization, apparently without ill effects. Although potential behavioral, genetic, population and/or vegetational perturbations through over-exploitation can only be implied, the Semliki kob provide a valuable paradigm for conceptualizing the significance of social behavior in the management of ungulates.

METHODS

Initially, the study of the kob in the Semliki was designed to determine the pattern of reproduction; and about 15 individuals, mostly females, were collected each month for a year, beginning in July 1957. In a preliminary study of the territoriality of the male kob, techniques were developed for capturing the animal with immobilizing drugs, using succinylcholine chloride administered by a projectile syringe (Buechner *et al.,* 1960). The orientation of sub-units around TGs emerged from this research, and more intensive study of reproduction and territorial behavior was carried out from 1962 to 1964. Tagged and naturally marked males and females were observed from 5-meter towers to obtain data on territorial behavior and to determine precise dates of copulation. Females with known-aged concepti, based on known dates of copulation, were collected at intervals to obtain a foetal growth curve, from which the ages of embryos and foetuses from females collected at random were calculated to determine the annual pattern of reproduction. Fawns were tagged within 2- 3 days after birth to determine: (1) the minimum breeding ages of males and females; and (2) the interval between parturition and subsequent conception. A few fawns were raised in captivity to obtain information on growth rates, horn development, and minimum breeding age. Surveys were made to ascertain the sex and age composition of the population, and simultaneously to locate tagged individuals. Tagged kob were also recorded in terms of distance and direction from their home TGs each time they were observed during the course of field work. Eight males were translocated to determine the degree of their attachment to their home TGs. The data from all of these studies have been organized and stored on computer tape.

THE STUDY AREA

The Semliki Plains are located in the Western Rift Valley, 1°N of the equator, at an elevation of 650 to 850 m (Fig. 1). Here the kob's environment is limited eastward by the Albert Escarpment (800 m); westward by the Semliki River, along which cattle are grazed intensively; southward by the more highly dissected topography toward the foothills of the Ruwenzori Mountains; and northward by the marshes along Lake Albert. Annual rainfall, varying from 75-90 cm at Lake Albert to ca. 125 cm at the southern end of the Plains, occurs in a long rainy season from late March through June and a short season in September and October. After periods of heavy thunderstorms, low-lying, poorly drained flats are temporarily inundated. The drainage pattern evolved in response to small-scale block faulting that occurred during the most recent upthrust of the Ruwenzoris (Bishop, 1965, 1967). TGs are located, in relationship to the tilt blocks and fault pattern, on well-drained sites where visibility is good and permanent water is available in small intermittent streams, in which pools remain during normal dry seasons (Fig. 2). Prolonged droughts occasionally occur, perhaps once or twice in a decade, and at such times the kob migrate temporarily to the lower land near Lake Albert.

The vegetation consists of open, sparsely wooded grasslands. Langdale-Brown *et al.* (1964) include only *Borassus-Hyparrhenia dissoluta* Palm Savanna, *Combretum-Hyparrhenia* Savanna, *Themeda-Heteropogon* Grass Savanna, and *Acacia-Imperata* Savanna in the Semliki Plains. Significant communities of *Hyparrhenia* Grass Savanna and *Themeda-Chloris* Grass Savanna also occur in the pattern of vegetation. During the long dry season from late December to raid-March the grass is burned in a patchwork pattern, and some of the driest areas are burned also in July. Regrowth is rapid, even without rain, and the burned areas become green within a week. Sufficient rainfall occurs during the dry season to maintain adequate forage production.

In response to good visibility and an abundance of short, fresh grass, the kob spread out widely during the dry season. With the onset of the long rains, the animals concentrate around the TGs where they are able to keep the grasses grazed down until the end of the rainy season, by which time the growth of grasses (up to 1-1. 5 m) is so rapid that close cropping cannot be maintained. The burning that follows, as soon as the grasses are sufficiently dry, produces new growths of grasses on which the kob concentrate.

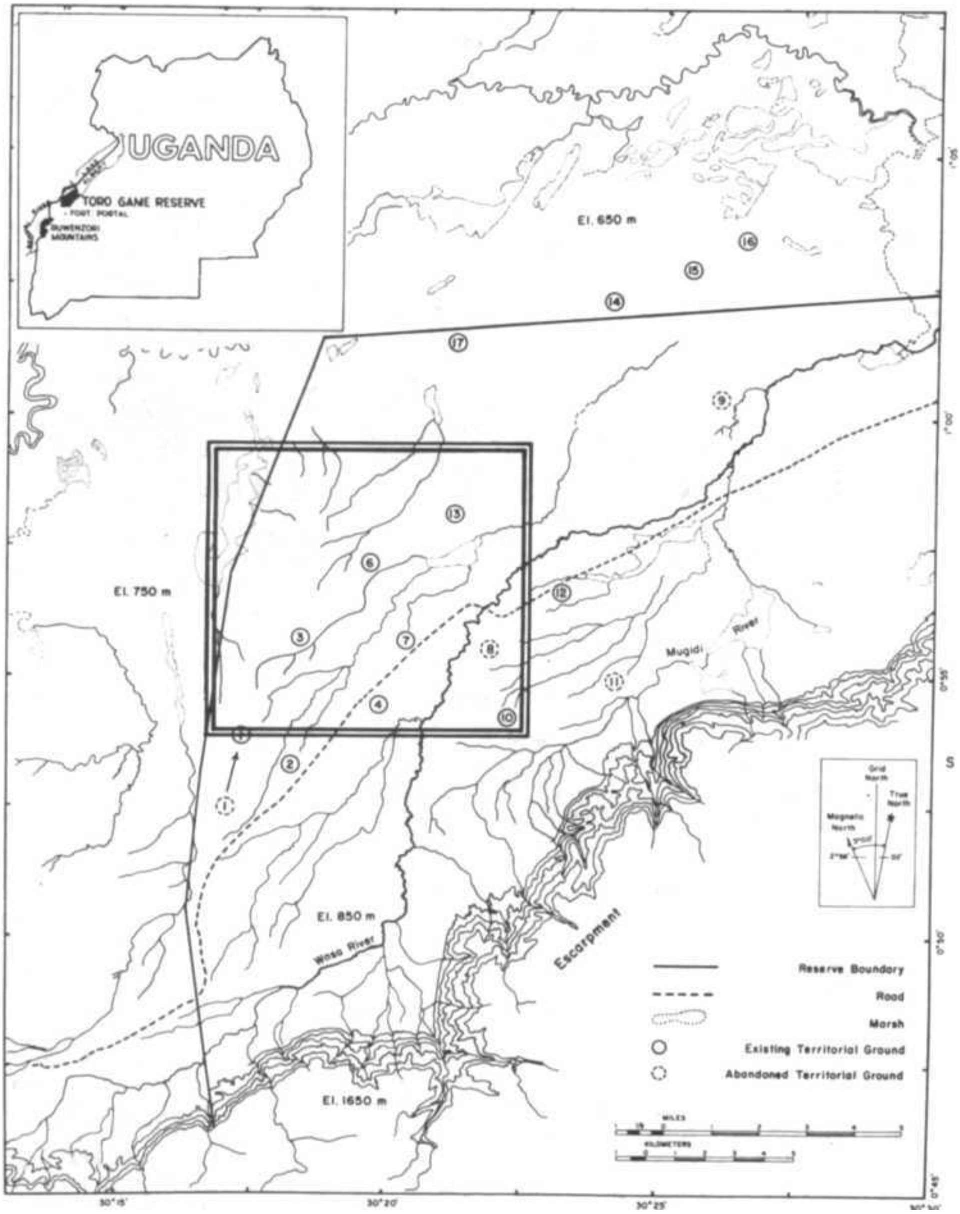

Fig. 1. Toro Game Reserve and vicinity in the Semliki Plains. Main research area in center inset.

Fig. 2. TG3: the location provides good visibility, excellent drainage and access to drinking water in adjacent draw. The TG is c. 200 m in diameter, these territories being approximately circular not elliptical as suggested by the foreshortening effect of a telescopic lens.

Besides the Uganda kob, which are numerically dominant, eight other species of ungulates occur in the Semliki: Jackson hartebeest, *Alcelaphus buselaphus jacksoni;* defassa Waterbuck, *Kobus defassa ugandae,*Bohor reedbuck, *Redunca redunca;* bushbuck, *Tragelaphus scriptus;* gray duiker, *Sylvicapra gimmia;* Cape buffalo, *Syncerus caffer;* giant forest *hog, Hylochoerus meinertzhageni;* and warthog, *Phacochoerus aethiopicus* Significant numbers of lions, leopards, spotted hyena, and elephants also occur.

SOCIAL ORGANIZATION OF THE POPULATION

Within an area of ca. 15 km by 30 km, conventional TGs or leks, serve as centers of orientation for sub-units of the kob population (Fig. 1). The locations of all of the TGs were plotted on a map of the area in 1959. The author's familiarity with at least five of the TGs dates from 1957, and through local inhabitants of Rwebishengo village several TGs were traced back to the 1920s. The positions of some leks shifted by 200-300 m between 1959 and 1962, but the locations were essentially unchanged. Gut of 16 leks located in 1959, four were abandoned by 1962, and the location of one shifted a distance of about 2. 5 km. One additional permanent TG that had been overlooked earlier was located in 1962. Thus there appear to be about 13 permanently located TGs in the Semliki Plains. A few additional temporary TGs seem to be formed continuously, and they may persist for a year or so. Each TG consists of a cluster of about 30 to 40 circular individual male territories, each about 8 to 18 m in diameter, within a TG about 200 m in diameter. Here the grass is closely cropped, and spots of bare ground appear in some territories. The boundaries of most territories are

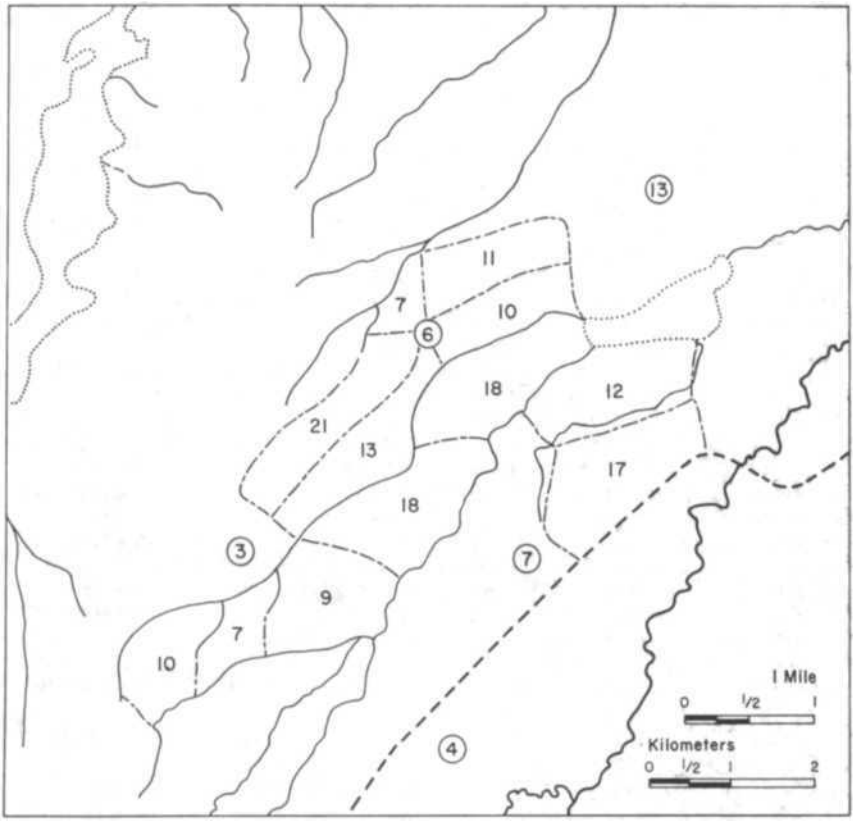

Fig. 3. Numbers of STs between TGs on 2-3 March 1964 (after Fig. 8 in Leuthold, 1966a).

TABLE 1. ORIENTATION OF ADULT MALES AND FEMALES TO TG

	Number of Males Observed within 500 m of TGs				
Territorial Grounds	90-100% of all Observations	80-89% of all Observations	70-79% of all Observations	<69% of all Observations	Total Number
TG 3	24	6	8	6	44
TG 6	17	3	1	3	24
TG 7	12	4	6	10	32
Total	53	13	15	19	100
	Number of Females Observed within 500 m of TGs				
TG 3	5	4	6	13	28
TG 6	3	5	2	10	20
TG 7	1	6	1	8	16
Total	9	15	9	31	64

clearly marked by longer grass; only where the most intensive fighting and breeding activity occur on the TG are boundaries difficult to see because of the closely cropped grass and trampled ground. Between the leks are scattered Single Territories (STs), as distinguished from the TG cluster, which are defended in the same manner as the territories on the TGs (Fig. 3). Precoital mating activity often occurs on the STs, but rarely with completion of copulation. Behavioral activity on STs and the significance of these territories in relationship to the TGs have been discussed by Leuthold (1966a). The attachment of both males and females to a 'home' TG was confirmed by 7, 844 observations of tagged kob (175 males, 72 females, and 54 fawns), mostly at three TGs (Nos. 3, 6, 7) over a period from July 1962 to April 1964. In addition 933 observations were made on 51 naturally marked males and 32 naturally marked females. An analysis of the data, in which observations made over periods of <50 days were excluded and the distance from the home TG was limited to 500 m, is summarized in Table 1. The figures show that 53% of the males were found within 500 m of their home territorial ground 90-100% of the time, whereas only 14% of the females were found within 500 m of their territorial ground 90-100% of the time. Besides spending some time on the lek when they are territorial, the males also graze in closer proximity to the home TG than the females. Although females graze at greater distances from the TG, they are strongly attached to the TG in that they return to the 'home' lek for mating. About 15 known females invariably returned to the same TG in subsequent periods of estrus. The males also are strongly attached to the home lek in terms of territorial and breeding activity. Only one male (No. 17/6) was observed holding territories on more than one TG (Leuthold, 1966a). The data for these interpretations are based on substantial periods of observations—54% of the males and 67% of the females were observed for more than 250 days. The data may be slightly biased, since more time was spent observing in the vicinity of the leks than elsewhere in the study area, but they indisputably support the concept of sub-units of population socially organized around the TGs. The strong attachment of males to their TG was confirmed by translocating eight adult males distances of 5-23 km (Leuthold, 1966b). Five returned to their home TGs within 5-26 days, and one within 4 months. None of the translocated males was observed holding a territory on a foreign TG, whereas joining the bachelor herd occurred at least temporarily.

The males on the TG defend their territories against neighboring males through ritualized displays, and they are replaced when defeated by a stronger male entering the TG to claim a territory (Buechner, 1961). The rate of interchange of males on the most active territories is high, and a male may be able to hold his territory only for a day or two. Less active territories may be held for a week or two, and peripheral territories may be occupied for a year or more. Defeated males return to the bachelor herd to recuperate.

ANNUAL RATE OF RECRUITMENT

Sex-and-age-composition counts, made in that part of the Reserve where the research was concentrated (Fig. 1), together with data from the study of reproduction, provide a basis for estimating the annual production of the kob population in the Semliki Plains. The four best counts, made after gaining familiarity with the distribution of the kob and experience in judging the size of young animals, are shown in Table 2. The average of these counts, 8, 278 animals, was somewhat less than half of the Semliki population. The largest number of uncounted kob were in the Hybali region near Lake Albert, and some smaller units were also missed southward from the primary research area. The counts also showed that about 1, 000 to 1, 500 animals were attached to each of the conventional TGs, indicating that the population undoubtedly exceeded 15, 000. The estimate of 18, 000 (Brooks, 1961) for the total population seems reasonable, and this figure is used by the Uganda Game Department as a basis for management.

Classification by sex is simple, since females normally lack horns. Only about one in a thousand females is horned, and these vary from fully reproductive females to individuals with completely underdeveloped ovaries and uteri (Buechner *et al.*, 1966).

Classification by age in the field is possible up to about 12 months. The growth rate of males and females is nearly identical up to 6-7 months of age. At 7 months fe-

TABLE 2. HERD-COMPOSITION COUNTS OF UGANDA KOB IN SEMLIKI PLAINS

Age Class	Number Counted (1963)					One Standard Deviation	% of x Total
	2-7 Apr.	2-4 Oct.	28-29 Oct.	6-8 Dec.	$\bar{x}$		
Males and females < 7 months (¼ + ½ grown)	1,491	907	1,245	1,439	1,271	229	15
Males 7-12 months (SC–)*	582	548	527	808	616	112	8
Mature females (>12 months)	4,247	3,323	3,987	5,178	4,184	769	50
Nonbreeding sub-adult males (1-3 years; SC+ and DC-)	1,468	1,129	1,260	1,723	1,395	259	17
Breeding males (>3 years;DC)	930	591	801	926	812	159	10
Total	8,718	6,498	7,820	10,074	8,278	1,304	100

* SC— = single-curved horns < ear length; SC+ = single-curved horns >ear length; DC— = approaching double curve; DC = double-curved horns.

males have reached about half (30-35 kg) of their potential weight, and males have reached about one-third of their full weight. In terms of body proportions, both males and females are about half the size of full-grown females at 6-7 months, providing a convenient breaking point for classification of young animals. Difficulty arises in distinguishing females as they approach three-quarters growth and blend into the proportions of full-grown females, and therefore females 7-12 months old were not classified. However, males of comparable age can be distinguished by horn development. The horns of a captive male fawn began growing at 5 months of age. At 6-7 months the horns of males are plainly visible under field conditions, and at this age many males leave their mothers to join the bachelor herds. Other males remain in the herds of females and young. Horn growth begins to exceed the length of the ears at about one year of age. One male (No. 517), tagged within a few days of birth and recaptured, had horns 19 cm in length, compared with an ear length of 12 cm, at 14 months of age. Thus juvenile males between 7 and 12 months of age can be distinguished in the field; and since the sex ratio is about equal at this age, the number of nonbreeding females 7-12 months of age can be estimated.

On the basis of the mother's lactation, it is possible to determine the mortality rate of young kob reasonably well up to the time of weaning, at which time fawns are 6-7 months of age and their mothers have reached 5-6 months gestation with their next fawn (Figs. 4, 5). The status of lactation in 248 randomly collected breeding female

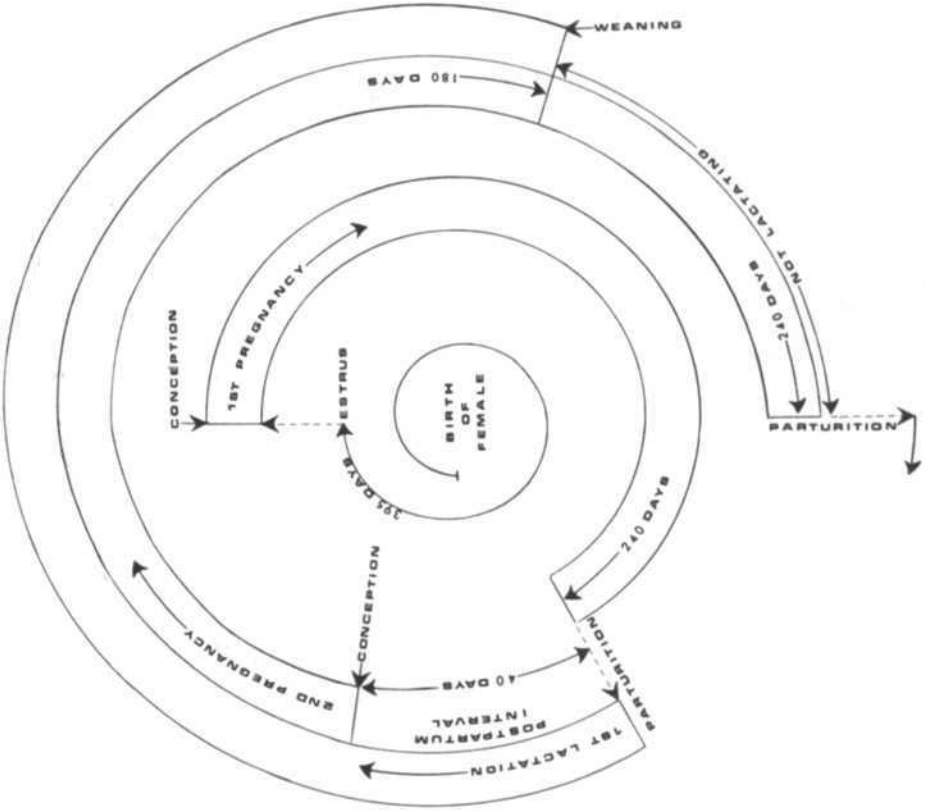

Fig. 4. Reproductive cycle: sequence of events and relationship between gestation and lactation (360° = 1 year).

kob beyond their first pregnancy was determined by classifying lactation into five categories (none, very slight and thick, slight and normal, considerable, and copious), based on the amount of milk that could be extruded from the teats. The fawns of mothers in lactation categories 1 and 2 were assumed to have died. All except eight out of 42 females in category 1 and 11 females in category 2 had udders weighing <200 g. In Fig. 5, udder weights <200 g for females ranging from postpartum to 160 days gestation represent cases in which fawns had died and regression of the udder was completed, or nearly so. Two of the 8 nonlactating females were postpartum, with udders weighing 402 and 1, 404 g, and mortality of their fawns is indicated by a square in Fig. 5. The other six were in the main transition range of regression of the udder (200-400 g). Eight fawns of 41 mothers in category 3 were assumed to have

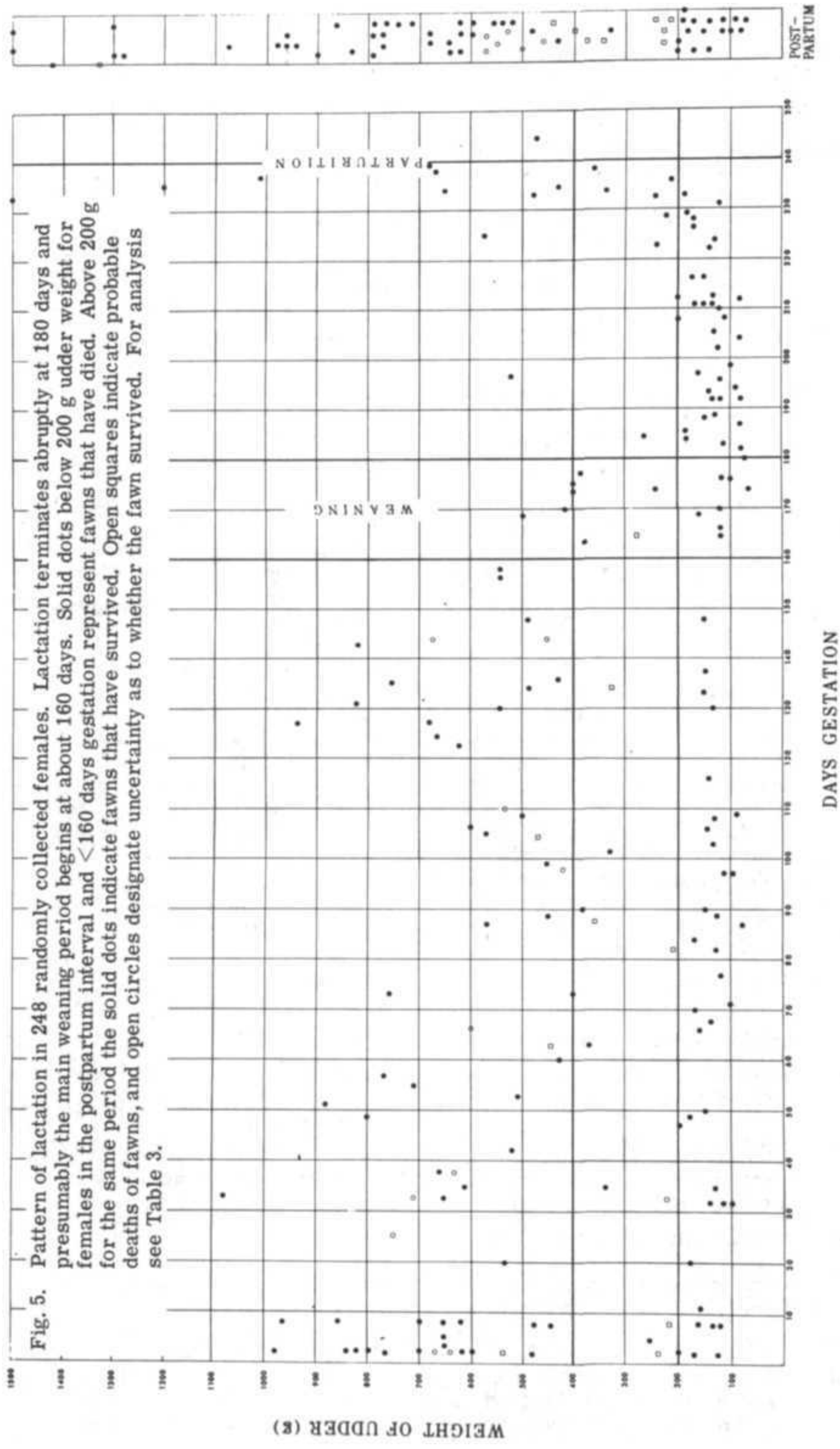

Fig. 5. Pattern of lactation in 248 randomly collected females. Lactation terminates abruptly at 180 days and presumably the main weaning period begins at about 160 days. Solid dots below 200 g udder weight for females in the postpartum interval and <160 days gestation represent fawns that have died. Above 200 g for the same period the solid dots indicate fawns that have survived. Open squares indicate probable deaths of fawns, and open circles designate uncertainty as to whether the fawn survived. For analysis see Table 3.

died, since the weight of the udder was <200g. The fawns of all 11 females that fell in the transition range and 4 females with udders about 400 g were thought to have died, based on information recorded in field notes. The survival of fawns of 16 females (open circles in Fig. 5) with lactation in category 3 was uncertain. The udders of these females may have been regressing following fawn mortality (or weaning) or they may have been drained of milk. Fawns of mothers lactating considerably or copiously were considered to have survived. In tabulating the data (Table 3) the 16 fawns of uncertain status were classified as having died. The data show a 47% mortality rate during the first 7 months of age. The mortality rate of 44 tagged fawns was somewhat higher: 50% to 6 months of age and 59% to 9 months of age, not including 5 tagged fawns that were collected for research. Mortality among tagged fawns, however, may have been somewhat higher as a direct result of the tagging process. Using lactation as a criterion for survival, Spinage (1968) found a mortality rate of 49% in the defassa Waterbuck in Queen Elizabeth (now Ruwenzori) National Park.

TABLE 3. JUVENILE MORTALITY BASED ON LACTATION

Age Class of Fawns (days)	Gestation of Mother (days)	Number of Females	Survival of Fawns: Survival No.	%	Mortality No.	%
1-40	Postpartum	68	37	54	31	46
41-80	1-40	46	26	56	20	44
81-120	41-80	20	10	50	10	50
121-160	81-120	24	8	33	16	67
161-180	121-160	21	14	67	7	33
Total		179	95	53	84	47

The breeding cycle of females is about 280 days (Fig. 4), and bears little, if any, relationship to the annual cycle of seasons here at 1°N of the equator (Fig. 6). A 365-day period in the life of a female kob includes: conception; 240 days gestation with 1 young; parturition; 40 days postpartum interval (average of 7 known intervals); conception; 85 days gestation with next young. This means that each breeding female produces 1. 35 young annually (1 young + 85/240 of another). The minimum breeding age for females, based on an individual tagged within a day of birth and later recaptured, is 13 months (Buechner *et al.,* 1966).

Using the data from herd-composition counts and reproduction in females, the annual rate of production can be calculated as follows:

4,184	females (average of 4 herd-composition counts, from Table 2).
–616	nonbreeding females 7-12 months of age, assumed to be equal to average of males of same age group in Table 2.
3,568	breeding females.
4,817	young produced annually (natality = 3, 568 × 1. 35 = 4, 817; natality ratio = 135 young; 100 breeding females).
2,264	47% mortality, from Table 3.
2,553	young surviving annually (ca. 5, 500 for total population of 18, 000 in Semliki Plains), or annual recruitment.
71:100	*expected* ratio young; 100 breeding females (2, 533 ÷ 3, 568 = 0. 71).
70:100	*observed* ratio young: 100 breeding females (2, 502 ÷ 3, 568 = 0. 70). based on averages of observed animals (Table 2) less than 1 year of age, including the assumption that the number of females >12 months of age was equal to the number of males in this age group.

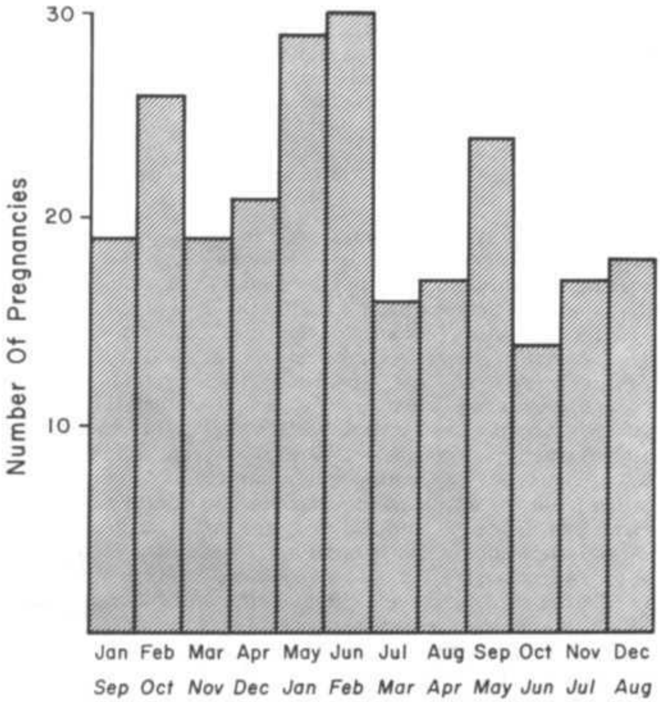

Fig. 6. Lack of seasonality in the reproductive cycle is shown by the distribution of conception dates (upper months) or parturition dates (lower months) determined from randomly collected pregnant females and birthdays of fawns examined within a few days of parturition.

In this calculation, the mortality rate of 47% for the first half-year of life for a given cohort is applied to the entire first year of life. The mortality rate is likely to decline after the first half-year, and 47% could be somewhat high for the whole year. On the other hand, the data from tagged fawns indicate that the mortality rate during the first year of life may be above 50%.

The annual rate of recruitment (71 young: 100 breeding females; 30 young: 100 individuals of total population) is near maximum for the population, as will be shown in the discussions that follow.

In terms of energetics, using a total population of 18, 000, the rates reported earlier (Buechner and Golley, 1967) have been recalculated, on the basis of refinement of the data and the correction of errors, in kcal/m^2/year as: standing crop 3. 7, ingestion 89. 1, assimilation 74. 9, respiration 73. l,and growth 1. 8. The population of kob in the Semliki Plains has rates of assimilation, respiration and growth more than double those realized by the population of elephants in Queen Elizabeth National Park (Bourlière and Hadley, 1970). The rates are also higher than those for the meadow mouse and white-tailed deer; and, insofar as is known, any other species of mammal.

ROLE OF TERRITORIALITY AND SOCIAL ORGANIZATION

Several ideas about the function of the highly developed system of territorial behavior on conventional leks have emerged from the study. Undoubtedly, one consequence is the maintenance of a high quality of genetic variability in the population, since natural selection of those males that are morphologically, physiologically and behaviorally fittest is accomplished through territorial behavior. Although males have viable sperm at 14 months of age (Buechner *et al.*, 1966), they are incapable of breeding until somewhat over 3 years of age under the kob's social system. Not all 3-year-old males succeed in winning a territory on a TG, and among those that do succeed there is considerable variation in the amount of breeding accomplished. Estrous females concentrate on only 3 or 4 of the 30-40 territories of a TG, and males on peripheral territories of the cluster rarely breed a female. Copulation is also rarely successful on the STs. Thus most of the transfer of genetic information is accomplished by a relatively small number of highly selected males.

Another function of the kob's social system appears to be in the maintenance of a high rate of natality. Although females can become estrous as early as 10-15 days after parturition, considerable variation occurs in the length of the postpartum interval between parturition and subsequent conception (Buechner *et al.*, 1966; Morrison and Buechner, 1971). The average of seven known postpartum intervals was 40 days, the longest being 65 days. Moreover, there is a proliferation of small corpora lutea associated with ovulatory cycles of 6-13 days. Apparently, if all systems function with maximum effectiveness, the uterus is prepared to accept implantation of a new embryo about 15 days after parturition; and if perturbations occur, due to cystic ovaries, diseased uteri or disruption of mating activities, the mechanism of short ovulatory cycles seems to provide for conception with a minimum of delay. Conceivably, stimuli emanating from the leks could be important in eliciting the short ovulatory cycles and estrous behavior. Stimuli that require investigation in this regard include: (1) male whistling, singly and in chorus; (2) visual aspects of copulatory behavior; and (3) odors from urine, feces and ejaculum. Besides stimulating the onset and repetition of short ovulatory cycles, the territorial system probably contributes in other ways to the maintenance of high natality. Non-interference by other males is guaranteed. The highly ritualized ceremonial mating behavior, in which the postcoital behavior is more elaborate than precoital behavior (Buechner and Schloeth, 1965), seems to be important in bringing the male and female into sexual synchrony and in transporting the sperm through the uterus (Morrison and Buechner, 1971).

The overall effect of the reproductive and territorial systems is that almost 100% of all adult female kob in the Semliki Plains conceive about every 280 days. The expected percentage of postpartum females is about 14% (40 ÷ 280 days); and the percentage in the random collection of 264 breeding females was 19% (Table 4).

TABLE 4. FEMALE UGANDA KOB COLLECTED RANDOMLY

Reproductive Status	Number of Animals 1957-1958	1962-1965	Total	% of 264 Breeding Females
Prereproductive	9	1	10	
First estrus	2	5	7	2.6
First pregnancy	11	9	20	7.6
Second pregnancy	11	4	15	5.7
Later pregnancy	124	47	171	64.8
Postpartum				
First interval	5	1	6	2.3
Later interval				
Near estrus	9	5	14	5.3
Non-estrous	22	9	31	11.7
Total	193	81	274	100.0

About one-fourth of the postpartum females collected were near estrus, most of which probably would have become pregnant within a few days, although some undoubtedly would have failed to conceive. Thus it appears that the females were reproducing at near the maximum rate, and it seems likely that the territorial system played an important role in maintaining this high rate.

Still another function of the social system in the kob may the spacing of the population, as a behavioral adaptation to regulate the use of forage in a confined environment (Buechner, 1963). Conceivably, this mechanism intensifies with an increase in population density; and under high densities, as in the Semliki Plains, lek behavior and the organization of a population around conventional TGs reaches its highest expression. Compared with the Semliki, lek behavior is not as well defined in the Queen Elizabeth or Murchison Falls National Parks in Uganda or in the Albert National Park in the Congo (Buechner, 1963; Leuthold, 1966a).

These functions, which admittedly must be clarified further, have an important bearing on the pattern of exploitation that man may impose on the population.

POTENTIAL EFFECTS OF EXPLOITATION

In view of potential adverse consequences of disturbing the social organization and behavior of the population of kob in the Semliki Plains, what proportion of the population can be exploited by man and what pattern of exploitation, with respect to sex, age and distribution, can be employed? The latter part of this question will be considered first, and the numerical aspects will be discussed in the following section.

Clearly, the shooting of those territorial males that breed on the most active territories of a given TG can adversely affect the genetic composition of the population. Full-grown males with double-curved, lyrate horns constitute only about 10% of the population (Table 2), or about 150 individuals at a conventional TG. Of the 150, not all succeed in winning a territory. Some are ST males that rarely, if ever, claim a territory on the TG; others succeed only in securing peripheral territories at a lek; and some males may never succeed in establishing themselves on a territory of any kind. Furthermore, most of the breeding takes place on but 10% of the territories at a given TG. There is a high turnover at these highly active territories, where males remain for <10 days during a given occupancy, and many males return to the same territory following recuperation in the bachelor herd. Probably < 50 males accomplish most of the breeding of 500-600 adult females. Although these figures are crude estimates, they illustrate realistically the importance of preserving the best territorial males in any scheme of exploitation One should also bear in mind that little interchange of genetic material seems to occur between the sub-units of the population. Only one male was observed holding a territory on two different TGs (Leuthold, 1966a), and the data on marked females show that they return to the same TG each time they breed. The primary gene flow between sub-units could be taking place through the shifting of young males between TGs, but the data on movements of young males and their establishment on TG territories are too limited to support or reject this hypothesis. Despite its apparent low rate, gene flow is probably adequate to maintain genetic viability in the population as a whole. Nevertheless, preservation of the fittest males at each lek seems to be worthwhile from the viewpoint of preserving the genetic potential of the socially isolated sub-units of the Semliki kob population.

Mature males holding STs form an essential part of the spacing mechanism and may contribute significantly to social stability among the kob. Leuthold (1966a) has pointed out that female herds preferred occupied STs to other areas for their daily activities. Here females are less subject to harassment by young males; and they may be somewhat protected from predation. What happens when a lion or leopard attacks has not been observed, but often the ST male was seen to remain behind on his territory when a herd of females and young left the ST and its vicinity. Furthermore, the distribution of the STs (Fig. 3) suggests that these territories are integral components of the structural fabric of the kob's social system in the Semliki. From the viewpoint of reproduction alone, Leuthold (1966a) notes, the STs would become obsolete once permanent TGs were established, and their continued existence implies that social factors, such as providing a 'feeling of security' to females, are important. In view of these ideas, it seems unwise to harvest ST males.

Distribution of the harvest among the sub-units of population is obviously important, since over-exploitation could seriously disrupt, or perhaps completely destroy, a sub-population oriented around a given TG. This might be an interesting experiment to determine the behavior of individuals from neighboring sub-populations in rebuilding a depleted social unit, but it would not constitute sound management of the total population over a long period of time.

The harvesting of substantial numbers of females undoubtedly would seriously reduce the annual recruitment of the total population. The data from the early 1960s show an annual natality approaching the maximum rate for the Uganda kob. Most females bred at the minimum age of about 13 months. Young females in their first estrus could be recognized by their small size, fear of territorial males, and lack of sexual experience. About 10% of the females in the random collection (Table 4) were in their first estrus (2. 6%) or pregnant for the first time (7. 6%). If the pre-reproductive, females (¾-grown, approaching 13 months of age), collected randomly are included with those breeding for the first time, 14% of the collection consisted of young, sub-adult females. This is about the percentage to be expected, according to the herd-composition counts (Table 2), which show about 15% sub-adult females. High natality was also maintained through a relatively brief postpartum interval—an average of 40 days for seven known individuals. It appears physiologically possible for the kob to increase natality somewhat by reducing the length of the postpartum interval, since the minimum time between parturition and subsequent conception is 10-15 days. Reducing the interval from 40 days to 20 days increases the total natality for a population of 18, 000 by about 684 individuals. Both the breeding of nearly all young females at the minimum age and the postpartum interval of 40 days indicate a high rate of natality for the Semliki population of Uganda kob; and it is unlikely that reduction of population density by harvesting females can stimulate a significantly higher rate, as in the case of overpopulation of white-tailed deer or elk (Buechner and Swanson, 1955). The harvesting of females must therefore be done with considerable caution, and with careful monitoring to determine whether annual production is impaired by the exploitation.

If fully mature males on leks and STs are to be protected and only a small number of females is to be harvested, the remaining group available for exploitation is the all-male bachelor herd. This group contains territorial males in the process of recuperating from activities on the lek and sub-adult males from 1 to 3 years of age, among which are the 'supreme' males destined to occupy territories in the future. Any male that is shot is likely to be a genetically effective individual in perpetuating the highly developed system of lek behavior. Under a system of purely natural selection, the trend would be toward survival of the fittest sub-adult males, but it is unlikely that such a trend would hold under a system of exploitation by man. First of all, the shooting is not likely to be completely random, since consciously or unconsciously man selects his target. He is likely, for example, to choose the larger sub-adult males, which would select the most vigorous, most rapidly developing individuals. Secondly, the selection pressure through shooting provides little opportunity for the kob to respond to his natural means of escape by using speed, position in the herd, knowledge of the terrain, and other mechanisms for evading non-human predators. Exploitation of sub-adult males in the bachelor herds undoubtedly removes a broad spectrum of individuals with respect to genetic endowment, probably with some bias toward the better individuals, but it provides a more random selection of the gene pool than exploitation of adult males in the bachelor herd or elsewhere. Somewhat over 3 years are required for a male to reach full maturity and acquire a territory, by which time natural selection has had considerable effect on the male populatioa Harvesting sub-adult males may, therefore, help to minimize the consequences of imposing anthropic exploitation on the population of Uganda kob in the Semliki Plains.

SUSTAINED EXPLOITATION

The total size and stability of the population have a bearing on exploitable numbers, along with social behavior and the dynamics of the population. Prior to the inception of exploitation in 1963, the population was estimated at 18, 000 kob (Brooks, 1961). An intensive ground count by the Uganda Game Department in 1969, indicated about 19, 000 kob (Sylvester Ruhweza, pers. comm.). An aerial survey made by William M. Longhurst, Frank Poppleton, and William Smith in October 1961, showed 7, 422 kob, about the same number found by Longhurst and myself in May 1958. The aerial surveys were not satisfactory, since many of the large, compact herds had to be estimated. Herd-composition counts in the research area, combined with estimates in the areas not covered, indicated more than 15, 000 kob, and possibly as many as 18, 000. The evidence indicates that the population of kob in the Semliki Plains has remained stable since the inception of the study in 1957, having reached a plateau following an epidemic of rinderpest and removal of cattle from the area in 1924.

TABLE 5. EXPLOITATION OF KOB IN SEMLIKI PLAINS

Type of Harvest	1963	1964	1965	1966	1967	1968	1969	1970
Cropping for Market	166	600	1,197	738	648	927	1,108	1,011
Licensed Hunting	114	94	58	91	112	74	79	43

Cropping for the market and licensed hunting were initiated by the Uganda Game Department in 1963, the results of which are shown in Table 5. The offtake of about 1, 000 kob annually over the past 3 years does not appear to have affected the social organization or behavior of the kob adversely, according to the Chief Game Warden, Sylvester Ruhweza (pers. comm.). Males on their territories are protected; but some adult males are harvested, particularly for trophies, out of the bachelor herds. The cropping is concentrated on young males in the bachelor herds, and 10-20% of the harvest consists of females.

In addition to the legal offtake, poaching is fairly common, a large percentage of which is on young fawns that can be approached within spearing distance as they lie quietly in patches of tall grass.

Predation by lions, leopards, hyena, and possibly white-headed vultures, accounts for most of the mortality among the kob in the Semliki Plains. Seemingly, the predators maintain their own populations somewhat below the potential annual removal of prey, as suggested by: (1) the distribution of ages well into advanced years among the female kob, judging by tooth wear in the random collection; and (2) the maintenance of population stability despite the exploitation of 1, 000 kob annually by man in recent years. Small but significant numbers of lions and leopards are taken in sport-hunting and to protect cattle that graze adjacent to the kob, west of the Reserve, thus making more kob available for exploitation by maa

Since reproduction seems to be near the maximum rate, the adjustment to the mortality imposed by legal cropping is most likely to be through the intercompensation of mortality factors, not only among the predators but also in terms of diseases, accidents and indirect influences, such as nutrition and social behavior. It is impossible, however, at this stage to ascertain precisely how well the Semliki kob are adapting to the mortality imposed by legal cropping.

Although the present level and pattern of harvesting seem to have had little influence on the kob's social system, subtle changes could be taking place. If so, such changes probably can be detected through annual herd-composition counts and monitoring of the locations of conventional and temporary TGs, the number and distribution of STs, and territorial and breeding activities. Until adequate information accumulates over another decade, or longer, it would be wise to keep the annual harvest below 1, 000 kob.

The number of males between the ages of 1 and 3 years that die annually in a population of 18, 000 is about 1, 700. Using the average of 1, 252 males (636 up to 7 months of age + 616 from 7-12 months of age) observed alive in the research area during the first year of life, and the average of 8, 278 for the total population counted (Table 2), the number of males in their first year of life in a population of 18, 000 is 2, 983. Applying an annual mortality rate of 33% to ca. 3, 000 males, reduces the population by 1, 000 during the second year of life, and by nearly 700 during the third year of life.

The mortality rate of 33% was estimated as follows. Taking all of the males in the first year of life collectively as a single cohort of yearling males (an average of 1, 252 males in the four herd-composition counts), the number surviving in the second year of life at a mortality rate of 33% is 835, and applying the same rate to 835 the number surviving in the third year of life is 557, or a total of 1, 392 sub-adult males surviving for the 2-year period. In the herd-composition counts the number of living males in the 2-year period from 1 to 3 years of age was an average of 1, 395 (1, 001 SC + plus 394 DC—).

How much of the mortality (1, 700 young males) can be diverted from natural mortality factors to cropping, on a sustained basis, without adversely affecting the dynamics or the social organization of the population, remains to be determined by trial and error over a period of years; but the number is probably small—perhaps about 500 individuals. An annual harvest of about 100 adult males >3 years old, taken from the bachelor herds, might be possible without jeopardizing the social organization and genetics of the population, at least for a short period of time, but sustained harvest over a long period of time may be impossible if the territorial system on both TGs and STs is to be preserved. The cropping of 100 to 200 adult females annually can probably be sustained.

OTHER VALUES

From the viewpoint of tourists, the numbers of kob in the Toro Game Reserve and its vicinity are impressive, and the phenomenon of territoriality is fascinating. The kob's social system, territorial behavior, and elaborate mating cermony provide insights that are stimulating, fulfilling and rewarding to the visitor, not only in terms of understanding the natural world in which we live but also in terms of possible implications with respect to human behavior.

From the viewpoint of science, the well-defined lek behavior of the Uganda kob holds promise for a deeper and more fundamental understanding of territorial behavior in the biology of animals, particularly with regard to its function as an ecosystem process in the natural regulation of numbers.

CONCLUSIONS

The Uganda kob live at a high density (45/km^2) in a confined habitat in the Semliki Plains, along with eight other ungulates, all of which are at lower densities, and a substantial number of lions and leopards. Under these conditions a highly developed social system, based on territorial behavior and the organization of subpopulations around conventional breeding grounds, has evolved in this species, apparently as a behavioral adaptation to the capacity of the ecosystem to support the population. Possible functions of the social system include: maintaining genetic viability, spacing the animals in relationship to food supplies, and maintaining a high rate of production.

Data from herd-composition counts and reproduction indicate that natality is near a maximum rate. This high rate appears to be in response to the mortality imposed on the population primarily by lions and leopards. Despite the legal harvesting over the past decade, which reached about 1, 000 kob annually in recent years, the population appears to have remained stable. Whether the population can continue to sustain cropping at this level without perturbations to the social system is still an open question. It seems logical, however, that cropping will have to remain at a modest level and within a specific pattern that takes social behavior into consideration, if the economic, esthetic and scientific values of the kob's social system are to be preserved in the Toro Game Reserve.

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Paper No. 50

Impala Behaviour and its Relevance to Management

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ABSTRACT

Impala are medium-sized, sexually dimorphic, gregarious antelope. Their group size is related to food availability and dispersion, and thus varies seasonally, as do other features of their feeding behaviour such as rate of movement and inter-individual distance.

In eastern Africa, where breeding may occur throughout most of the year, a proportion of adult males hold territory at any one time. From this territory a male will exclude other territorial males, and he will herd any females entering the territory, attempting to keep bachelor males away from the females although not necessarily excluding them completely from the territory. Within the local bachelor population there is a linear hierarchy among the non-territorial adult males, and a hierarchy based upon age among the sub-adult males. Only individuals high in the hierarchy challenge for territory. On losing his territory a male returns to the bachelor society, sometimes quite low in the hierarchy, having lost condition while holding territory. Females and bachelor males utilise home ranges that cover several territories. Their herds are of open membership. In the dry season this typical social organisation, produced by the segregating activities of territorial males, may break down with all social castes mingling as territoriality wanes.

In southern Africa, where breeding is confined to generally less than 3 months in the year, full territorial behaviour is compressed into a short rutting season, although some aspects of territorial activity may be observed at other times of the year.

It is emphasised that organisation is imposed on impala society by the activity of territorial males only when environmental conditions permit, but that aggregating aspects of social behaviour, which are related to feeding and anti-predator behaviour, apply under all circumstances. It is, in general, these types of behaviour, in which impala are responding to their environment rather than to each other, that are most relevant to management.

INTRODUCTION

Impala (*Aepyceros melampus* Lichtenstein) are found throughout most of the deciduous woodland and savanna zone of eastern, central, and southern Africa. They are medium-sized antelopes, displaying considerable sexual dimorphism. Adult males weigh 60-65 kg, females 40-45 kg; there is some regional variation in weight. Only male impala carry horns. The colouring of both sexes is the same, a rich rufous over most of the body, contrasting with paler sides and a white belly. There is nothing obviously cryptic about their colouring or marking.

This paper summarises some of our findings during six years field work in various parts of Africa. For three years one of us (M.V.J.) made an intensive study of the behaviour of a population of impala in part of the Serengeti National Park, Tanzania. Her study relied upon individual recognition of several females, many sub-adult and non-territorial adult males, and all territory holders; the detailed findings will be published elsewhere (Jarman, M. V., in prep.). The rest of our programme consisted of an intensive study of the ecology and social organisation of the species in the Serengeti, and extensive sampling of social organisation in about twenty other study areas, from Kenya to Natal.

SEASONALITY

Impala feed quite selectively upon a catholic diet of grasses, herbs and shrubs. In habitat choice they avoid forest, dense woodland and dense thicket at one extreme, and open grassland and semi-desert scrub at the other. They are commonly associated with light deciduous woodland (especially mopani) or *Acacia* savanna, vegetation types whose ground storey carries a diverse community of grasses, herbs, shrubs and young trees. This diversity is necessary to the impala, which depend upon the resources of a familiar home range throughout the year. By changing their preference seasonally and by shifting their preference for vegetation type up or down the catena, impala are able to subsist on the resources of their confined home range in all seasons. This ecological flexibility is a notable feature of the species, and is paralleled by social flexibility. Both reflect the marked seasonality in availability of resources for the species, which results from the alternation between wet and dry seasons each year. During the wet season food and water are abundant and well distributed; during the dry season they are not. These basic differences have profound effects on all aspects of the impala's life.

Most impala are able to put on fat and muscle tissue during the wet season, and to lose both if their daily food intake falls below maintenance requirements in the dry season. The requirements of lactating females seem to be higher than for any other class of impala (in common with most ungulates—Sadleir, 1969), and they and their unweaned offspring will be the first to suffer the effects of dwindling resources. In southern and central Africa where rain falls in one, short, confined period each year, selection has favoured only those animals calving at the start of that short period, whose offspring are weaned before the full severity of the dry season is felt. In eastern Africa, where rains fall over a greater part of the year or occur in more than one wet season, calving occurs throughout the year. However, there is still a tendency for most calves to be born just before, or at the start of, each rainy period.

So there are two distinct modes of distribution of calving in impala, and these call upon two different distributions of mating to produce them. As in most antelopes, the social organisation is in part based upon the behaviour of males in securing mating rights. As the socio-sexual behaviour of males fluctuates seasonally, so does social organisation vary.

BEHAVIOUR

Two sets of interactions combine in the observed social organisation of impala, and these have been called socio-ecological and socio-sexual interactions (Jarman, P. J., 1968). Socio-ecological interactions include the interactions between impala and their environment which, to a great extent, determine the typical size of group in which animals aggregate. Socio-sexual interactions are those involved in the behaviour by which a proportion of males achieve mating rights. While socio-ecological behaviour occurs wherever and whenever impala are found, socio-sexual behaviour is apparent only under certain ecological conditions.

(i) Socio-sexual behaviour and organisation in eastern Africa

In Kenya, Rwanda and the *Acacia-Commiphora* zone of northern Tanzania, impala drop calves in nearly all months of the year, but with peaks of calving just before, or at the start of, the rains. Rains are well distributed throughout the year in these regions. At all times except the extreme dry season, impala society in these areas is organised by conventions imposed by the behaviour of adult males, a proportion of whom hold territory. The proportion varies, but is usually about one third of the adult male population at a time. The rest of the adult and the sub-adult males are found in bachelor herds numbering a few to several score animals. Females and juveniles form a third social category, and are found in herds numbering from ten to over a hundred individuals. It is the activities of the territorial males which bring about these social divisions. The following description is based mainly upon the intensive study in the Serengeti (Jarman, M. V., in prep.), but with additional information from observation of impala in other parts of East Africa. Observations fully confirmed the suggestion by Leuthold (1970) that impala males were territorial at times. While the accuracy of the descriptions of many of the elements of behaviour given by Schenkel (1966) was borne out by our observations, his interpretations of social behaviour and organisation seem to us at times to have been erroneous.

(*a*) *Territory holding*

In the intensive study area, each male's territory was a piece of ground that he defended against other adult males of a comparable social status. Territories were contiguous and formed a mosaic covering most of the area occupied by impala. Female's and bachelor male's home ranges were superimposed upon this mosaic, and were much larger than any single territory. A typical female's home range covered about ten territories, and most bachelors' ranges were of a similar size.

Each male's territory was defended against males holding or attempting to gain territory. All other males were subordinate to a territorial male within his territory, and neighbouring territorial males did not trespass far inside each other's territories. Ownership of a territory was advertised in several ways. Scent marks, in the form of dung heaps and deposits of secretion from a glandular area on the forehead, were distributed throughout the territory and not confined to a boundary zone. The dung heaps resulted from linked defaecation-urination repeated on one spot, although the heaps might be used by females and bachelor males as well as by the territory holder. The oily, smelly secretion from the glandular area on the forehead was rubbed onto low bushes and herbs, the male often smelling at the plant before, during and after the rubbing. A lone territorial male frequently stood in a position in which he could be seen from most parts of his territory, in an attitude which, at least to the human observer, clearly distinguished his status. Apart from this, most visual and auditory displays of territorial possession tended to be used only in the presence of other impala. There were many visual displays, some of which have been well described by Schenkel (1966), each appropriate to a type of encounter with conspecifics, and one particular auditory display, the roar, which was used in several situations in which the male was expressing some aspect of his territorial status (Jarman, M. V., in prep.). Territorial males often became visibly different from other adult males of the same age by developing dark areas around the eyes and significantly thicker necks. The thickened neck probably has importance in the lateral displays of dominance in which a male stands sideways to a rival and flexes his neck. These symptoms were gradually lost when a male lost territory.

By a combination of these passive and active displays, a male advertised his possession of territory. When this possession was finally challenged, the outcome of the challenge eventually depended on the holder's fitness compared with his challenger's; but until they actually fought, a holder might outface a stronger male for several weeks simply because of his dominance as the established owner of the territory. Lengthy sessions of display usually preceded fighting. Bouts of display and fighting might alternate over a period of hours, and the whole performance be repeated for several days, even a few weeks, before the outcome was clear. Fighting was intense and often left minor wounds; it can result in more serious injuries or death (Jarman, M. V., 1970; Jarman, P. J., in press). The loser might remain near his old territory or might leave the vicinity, but sooner or later he usually rejoined a bachelor herd.

(*b*) *Bachelors and the territorial male*

Bachelor herds consisted of the sub-adult and non-territorial adult males of the population. Herds were temporary, loose associations of individuals, without fixed membership, but, because they might share a common home range, there was a strong tendency for some animals to encounter each other repeatedly in the herds. Most young males in eastern Africa joined bachelor herds when six to nine months old, having been evicted from female herds by territorial males. If territoriality was in abeyance when a male reached this age his eviction would be delayed. Within bachelor herds the young males continued to be wary of any older males, to whom they were submissive. They groomed and sparred with other young males of a similar age, and tended to stay near such males when feeding or walking. As they grew they themselves dominated younger males joining the herds, but remained subordinate to full adults. The sub-adult males' society was organised by like-age association and a hierarchy based on age distinctions. Age distinctions were easily detected by body size and stage of horn growth. Those clues to rank did not apply to full adults, and we found that their society was organised as a linear hierarchy based upon individual status. This hierarchy may have involved a certain amount of individual recognition within the local population, since individuals did not go through lengthy display sequences to establish relative ranks every time they met. Rank was usually determined by encounters involving display, but sometimes fighting as well, and was maintained by the individual's attitude at all times to adjacent animals. Size of horn did not determine rank. Some activities which were most typically used by territorial males were also seen in a preliminary form among bachelors. Among these were soil-horning, bush-thrashing, and frontal-rubbing (see below), but roaring, the vocal display typical of territorial males, was rarely used by bachelors. Frontal-rubbing is the action of depositing the oily secretion from the forehead onto vegetation. This secretion was also smelled by subordinate males in a characteristic rank-testing behaviour, in which the subordinate would approach a dominant slowly, sniff at his face, and then retreat. When deposited on vegetation the secretion might still indicate the depositor's dominant status, making it a very suitable territorial marker.

Only animals near the top of the bachelor hierarchy were in a position to challenge for territory. Most tried to gain a territory within their bachelor home range, so that if one succeeded it would mean that his dominant status was already known to the bachelors most likely to pass through his territory. On losing territory and rejoining bachelor society, a male reverted to using a home range similar to that used before he became territorial. Entering the bachelor hierarchy at a low position, he had once more to rise in rank before he could again challenge for territory. When he did this he was very likely to challenge for a territory he had previously held. Thus we found considerable attachment both to home range and to site of territory among impala males. A local population of males can be seen as a reservoir of bachelors developing skills and dominance in preparation for temporarily holding a limited number of posts as territorial males.

A territorial male would frequently allow bachelor herds to enter his territory, and might join them while they were there, although still asserting his dominance over them. His attitude changed when a female herd was in his territory. Then he attempted to keep bachelors at a reasonable distance from the females, although not necessarily driving them from the territory. The zone he defended around the females varied seasonally, decreasing in extent in the dry season. The territorial male also evicted young males from the female herd, generally chasing out those six months old or older. There was no obvious dividing age before which young males were tolerated and after which they were evicted; tolerance varied with a range of circumstances. Eviction was a gradual process, since at first the young male rejoined females whenever he could, spending the rest of the time near females or near bachelors. As he grew he was tolerated in female herds progressively less often. It might be two or three months before he no longer entered female herds and joined bachelor society full-time.

(*c*) *Females and the territorial male*

A territorial male attempted to herd nearly all females which entered his territory, rounding them up and encouraging them to move away from the boundary. When they moved towards the boundary he would try to stop them, using a variety of displays, as described by Schenkel [1966], but not employing his horns to compel them. As long as they were within his territory but away from the boundary he did relatively little to influence the direction in which they moved and fed; but he would expend much effort in keeping them together and in particular in preventing single individuals from breaking away from the herd. One such escaping individual often started a stream of others. When a male had guided a female herd away from his boundary, had ensured that any bachelors were at a reasonable distance, and had evicted from the herd any juvenile males that attracted his aggression, he would turn his attention to detecting any oestrous females in the herd. He would check for these by sniffing at their vulvas, or testing their urine. He would continue to check the herd periodically for as long as they remained in his territory. On finding an oestrous female he would court her by following her, licking at her vulva until she stood to let him mount. This following phase takes time and space, and emphasises the need for the male to be in undisputed possession of his territory to enjoy uninterrupted mating. Courtship and copulation would be repeated at intervals for as long as the oestrous female was in his territory.

Females, like bachelors, associated in groups without fixed membership, although animals sharing similar home ranges might repeatedly occur in the same herds. A majority of females in a herd often shared a common physiological state, such as late pregnancy, or even good or poor physical condition, which distinguished the herd from others in the population at the same time. The most obvious example of this type of association was the aggregation of females with new-born young. These tended to gather in nursery herds within which the juveniles formed creches. The activity of a creche was often different from that of the rest of the herd, and creches were sometimes left in the care of a few females while the rest of the herd moved away to feed or drink. This commonly happened when females were feeding in an open area where juveniles would be particularly exposed to predators. Females normally left the herd to give birth, trying to hide themselves in bushes or thicket. The inquisitiveness of other impala and interference by the territorial male made the rare female giving birth within the herd very obvious and vulnerable. Distrubance by other impala at this critical time might disrupt the formation of the mother-juvenile bond. Normally the calf lay out for several days after birth, in bushes or long grass. The mother might either hide with it, or feed nearby or with a female herd, returning to suckle it at intervals. In eastern Africa the mortality during the first days of life is very high, and much of it is caused by predators. In the study area the interval between birth and the juvenile's joining a female herd seemed to be related to the numbers of juveniles already in the local herds, the juvenile being introduced sooner when there were already several juveniles in the herds.

Females wandered almost at will, selecting the areas that most fully met their resource requirements. Requirements, and hence preferred areas, changed seasonally. Territories falling within the preferred areas most often had females in them. Males holding those territories would spend more time herding females, chasing away bachelors, evicting young males and searching for oestrous females than would males holding territories in less preferred areas. This multiplicity of strenuous, time-consuming activities exhausted males, and holders of favoured territories tended to lose condition and territory sooner than holders of territories in less preferred areas.

We found that the majority of conceptions occurred in March and April in the Serengeti study area, although the territorial system had been operating since October or November. So, to produce the maximum number of offspring, a male should hold territory both in the right place, an area preferred by females in that season, and at the right time, when the greatest number of females were in oestrus. It appeared that, during the whole period of territoriality, there were three successive phases of males holding territory; the first and third phases at the start and close of the period contained young and old males, while the second phase contained prime-age males of 4. 5-6. 5 years old. It was this second phase which held territories during the March and April peak of conceptions. It must be emphasised that there were many exceptions; some males held territory in two or even all three phases, especially those in marginal territories, and some prime-age males held territory in the first or third phases. We do not yet know the behaviour which led to the prime-age males delaying gaining territory until the most suitable time of year.

(*d*) *The non-territorial period*

In parts of the eastern region, especially those with a relatively long dry season, the territorial system is not maintained throughout the year. Collapse of territoriality probably results from exhaustion of males, and some of the causes of this are discussed in the section on socio-ecological behaviour below. When the restrictions of territoriality are removed all males can mingle with the females, there being no territorial males actively trying to separate them. However various aspects of social organisation persist. Males still maintain greater inter-individual distance within groups than females. Association between animals of similar age or physiological state is still found. Elements of male hierarchy are still apparent. Impala still aggregate in groups. The collapse may not be total; a proportion of males may still be found single, and a proportion of females may be herded and segregated by such males. This state of affairs continues until renewed rain improves the availability of food, and territories are once more established.

(ii) Central and southern Africa

In central and southern Africa rainfall is confined to one period each year, which is relatively shorter than in eastern Africa, and the dry season is correspondingly longer and more severe. Calving is confined to one peak at the start of the rains, and in most areas the great majority of calves are dropped within two months. There is a similarly limited mating season, the rut, at the end of the rains or early in the dry season.

(*a*) *Social behaviour and organisation in the rut*

During the rut a social organisation is found that seems to us entirely homologous with that described above for eastern Africa. Dasmann and Mossman (1962) recognised that some males were probably territorial during the rut, and our observations confirm this. In Mkuzi Game Reserve, South Africa, we observed behaviour of males a few weeks before the start of the rut. A proportion of the adult males were separate from the bachelor herds, and were found alone, spaced rather regularly through the area. They were seen to use dung heaps, to thrash bushes, to horn soil and to frontal-rub, and were seen and heard roaring. Most interestingly, they distributed themselves in relation to each other and appeared to be marking territory without taking any notice of the female herds wandering through their territories. In the rut itself, in Rhodesia, territorial males, like those in eastern Africa, herd female groups intensively and are hostile towards bachelor herds. Bachelors in central and southern Africa may be driven into marginal habitat more commonly than in eastern Africa, perhaps because of the tendency of southern impala to occur at greater density and to hold smaller territories. In Mkuzi we saw behaviour which indicated that a hierarchy could exist among bachelors, but since we were not watching known individuals we could not establish this. We do not know whether males hold territory throughout the rut, or whether there is a succession of holders.

At the start of the rut juvenile males born the previous year are at most six months old, and territorial males do not appear to evict these as they might in eastern Africa. However in some areas these juvenile males, together with females of the same age, form groups separately from the adult females for the duration of the rut.

(*b*) *Organisation outside the rut*

Although the majority of conceptions have occurred within two months of the start of the rut, a few arise from matings up to four months from the start. The observed social organisation suggests that some males continue to herd females and repel bachelors for as long as this, or longer. In nearly all studied populations a proportion of males were found single, and a proportion of the females were accompanied by only one adult male, at any time of year. The proportions fall in the dry season to about 20% of the populations in both social categories, the rest of the males being in multi-male groups, and the rest of the females being with several males or no male. At the start of the rains females begin to drop calves. There is a slight resurgence of single males in the samples, and a higher proportion of the females, perhaps 70-80%, are found with only one adult male accompanying the herd. Young males had joined the female herds again after the rut, and tend to separate from the females again during the calving period, forming bachelor groups. Young females tend to form distinct groups within the female population. By the middle of the rains over 90% of females may be seen in groups accompanied by single adult males. Creche groups are very obvious at this time. The proportion of adult males found single rises to a peak at the time of the rut.

(iii) Comparisons between the eastern and the southern and central African systems

Because our southern African observations were discontinuous and were mostly made before we had learned to recognise territoriality, we can make only limited comments on the data. There was a fluctuation in the proportion of adult males found single, the proportion rising in the rains, particularly during the rut, and falling in the dry season. During the rut our observation indicated that these males were holding territory; for the rest of year they appear to be localised, may attach themselves to and exclude bachelors from female herds, and use dung heaps to some extent. Yet roaring is heard only during, and just before, the rut, and fighting is also most common then. It seems that elements of territorialism, most obviously the tendency to isolate themselves, occur in some males in the population at any time of year, but that its full expression is confined to the rut. This makes the southern system directly comparable to the eastern African, differing only in the highly concentrated form of the mating season in southern regions.

SOCIO-ECOLOGICAL BEHAVIOUR

(i) Anti-predator behaviour

Impala tend to aggregate, and it is probable that this has value for the species in reducing each individual's chances of being killed by a predator. Although a mother can defend her calf against a jackal-sized predator, impala do not generally co-operate aggressively against a carnivore. Aggregation seems to benefit them in the presence of predators by increasing the chances of detecting the predator, decreasing the average individual's chance of being the victim of an attack, and making it more difficult for the predator to isolate or distinguish an individual target. If the predator's success depends upon surprise, so that a herd that has detected it is immune from attack, then the impala population will keep the predator population low by aggregating, so that the daily number of opportunities for surprise (i.e. the number of groups of impala) is reduced. Thus the formation of herds is a passive as well as an active form of anti-predator behaviour. It is reinforced by a variety of calls and displays, and special activities, which co-ordinate animals within a group in the presence of a predator

(ii) Group size and feeding behaviour

While anti-predator behaviour sets a lower limit to effective group size, an upper limit is imposed by the animals' behaviour in response to the abundance and dispersion of acceptable food items. Availability of other resources has similar effects, but they can best be shown for food supply. It is clear from a knowledge of the food eaten by, and available to, impala that the quality of food intake declines from wet to dry season. In some areas the total quantity of food eaten may increase slightly over this period, yet in all areas the final effect is that animals lose condition, and some may die of malnutrition by the end of the dry season. Impala in the intensively studied population in the Serengeti modified their behaviour to counteract declining quality of intake and quantity of available food in several ways. Their rate of movement and total distance moved daily while feeding increased from wet to dry season; the separation of individuals within groups increased from wet to dry season; and the size of groups declined from wet to dry season. What seemed to be happening was this: as the abundant, highly nutritious food supply of the wet season decreased in quality and quantity, impala changed their diets to maintain quality of intake. In doing this they came to utilise more dispersed food items. To feed on these, groups spread out more widely and moved further each day for the same quantity of intake. As quality of items declined, even greater daily movements had to be made to maintain quantity of intake. The combination of increased inter-individual distance and increased rate of movement made groups less cohesive and co-ordinated, and groups tended to split into smaller units. The effectiveness of this strategy was seen in the maintenance of good condition by the animals for a prolonged period after food supplies had begun to decline, although animals' condition did finally start to fall as the strategy could no longer compensate for the worsening supply.

Rate of movement and distance moved while feeding, and inter-individual separation within groups, have been measured only in the Serengeti, but seasonal variations in group size have been recorded in many populations. Food supply is dependent upon rainfall, and group size upon food supply, so group size is secondarily dependent upon rainfall. Although measurements of food supply are rarely available, relationships between group size and local rainfall can be derived for most populations studied. When this is done, we find that correlation of group size and rainfall has characteristic values for different climatic regions. There is generally a time lag between the curve for monthly rainfall and the curve for monthly group size, so that the biggest groups occur some time after the wettest month. Where rains are well distributed through the year the lag is great compared with those areas where rain is confined to a short period each year. Thus in the Serengeti, with well distributed rain, the best correlation was found between group size and rainfall summed over the previous three months; in the Selous Game Reserve, Tanzania, with a limited wet season but similar total rainfall, the best correlation was found with rainfall over the previous two months. So in areas of strictly seasonal rainfall impala's aggregating behaviour responds faster to the onset and cessation of rain than in regions of better distributed rain.

There may come a time at the end of the dry season when the only available food is to be found in a few limited patches. In these circumstances the trend in group size will be reversed, and animals will congregate in large numbers on these localised abundances. Water also tends to become more and more patchily distributed in the dry season, and in many areas impala tend to congregate around available sources of water. In doing this they form larger groups near the water source than further away, as shown by Young (1970) in the Kruger National Park.

Other behavioural relations between resources and society are found in habitat preference and home-range behaviour. In the first, animals respond to differences in the availability or suitability of resources by apportioning their activities differentially between habitats. This may lead to the local society being divided according to resource requirements; for instance, herds containing creches may prefer vegetation types containing bushes, which other female herds might avoid. It also leads to seasonal changes in the areas in which females are found, with consequent differentiation between territories. In showing habitat preference an impala distinguishes between areas on criteria of resources; in showing home-range behaviour the animal further divides the area apparently according to familiarity. Juveniles, especially females, may adopt a home range similar to their mothers'. Size of home range is related to availability of resources throughout the year. Although animals may leave their home ranges when forced to, the tendency to return is very strong (Jarman, M. V., 1970). Home ranges, especially of males, may change with time. Home-range behaviour and habitat-preference behaviour are both involved in ensuring the most efficient distribution of the population through its environment.

We can now see some of the pressures upon territorial males which may be responsible for ending territoriality, or reducing its expression, in dry seasons. As female groups become more numerous by splitting-up in the dry season, and as they move faster, more of them will pass through each territory daily. Habitat preference on the part of the females, and often the need to concentrate near water, mean that certain territorial males are receiving most of the female herds. These males suffer from exhaustion because of the ever-increasing numbers of female groups they try to herd. Territories which do not receive females are clearly in unfavourable habitat at that season, often having no watering place in them; their holders must leave them to drink or feed, thus forfeiting their territorial status.

(iii) Aggregating behaviour

Aggregation into and cohesion within groups is brought about by behavioural actions, distinct from those, called socio-sexual above, which produce division into the social categories of territorial and bachelor males, and female herds. Impala are particularly allelomimetic in many activities, like feeding, ruminating, moving, playing, defaecating and urinating, and especially in responding to alarm. It is obviously essential for group cohesion that they should be. Where there are departures from co-ordination they are generally made by sub-groups of several animals, like creches, rather than by single animals. The exception to this is the territorial male whose activities are often rather different from those of the herd he is with. Co-ordination of activities in herds is aided by the adoption of postures typical of each activity, making its nature obvious to the other animals. Displays may re-inforce co-ordination, particularly in anti-predator behaviour and situations of alarm.

Impala maintain inter-individual separation within groups partly by mild aggresion towards animals coming too close while moving and feeding, although this is less apparent when they are resting. Aggression may rise sharply when animals are forced close together at a restricted resource, such as a water-hole or salt-lick. Certain activities bring animals together, such as play in juveniles, sparring in young males, display in older males, suckling and grooming between mother and calf, and grooming between like-age like-sex partners in all social categories except territorial males. A variety of quiet calls is used within impala herds, notably between mother and offspring; these may become very loud if mother and young are separated and are trying to make contact. An impala's social life begins with the formation of a bond with its mother, and mother and young seem able to recognise each other by smell, sight and sound. Even when this bond ceases to operate, all impala of both sexes show a tendency to associate with adult females. Thus bachelor herds join females when given the opportunity, and a small female group will join a larger one. This general tendency to aggregate is the most pervasive of all aspects of impala behaviour; so much so that we do not normally describe it as a distinct behavioural action, and much of this paper has been concerned with describing departures from or modifications to it.

RELEVANCE TO MANAGEMENT

Impala are among the most numerous antelope in Africa, important members of many of the best surviving communities. They are aesthetically attractive, have palatable flesh, complement domestic stock as utilisers of range, and are favoured prey of several large carnivores. Anywhere within their range they can be found in one of the following systems of management:-

(i) natural, unexploited system; animals living in near-natural conditions, regulating their own populations. This system applies in a very few reserves.

(ii) unnatural, unexploited system; animals living in an environment modified by man, but being left to regulate their own populations. The most common system in most reserves, on farm or ranch land, and in restocked areas.

(iii) natural, exploited system; animals living in near-natural conditions, but with man acting as a predator, removing a few through hunting or light cropping.

(iv) unnatural, exploited system; animals in an environment modified by man, which are cropped, ranched or captured.

In system (i), in reserves where no intentional interference with either habitat or animals is undertaken, a knowledge of the behaviour of impala has relevance only in monitoring the population for possible unintentional interference. This kind of management, preserving a wilderness area, is unfortunately rare, and most reserves are nearer to system (ii), in which the environment is modified by the creation of roads, erection of fences, provision of watering places and slat-licks, usually by the use of fire, and by the frequent presence of men and cars. Aspects of the socio-ecological behaviour of impala are relevant to such management, as they are to the introduction of impala to new reserves. For instance, the behaviour involved in habitat preference and establishment of home range should be borne in mind when trying to influence the dispersion of impala through a reserve. A good diversity of vegetation types per unit area generally allows impala to use small home ranges, and to be found distributed throughout the reserve in most seasons. Any need for animals to congregate at limited resources, such as water, tends to break down the socio-sexual organisation, and if this happens too early in the dry season reproduction may suffer. Ideally watering points should be distributed at intervals of one home-range diameter apart to keep animals well dispersed throughout the year. Constructive steps can be taken to induce vegetation types suitable for certain actions; for instance bush clumps for parturition, and grassy glades on which impala congregate in the evenings, spend the night, and perform many social displays in the mornings. Anything which adversely affects feeding behvaiour, making groups move further daily or split up more, is detrimental and should be avoided if the growth of the population is to be encouraged. When impala are introduced to restock an area their normal attachment to a home area should be remembered, and stock distributed in groups throughout the reserve rather than all released at one point.

For many reserves predators are treated as a raison d'être. A dense, well-dispersed population of impala is an ideal encouragement for lion, leopard and cheetah in some areas, impala being the right size as prey and, if managed suitably, resident.

Impala can modify their daily activity pattern to cope with a regular disturbance. We have found them, when sharing their range with cattle, altering their time of drinking to avoid coinciding with cattle and herdsmen at the watering points.

All these points apply equally to the forms of management in which impala are exploited by hunting, cropping, capture or ranching, and in these systems other aspects of the species' behaviour also become relevant. Most of the behaviour invoked above has been socio-ecological, since it is the environment that has been managed in those systems. Where systems (iii) and (iv) impinge upon the individual impala directly, the socio-sexual behaviour becomes relevant. The most obvious points here relate to selection of the animals to be removed. For instance many hunters have assumed that lone males were 'old' and evicted from society, hence ideal targets as trophies or worse. Our research shows that these are the very animals that are actively reproducing. Similarly a cropper or rancher should not assume that a female is sterile just because she does not have a calf at heel; it may be lying up with a creche a hundred metres away. A knowledge of the annual cycle of socio-sexual behaviour suggests some times of year as better than others for cropping or capture; obviously not during the calving season, the pre-weaning period, or the rut. Several results of the disturbance caused by exploitation are undesirable. Repeated distrubance disrupts normal socialising within a herd, drives animals out of their home ranges, disturbs daily activity patterns, and causes herds to move further and split up. We recommend that, as far as possible, cropping or capture should take place in any area in as short a time as possible, with the offtake well distributed throughout the area, and at a season when most of the socio-sexual behaviour linked with mating peak or rut has passed. This should have less detrimental, long-term effect than the same proportional crop spread evenly throughout the year; this latter will be particularly disturbing if the cropping is done from fixed points, such as hides at water holes. In selecting number and composition of the crop, behaviour that leads to differential distribution of the sexes or ages should be remembered.

The behaviour of impala does not seem to be compatible with their domestication, for which animals with fixed-membership herds, like buffalo or eland, are more appropriate. The problems experienced by a territorial male impala trying to restrict the movements of a female herd should be observed by anyone who wishes to put himself in the male's position.

ACKNOWLEDGEMENTS

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Paper No. 51

The Development of a South African Game Ranch

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ABSTRACT

The first five years of a 2, 700 acre game ranch in Zululand are described. A brief outline of the environment, both ecological and economic, is included. Data on the build-up of populations; species being used; yield, population structure and biomass are shown and discussed. The influence of certain behaviour on management practice is described, particularly the necessity for ensuring that flight distance is minimised.

INTRODUCTION

The ecological justification for game ranching in Africa has been argued convincingly and at length. There is, however, little information on the results of game ranching in practice. Yet such data are necessary to an appraisal of the value of this form of land-use. This brief history of the Ubizane Game Ranch is, therefore, offered as a contribution to such data.

LOCATION AND ENVIRONMENT

The Ubizane Ranch comprises 2, 700 acres (1, 080 hectares approx.) of privately-owned land in north central Zululand, Province of Natal, South Africa. The surface is undulating from 200 to 700 feet (60. 9-213. 2 m) above sea level. The underlying rocks comprise basalts interspersed with rhyolite dykes of the Stormberg system. From these are derived a red to dark brown heavy clay soil, displaced in the valleys by a very heavy, deeply cracking, alluvial black clay. The climate is tropical and semi-arid; aridity being increased for vegetation by the nature of the soil. There is no natural surface water. Fifty-five per cent of the ranch area, along interfluvial ridges, supports a short, tree savanna of *Themeda triandra* and *Acacia nilotica.* Forty per cent, along the valleys, supports a low, wooded savanna of *A. nilotica* with *Sekima galpini* the main grass. The remaining five per cent comprises riverine woodland and forest along the largest watercourse, dominated by *Acacia xanthophloea* and *Ficus sycamorus*;and thickets either of *Euclea* or *Dichrostachys* and *Acacia karoo.*

REGIONAL LAND-USE, HLUHLUWE DISTRICT

Cattle ranching has been the longest and most widely practised land-use. But with profitability at best about 2 per cent on capital invested, increasingly larger areas of natural vegetation have been replaced by plant crops in hope of a better return. These are sisal and cotton on the basalt, and pineapples on the sandy coastal plains. The fibre crops have been hard hit by competition from artificial fibres, but pineapples on the less arid sands are giving a better return. Tribal lands of the Zulu people are used in the traditional manner for subsistence crops of maize and millet, with cattle and goats playing a vital role in the social system but not as producers, other than of some milk for domestic use. Game ranching in the district is now being practised on some 20, 000 acres (8, 000 hectares). The district is bordered on the west by the Hluhluwe Game Reserve, to the north-east by the Mkuze Game Reserve and to the east by Lake St. Lucia Game Reserve. Communications are linked primarily to Durban by rail and tarmac highway, via which virtually all produce is marketed, 170 miles to the south-west. This city is the major sea port in South Africa (and on the continent) with a population of about one million of whom many are most partial to game meat.

ESTABLISHMENT OF GAME POPULATIONS

The large mammal fauna of the area when purchased in 1966, was sparse and the species spectrum impoverished. This resulted from the policy of game eradication between 1918 and 1952 intended to eliminate the tsetse fly *Glossina pallidipes*. The fly was finally removed by insecticide applications, between 1946 and 1954. Only some smaller ungulates survived in fair abundance, together with relic stocks of impala, nyala and greater kudu. The first problem was therefore to re-introduce as rapidly as possible an exploitable game population and to prevent it from emigrating. An eight foot perimeter game fence was therefore built, whereupon animals were moved in. The major source of most species in economic numbers is the annual surplus of the nearby game reserves, including Umfolozi, administered by the Natal Parks, Game and Fish Preservation Board. The build-up of the populations is detailed in Table 1, which shows the populations of species at each year end. At this time the seasonal breeders, most importantly impala and blue wildebeest, have dropped the annual calf crop. At the time, the movement of game to this ranch constituted the greatest translocation of game to a single destination in South Africa. Subsequently, even more efficient capture techniques have made larger movements possible. Table 2 describes the increase in the *average annual* ungulate population in numbers and as pounds per square mile. This average is determined by dividing the sum of the population at each month end by 12 and is, we believe, the best indicator of the population actually carried on the land.

TABLE 1. NUMBERS OF EACH SPECIES AT YEARS END

	1966	1967	1968	1969	1970	JUNE 1971
White Rhino	0	8	8	11	8	8
Giraffe	0	2	2	2	3	3
Zebra	0	19	75	205	229	206
Blue Wildebeest	0	5	183	313	460	376
Greater Kudu	2	5	12	14	26	26
Eland	0	4	1	2	6	6
Nyala	2-1	57	158	240	223	221
Impala	12	341	894	1970	2285	1827
S. Reedbuck	10+	10+	20+	30+	14+	19+
Common Waterbuck	0	0	5	6	9	9
Grey Duiker	12+	12+	50+	60+	48+	59+
Steenbuck	6+	6+	20+	30+	27+	26+
Warthog	0	38	41	70	120	111
Blesbuck	0	0	67	91	100	89
TOTAL	42-3	507	1536	3044	3558	2986

Note: It is estimated that the year-end figure 1971 will approximately equal that of 1970.

TABLE 2. AVERAGE ANNUAL BIOMASS AND POPULATION

	1967	1968	1969	1970	1971
Population—game	326	1,087	2,341	2,916	3,280
Population—cattle	0	374	41	0	0
TOTAL	326	1,461	2,382	2,916	3,280
Biomass—game	8,746	32,641	78,780	102,297	110, 706
Biomass—cattle (lbs/sq. mile)	0	71, 578	7,890	0	0
Biomass—grazers	5,471	95, 054	68,234	80,643	84,573
Biomass—browsers	3,275	9,179	18, 436	21, 654	26,133
TOTAL	8,746	104, 233	86,670	102, 297	110,706

Notes: (1) Figures for 1971 are the half year averages, the annual averages will be about 10% less.
(2) In calculating grazing biomass half of impala and one third of nyala included, balance to browsers.
(3) To convert to kg/km^2—multiply by 1.1363.

The necessity for re-stocking places South African game ranches in a different category to those elsewhere in Africa from which original populations have not been removed or badly decimated. Economically the most important distinction is in the long interval between commencement of the enterprise and attainment of an exploitable abundance. This is also a handicap in comparison to the use of domestic stock. We, therefore, found it necessary initially to use cattle to generate income before game commenced to do so. This is true of virtually all game ranches in the country, except that sheep replace cattle in the temperate semi-arid and sub-humid areas. Integration of domestic stock with game utilization is also practised—particularly sheep with blesbuck and/or springbuck.

OPTIMUM ABUNDANCE

Initially our intention was to maintain an average annual grazing bio-mass of 70, 000 lbs per square mile. As Table 2 indicates, during 1968 the ungulate biomass, including cattle, greatly exceeded this figure due primarily to a much more rapid inflow of game than we had anticipated. At the same time the rainfall from the 1966/67 season onwards progressively decreased to the lowest ever recorded, in 1969/70, a season only slightly improved upon by the last (70/71). The average of these four seasons has been less than 60 per cent of the average rainfall since 1923 when records were inaugurated. Above-average rainfall has not been experienced since 1963. We have therefore revised the target figure to 60, 000 lbs grazing biomass until this drought cycle is broken and the extent of recovery of the vegetation justifies an increase. Nevertheless with unreliable rainfall of this nature the average biomass maintained cannot be constant and will have to be varied in response. A factor which can also never be disregarded is the minimum economic abundance.

YIELD

Table 3 describes average annual population, since establishment, of those species presently being cropped or to be cropped from 1972, together with the yield in numbers of animals. Table 4 shows production in terms of dressed carcase weight (weights of animals taken by sport hunters are estimated). The figures for 1971 are incomplete in so far as the annual crop has not been fully harvested but this figure—weights estimated—is also shown. Only one species, blue wildebeest, has already reached the abundance and population structure to allow of the sustained yield being taken this year. Zebra and impala will do so in 1972. Table 5 describes the population structure for the blue wildebeest and impala at the beginning of 1971 and what it is expected to be when the full yield has been taken before the next calf crop. It will be seen that the number of reproductive females almost equals the yield in the wildebeest at the end of the year, but exceeds yield in the impala. The crop of impala in 1972 will be increased to its maximum. Ten per cent mortality in the calf crop is allowed for. Table 6 indicates the ratio of reproductive males to females in these 2 species for January of each year since 1967, indicating the aims of our culling policy during the establishment phase as well as the final ratio which we believe is optimal. Reproductive males are arbitrarily classed as over two years old, and females being those older than one year. More accurate determination during counting is not possible.

TABLE 3. AVERAGE ANNUAL POPULATIONS OF 4 MOST ABUNDANT SPECIES AND NUMBERS REMOVED FROM POPULATION

	1967	1968	1969	1970	1971
Impala	226(10)	696(61)	1, 454(151)	1, 811(436)	2, 065(425)
Wildebeest	4(1)	54(14)	278(28)	398(117)	407(77)
Zebra	14(1)	47(8)	145(19)	187(64)	207(3)
Nyala	35(1)	89(2)	188(15)	199(87)	222(7)

Notes: (1) Figures for 1971 are the half year averages, the annual averages will be about 10% less.
(2) Numbers removed include those shot, natural deaths, and losses through fence; shown in parenthesis.
(3) No animals introduced in 1970 and 1971.

TABLE 4. TOTAL DRESSED CARCASE WEIGHT SOLD PER YEAR/LBS, AND YIELD PER ACRE: GAME ONLY

	1967	1968	1969	1970	1971
Total	0	1250	15,200	41, 880	35, 160 (61, 000)
Yield/acre	0	0.4	5.4	14.8	12.5 (21.8)

Notes: (1) Includes animals killed by sport hunters
(2) Figures in parenthesis include estimated weight of remaining animals to be culled in 1971.

BEHAVIOURAL LIMITATIONS TO RANCHING PRACTICE

The most important limitation of wild ungulate behaviour is fear of man. Unless properly regulated, human predation rapidly increased the flight distance (as defined by Hediger) of all prey animals. This, in inverse ratio, reduces hunting efficiency to the point where it is uneconomic. It is essential, therefore, that hunting be compensated by constant harmless activity by day and night; be restricted to short, well-spaced periods; and be practised in the most innocuous manner possible. All human

TABLE 5. POPULATION STRUCTURE OF IMPALA AND WILDEBEEST BEFORE AND AFTER CULLING-1971

	Ad Male	Sub-ad Male	Juv. Male	Ad/sub adult female	Juv. Female
Impala—before	142	133	250	1, 260	500
Impala—after	122	90	240	870	480
Wildebeest—before	145		60	195	60
Wildebeest-after	80		55	105	55

Note: after culling figure includes estimated losses from all causes.

TABLE 6. SEX RATIOS, ADULT MALES: ADULT FEMALES, OF IMPALA AND WILDEBEEST, IN JANUARY

	1967	1968	1969	1970	1971	1972
Impala	1 : 2. 5	2.5	2.8	2.9	8.9	4.0
Wildebeest	1 : 1.0	3.0	2.9	1.9	2.2	2.0

Note: Figure for 1972 estimated on total crop culled in 1971.

activity must be carried on in such manner as will reduce flight distance. This distance must not exceed 150 metres in daylight, or for those species dazzled at night 20 metres under illumination.

The reduced carcase quality caused by fear must also be minimised.

Practical recognition of these limitations is the *sine qua non* for efficient operation of a game ranch. Failure to do so will result in an operation being abandoned. It is the primary reason for the disfavour in which some game utilization schemes are already held. This cannot be too strongly stressed.

Another facet of ungulate behaviour of practical importance is the hierarchical ranking of adult males in many social species. This results in only a small proportion of potential breeders actually breeding. Not more than 20 per cent per year of these dominant animals ought to be removed. In those species for which rutting is seasonal no removals of dominants should be allowed during this season.

The remaining behavioural characteristic of importance which we will mention here, is home range. All of the species we are using have a defined and quite limited home range. It is, therefore, essential to vegetational management that the population of each home range be proportionately culled, and not only those in more accessible areas. Failure to do so rapidly results in overuse of vegetation in those home ranges neglected by hunting, with all the ill-effects to which this leads.

ECONOMIC RESULTS

These, of course, reflect the size of the crop. Our operation achieved a balance between income and recurrent expenditure in the fifth year. To ensure a good and sustained market, it is essential that the product is offered in prime condition. Carcases must be properly butchered and delivered in the manner usual for domestic stock, i.e. without wounds, in mutton-cloth, fresh and hanging by the rear legs. This requires head shots and constant supervision of butchery staff. Attention to these details ensures that demand, at a good price, exceeds supply. Failure to do so results in great wastage and loss of income, and low prices. Similar considerations apply to the proper handling of skins. Too many producers are still ignoring these requirements.

CONCLUSION

We are now confident, from results achieved, that game ranching on this property will provide a satisfactory return on capital employed.

Paper No. 52

Wildlife Husbandry on a Rhodesian Game Ranch

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ABSTRACT

The continuing existence of wildlife in the Matetsi district of Rhodesia generally and on Rosslyn game ranch in particular has been ensured because of the failure of conventional farming in this area. The initial production of venison and skins gave way to safari hunting and other tourist uses of the wildlife, since these mean more income with fewer animals shot and subsequent better biological manipulations of the population.

Extensive and intensive veld and game management are of the highest importance to ensure a sustained yield with no degradation of land. Hunting techniques and carcass processing are also important and the financial results offer great hope for this kind of marginal land use.

INTRODUCTION

The paper describes a Rhodesian wildlife utilisation unit, privately owned by Rosslyn Hunting & Wildlife (Private) Limited, and managed by the writer, primarily for sport hunting of large ungulates and their predators. The land is in the north-western part of Rhodesia, bounded on the south by the Wankie Game Reserve, on the west by Botswana and elsewhere by other game ranches at various stages of development. The boundaries with Botswana and the Game Reserve are defined by an effective game fence through which very little game movement takes place, apart from predators such as lions and hyaenas. The main ranch is 51, 000 acres and about 20 miles long and there is a separate unit of 6, 000 acres.

Average rainfall is 27. 35" per annum, falling mainly in the summer between November and March (the rainy season). There is also a cold dry season and a hot dry season. Mean maximum temperature is 87.7°F (absolute maximum 108. 7°F) and the mean minimum is 57. 7°F (absolute 27°F). Altitude varies between 3, 200 and 3, 600 feet.

HISTORY

The ranch was originally managed conventionally for cattle, vegetables and dry land crops. The low carrying capacity of a major part of the ranch, owing to erratic rainfall, shallow soils and fire climax grasses of poor food value, together with the predator problem to a lesser degree, gave poor financial results. By May 1967, all conventional farming had ceased and the company commenced game ranching on a meat and skin production basis. Although production of game meat could be maintained at around 11b per acre per annum, current low venison prices make a meat and skin economy unsatisfactory. It was therefore decided to go over to sport hunting, since this allows a good financial return from a few animals, leaving room for biological manipulation of the population according to the ecological rather than the financial needs.

STAFF

Management of the ranch is directed by the writer with the assistance of his wife and some twelve Africans. These Africans have been chosen and trained to do specific jobs but are able to assist in any work which requires extra help, such a fire fighting. Outside the hunting season they all work on veld reclamation, road and building maintenance, and so forth.

VEGETATION AND TOPOGRAPHY

The ranch consists of broken basalt hills and open woodland savannah (74. 5% of the land). These generally shallow-soiled areas have varying proportions of *Combretum, Commiphora* spp., *Kirkia acuminata, Bauhinia* spp. and *Colophospermum mopane.* The dominant grass is usually the *Aristida* spp., fire resistant and of low food value but with varying proportions of *Chloris gayana, Eragrostis* spp., *Digitaria* spp., *Urochloa bolbodes* and *Heteropogon contortus,* with *Tragus berteronius* and *Rhynchelytrum repens.*

Interspersed among the basalt woodland areas are grassy drainage valleys known as vleis (15. 5% of the ranch). Vleis are cold air drainage lines and therefore winter frosts are common and often severe. Frost and fire (fire in the long-grass vleis are fierce) are major factors in maintaining the vleis as grassland. Dominant grasses are *Setaria* spp., fire climax *Hyparrkenia* spp., with *Sorghum halapense, Robellia exaltata* and *Cynodon dactylon* in the disturbed areas, e.g. old crop lands. *Imperata cylindrica* is dominant in the wetter areas. All the ranch's permanent springs and sponges are found in the vleis.

VELD MANAGEMENT

The object of veld management is to maintain optimum balance between the wildlife and its habitat. This is achieved mainly by fire control, cropping of surplus animals in overgrazed areas, manipulation of grazing, plant conservation, termite control and measurement of long-term trends.

Fire control. The widespread annual fires in the district, while helping to maintain the veld as open woodland savannah, have also reduced its carrying capacity. With fire control becoming effective on Rosslyn, animals, once common, are now rarely seen and the proportion of palatable-grass species is increasing so that the number and variety of large animals is gradually increasing also.

Chief among fire management techniques is the construction of firebreaks, which consist of double tracks 75 yards apart on boundaries and 30 yards apart for internal firebreaks. These tracks are mown towards the end of the growing season and the hay burnt before the standing grass dries off. By July-August the area between the tracks must be burnt.

Cropping. When plant trend checks indicate a build-up of grazing pressure in an area, cropping of the dominant species is undertaken. Cropping methods are discussed later in the Game Management section.

Manipulation of grazing. Salt (NaCl) blocks are placed at points preferably about a mile from water to encourage the animals to graze away from the water and thus spread out grazing pressure.

No serious attempt has yet been made to feed a dry-season protein supplement to the animals, which would help make better use of available coarse dry grasses. This could be another important method of influencing grazing behaviour.

Vlei grazing is improved when the long coarse grasses are trampled down into contact with the decomposing micro-organisms in the soil, stimulating green shoots and reducing the fire risk. Buffalo (*Syncerus caffer*) are the most effective animals for doing this, but since there are not sufficient on Rosslyn the wetter vleis are burned about once every two years (in August after the frosts) to remove the moribund material; drier vleis are burned less frequently and only after several showers of rain have fallen. The burn stimulates green shoots, much liked by the game, and similar results are obtained by using a rotary mower to cut the grass, but this is expensive. The game like these mown areas too and, as on the burns, can do damage by concentration. Evidence is not yet conclusive but the best answer may well be to encourage the buffalo to build up, especially as they are valuable trophy animals.

Plant conservation. On the basalt woodland, bare patches are found where the successful re-establishment of grass is prevented by some cause such as soil capping or concentration of mineral salts. Covering part or all of these areas with cut brush helps greatly by providing shade for seedlings and catching windblown litter which holds moisture. Before putting down the brush, the soil surface may be broken up or covered with mown grass.

Termite control. Hodotermes sp. are troublesome, especially in degraded areas. Control methods consist of attempting to upgrade such areas; grassland in good condition does not have termite problems.

Measurement of long-term trends. One method of assessing veld trends is from the fixed-point transects which are scattered throughout the ranch and from which comparisons from photographs, basal cover measurements and species composition of the grasses are made annually. One-acre exclosures are also used to help determine the causes of veld changes in particular areas.

ANIMALS ON THE RANCH

There are 17 big game species and four species of large mammalian predators. The ten most important ungulates are:

Sable	*(Hippotragus niger)*
Zebra	*(Equus burchelli)*
Waterbuck	*(Kobus ellipsiprymnus)*
Reedbuck	*(Redunca arundinum)*
Impala	*(Aepyceros melampus)*
Kudu	*(Tragelaphus strepsiceros)*
Eland	*(Taurotragus oryx)*
Warthog	*(Phacochoerus aethiopicus)*
Duiker	*(Sylvicapra grimmia)*
Grysbuck	*(Raphicerus sharpei)*

— and the predators are:

Lion	*(Panthera leo)*
Leopard	*(Panthera pardus)*
Wild dog	*(Lycaon pictus)*
Hyaena	*(Crocuta crocuta)*

Other game present but marginal to the area are:

Roan	*(Hippotragus equinus)*
Tsessebe	*(Damaliscus lunatus)*
Wildebeest	*(Connochaetes taurinus)*
Bushbuck	*(Tragelaphus scriptus)*
Klipspringer	*(Oreotragus oreotragus)*

While there are seasonal movements around the ranch and to varying degrees on and off it, the extent of movement about the district is not fully understood and there is urgent need for a research project on the subject. On Rosslyn, observation of known animals indicates that the movement is probably not as extensive as some landholders believe. The distribution of animals on the ranch is limited by water supplies and the required habitat, so that increased water supplies will increase the range of some species such as sable, impala and zebra. Human habitation does not seriously affect the game, which continues to live near buildings.

GAME MANAGEMENT

The number of animals to be cropped or shot in any year is largely determined by the degree of veld utilisation. The object of management is to keep the numbers and variety of the game population as high as possible consistent with good veld condition. At present on Rosslyn ungulate species are cropped at roughly 3% of the estimated herd size, a low figure to enable herd strengths to increase. As the land approaches maximum utilisation with good veld management (particularly fire control and culling from overgrazed areas) this figure should increase to around 10%, even with the loss to predation.

It is well known that it is impossible to obtain exact counts of free-living wild animals but careful and regular counts over a period of time do give a good indication of density trends. The method used on Rosslyn is a modification of Mossman and Dasmann's road strip technique and the area of the true visible strip width is measured on routes selected to give a representative sample of the ranch. Care must be taken to allow for species habitat limitations, varying visibility range and the difficulty of seeing the smaller species. Animal counts are taken at regular intervals along these strips and extrapolated to the whole ranch.

During the meat production phase at Rosslyn, these counts were used as a basis to crop between 5% and 10% of the ten main species. Waterbuck were cropped at the rate of one male to two females in an effort to reduce the population, though this has not in fact happened appreciably even with 200 Waterbuck removed in four years. Other species were cropped with a male bias to achieve reduction less rapidly.

The ideal cropping age for venison production is about 30 to 36 months, but for trophies older animals up to 84 months are taken. Cropped animals are generally females or males with poor quality horns or other defects.

Both cropping and sport hunting are conducted so as to minimise disturbance of other animals and, in the case of sport hunting, mainly lone males are taken. Nevertheless, sport hunting is usually more disturbing to the animals than cropping, which is mostly carried out at night with the aid of a powerful hand-held light and a telescopic-sighted 30. 06 rifle from an open Land Rover. This system allows careful selection of age and sex classes and is only used on the darkest nights so that the animals cannot identify vehicles or humans. Wounding rates by the writer are less than 1% for night shooting but can rise to around 10% for day foot shooting, a much less efficient method except for zebra.

With night shooting, animals are killed instantly with head shots, using a 30. 06 with softnose bullets. When many impala are to be culled the writer's experience is that an autoloading 12-bore shotgun with AAA shot is most efficient. A . 22 rifle and silencer is adequate for the smallest antelope.

Cropping animals from blinds at waterholes is a useful method in drier parts of Rhodesia because of the consequent concentrations of game but is unproductive on Rosslyn because of the abundance of water. Blinds can be used at vlei burns when the green grass sprouts, but this method is disturbing if used more than a few times in any one season; however, it is a useful way of collecting several zebra at one time.

When the ranch was managed for meat, predators were shot on sight but not poisoned or trapped. However, these animals are now valuable trophies and as such only a few are shot by sportsmen, with the exception of hyaena which may quite seriously reduce the calf crop of a species and are therefore not protected.

CARCASS PROCESSING

To produce quality meat, the animals should be killed as humanely and quickly as possible, without disturbance, should be bled well and gutted immediately after, the skin removed and the quartered carcass hung to cool and set. Hygiene for both meat and skin processing is vital for a good product and there are rigorous Government regulations and inspections of facilities and meat: as a result, insecticides are not needed at the processing facilities.

Most meat is quickly processed into biltong (jerky) on the ranch. This is a dried meat product in high demand, produced in two grades: stick, which is top quality, and scrap, consisting of the trimmings. Biltong has several advantages over fresh meat, being more economically transported, not requiring refrigeration and currently having an excellent market. Damaged quarters are more productively used too.

A detailed system of recording is used for every stage of management and processing of wildlife and may be found in 'Game Ranching Recording System', a manual on the methods developed by the writer and published by the Game Ranching and Safari Association of Rhodesia.

FINANCIAL PERFORMANCE

In 1970, about 130 animals of all species were taken by sportsmen on Rosslyn. The total including those cropped was 190 animals, with a yield of . 7 lbs per acre. Gross ranch income including safari fees, sale of meat and skins and other by-products, was R$0. 37 per acre and this is expected to increase in the future as land management techniques take further effect. In addition the ranch provides a living for about 60 indigenous Africans.

Although this yield is low from a purely investment viewpoint, previous types of land use both degraded the veld and resulted in year to year operating losses. For this type of marginal land it is the writer's opinion that recreational use, by giving the best sustained financial return, offers a great hope for the future of our wildlife.

Paper No. 53

Game Ranching in Texas

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ABSTRACTS

Commercial hunting of native and exotic game has developed in Texas since the early 1920's, and today leasing of hunting privileges is involved in the harvest of practically all of the big game animals on ranges west of the 98th meridian. While leasing systems developed in this area, the commercialization of hunting has spread to practically all important game ranges in the state. Commercial hunting of big game, waterfowl, small game, including quail and doves, is practiced extensively at the present time. Season leases, dayhunting leases, and the 'hunting broker' or 'outfitter' system are the principal leasing plans. Commercial hunting of exotic animals, which are not classed as game animals or regulated as such, may be undertaken at any time with any method, and is growing in Texas and the southwestern United States generally.

Over 26 species of big-game mammals have been introduced into Texas, with varying degrees of success. Eight occur in large numbers: axis deer, blackbuck antelope, aoudad or Barbary sheep, mouflon sheep, European wild boar, nilgai antelope, Sika deer and fallow deer. All of these are Eurasian in origin. While many transplants of large mammals from Africa have been tried, none have successfully established themselves in unhusbanded or wild populations..

Introduced animals are presently used only in sport-hunting programs and as brood stock for translocations to other ranges. Some have a potential for furnishing meat in ranges that are marginal for domestic livestock or in multiple-use rangelands where diversity in forages might be more efficiently used by animals with varied feeding habits and nutritional requirements. At this point, it is difficult to predict the economic values and biological uses of such animals in highly developed countries where protein is efficiently produced by domestic livestock of several kinds. Nonetheless, we should not overlook the potential. Over 22 million pounds of white-tailed and mule deer meat is harvested from Texas ranges each year, and this from ranges where other agricultural production forms the primary forms of land-use. This amount of red meat represents more protein than is produced from domestic livestock in many of the larger developing countries of the world.

As suggested by some wildlife scientists and geographers, fitting the animal to the vegetation might be a better approach than trying to fit the vegetation to the animal, especially on ranges that have been changed or degraded by man.

INTRODUCTION

The State of Texas is richly blessed with a great variety of game habitats and associated game animals. Of the more than 160 million acres of land in the state, at least two-thirds or 110 million acres can be considered Wildlands in pastures, rangelands, forests and woodlands. Large, wild herbivores and several species of small game occupy these ranges. The remaining one-third of the land in the state is in cropland, and these agricultural areas can and do support huntable populations of upland game birds and small mammals.

The purpose of this paper is to give a short review of game ranching programs in Texas where introductions of various kinds of ungulates have resulted in successful establishment of several species of antelope, sheep and cervids. It seems appropriate to state that game ranching, under Texas conditions, also means the production of game animals in ranch environments, where grazing schemes include domestic livestock and wild ungulates on the same ranges. Game ranching can also be applied to populations of native game because of the economic values of commercial hunting programs in the state. Game cropping or culling is not an appropriate descriptive term for the Texas situation because cropping and culling is usually referred to the taking of animals from wild environments such as those in African savannas and grasslands.

I will first discuss the commercial hunting systems in Texas because the value of wildlife to ranch operators is the foundation for the growing industry surrounding the hunting of both native and exotic animals.

COMMERCIAL HUNTING PROGRAMS

Commercialization of hunting in Texas was made possible by trespass statutes, the American's traditional respect for private property and, perhaps most important, by the virtual lack of public lands on which the public had free access to hunt. Title to all public lands was retained by the State of Texas when she entered the Union in 1846, and less than 1, 000 square miles of public lands now remain on which hunting is permitted. Thus a market for hunting rights on privately owned lands developed, and even though game is held in trust by the State for the people, access to game ranges is controlled by the landowners. Control of access has, for all practical purposes, transferred the custody of game animals from the State to landowners (Teer and Forrest, 1968).

From the small numbers of leases for taking white-tailed deer in central Texas in the early 1920's, commercial harvest programs have spread to other important game ranges. The number of game species involved has also increased. Today, leasing programs are involved in the harvest of practically all of the big game (white-tailed deer, mule deer, and pronghorn antelope) on ranges west of the 98th meridian. The harvest of deer was estimated at near 290, 000 in 1970 in Texas, and of this number probably two-thirds were killed in that area west of the 98th meridian. Those ranges comprise the great ranching area of Texas and such large land holdings lend themselves to leasing programs.

Leasing systems have spread to the Rio Grande Plains, the timberlands of the Post Oak and Pine Belts and Cross Timbers of east Texas, and to all other game ranges of the state that support huntable populations of deer and other game species. East Texas has been traditionally an open range for hunting. There, most private land holdings are small, but leases by groups of small operators as well as by large timber companies are increasing. Timber companies with large acreages are just now beginning to develop hunting programs through leasing for financial gain. In the past, most timber companies allowed free hunting primarily for public relations reasons. They now see opportunities for substantial income through sales of hunting rights.

Returns from the sale of hunting privileges vary with the type of leasing arrangements. A typical season-long lease (about 45 days) for white-tailed deer in the Edwards Plateau and Central Mineral Region of Texas will involve about ten hunters per 1, 000 acres. The hunters pay about $2. 00 per acre for the lease, and they can kill 20 fork-horned bucks and 10 antlerless deer under present hunting regulations set by the state. Total gross income from livestock and deer leases among several representative ranches in the Edwards Plateau and Central Mineral Region ranges from $1. 53 to $5. 92 per acre in 1965 (Boykin and Forrest, 1971). Thus the sale of hunting leases is often a substantial portion of the rancher's total income, and the worth of the deer hunting enterprise is increasing every year. Teer *et al.* (1965) and Teer and Forrest (1968) discuss the growth of the economic value of game to landowners in Central and west-central Texas.

TYPES OF LEASING ARRANGEMENTS

Four general types of leasing programs, with several modifications for special situations, are used in commercialized harvest systems (Forrest, 1966). The first, and perhaps the most important, is a 'season-lease' arrangement. Season leases usually provide that a hunter or group of hunters will have exclusive hunting privileges for specified game species for the season. Harvest quotas for the hunters are established by state game regulations. The season-lease system has been and still is the most common hunting scheme used in big-game harvest programs in the western half of the state, and many landowners provide hunting privileges for other species under similar arrangements.

Most landowners provide hunters with a camphouse or some type of living accommodations on the leased land. Some of these are little more than shacks, but others are fine lodges indeed, and it is not uncommon to find that many of them have been constructed by the hunters themselves. However, the stipulation is usually made that all permanent construction becomes the property of the landowner when the lease is terminated.

Some of the season leases go much beyond providing hunting recreation. Leases are becoming family-oriented weekend and holiday recreation centers. Landowners are beginning to attract more of the recreation market by improving facilities and offering additional activities for all members of the family. Fishing in streams and stock-ponds, horseback riding, hiking, camping, and photographing wildlife and nature are other facets of leasing programs that are becoming important.

The second, or day-hunting system, is becoming more popular with landowners in big game ranges and especially with landowners in wintering areas for waterfowl. This leasing system allows hunters access to game on a given area on a per-day basis. Hunters are usually not guided or provided with any particular equipment under day-lease arrangements for taking deer, but many landowners with waterfowl hunting may guide, and provide decoys, boats and other equipment to, the guests.

The hunting 'broker' or hunting 'outfitter' system is the third type of leasing system commonly used in the state. This system is being used predominantly in harvesting geese and ducks in the ricelands, marshes and rangelands along the coast. Under such a program, a hunting outfitter will lease large blocks of favored wintering areas from the landowners. These blocks of wintering habitat will involve as many as 25 or more landowners' properties, and may be as large as 50, 000 acres. All hunting rights are assigned to the outfitter, who operates the entire area under lease as a shooting preserve.

Outfitters offer waterfowl shooting on a day-hunting basis. Ordinarily all equipment for hunting except guns, shells and dogs is provided; and often food, lodging and other services are catered.

Outfitters manage their hunting programs to hold waterfowl throughout the season. Commonly, a mosaic of rice fields and irrigation reservoirs is flooded or filled to serve as sanctuaries and roosting sites for the water-fowl. Game laws allow morning and afternoon hunting, but most outfitters stop hunting at noon. The hunters are often distributed from day to day after the field-feeding patterns of waterfowl have been established by aerial or ground reconnaissance.

The fourth type of commercial hunting program is only now becoming important, and this is one in which the charge is made directly for the animal. These types of programs involve hunting introduced big-game animals. Such animals presently are not classed as game species under Texas statues. Landowners or hunters can take them in any season using any means or methods desired. Such programs have a certain kinship to the traditional shooting resorts, but no regulations, such as are in effect for operating shooting resorts, are applied to hunting of exotic big game animals.

Axis deer (*Axis axis*), blackbuck or Indian antelope (*Antilope cervicapra*), aoudad or Barbary sheep (*Ammotragus lervia*), mouflon sheep (*Ovis musimon*), Sika or Japanese deer (*Cervus nippon),* and a few other antelope, cervids, and sheep are sold in these hunting programs. The quality of hunting in terms of natural conditions attendant to the hunt and the 'wildness' of the game are sometimes below that of populations of native game animals. Yet the demand for such hunting seems to be increasing.

GAME RANCHING AND INTRODUCED ANIMALS

It is not appropriate to discuss in this paper the risks, benefits, and ecological morality of introducing organisms or moving them about from one place to another. One must accept that the animals are established now in Texas, and it is purely a philosophical question, under present laws and conditions, when one discusses whether exotic animals should or should not be introduced. The subject has received a great amount of attention by various authors (Craighead and Dasmann, 1966; de Vos and Petrides, 1967; Elton, 1958; Howard, 1965; Petrides, 1968; and Teer, 1971). The symposium entilted *Introduction of Exotic Animals: Ecological and Socioeconomic Considerations,* published by the Caesar Kleberg Research Program in Wildlife Ecology at Texas A&M University in 1968, also gives a good review of the matter as it relates especially to Texas conditions.

Stocking and use of foreign big game animals for sport hunting has been an important consequence of the economic value of game animals in Texas. Recent surveys of the important big game ranges in the state suggest that the number of ranches with one or more species of exotic, hoofed animals has increased at least tenfold since the end of World War II. The stimuli of the hunting lease system and commercialized harvest programs of the large ranching areas in south and west Texas seems to have produced the impetus for more ambitious introductions of big game animals from other continents.

Interest in big-game animals from foreign lands is not confined to the private rancher. Several state game and fish departments, notably those in the semi-arid southeastern United States, have programs of introductions that are designed to fill 'vacant niches' with game species.

Apart from the recreational and sporting values of these introduced animals, they also may be capable of producing meat and other products on the same ranges where conventional grazing schemes with domestic livestock are the chief land-use programs.

While quite a number of exotic ungulates have been tried in Texas, only eight species of large hoofed animals have succeeded in establishing themsleves in large herds without close husbandry.

Ramsey (1970) listed 26 species of introduced big-game mammals in Texas, of which only eight occurred in the hundreds in total numbers. The eight most important species were: axis deer, 6, 450 on 69 ranches; 4, 125 blackbuck antelope on 56 ranches; 1, 300 aoudad sheep on 40 ranches; 10, 000 mouflon sheep on 121 ranches; 10, 000 European wild boar on over 100 ranches; and 4, 000 nilgai antelope on seven ranches; 875 sika deer on 22 ranches; and 445 fallow deer on 43 ranches. It is worth mentioning that all of these animals, except the aoudad, are Eurasian in origin and that, at the present time, none of the large African antelopes and other bovids are successfully established in Texas. However, African species, including the impala, eland, gemsbok and kudu, are now being introduced and tried. Meanwhile, there are several ranches in Texas where one or several of the eight species listed above are established in sizeable numbers. Some ranches have sport harvest programs of economic importance, and other ranches are engaged in the production of brood stock for sale to landowners desiring to establish huntable populations.

Descriptions of four of the most important species and their uses follow.

Nilgai Antelope

The nilgai antelope or blue bull is the largest of the Indian antelopes, and it is the oriental representative of the larger Africa forms of tragelaphine antelopes. A grazing and browsing herbivore, it was first stocked in 1924, and it is now established in large numbers on parts of the King Ranch and adjacent ranches in south Texas. Its numbers have been placed at near 4, 000 head, and it has spread and is still spreading quite extensively from the orginal transplant site on the Norias Division of the King Ranch. A census of occupied nilgai range was made by helicopter in 1969 and 1970, and results show a density of about 9 animals per section on the Norias Division (Sheffield *et al.,* 1971) in a population of about 2, 300 animals. Population levels are somewhat lower on ranges outside the Norias Divison.

The animals are little hunted on the Norias, and they are obviously increasing to a point to where they must be used in some manner. Dr. E. D. Abies and others of our staff are working with meat qualities of the animal, and it would seem that this species has the highest potential of any of the introduced ungulates to furnish protein in a commercial program. Bulls attain weights of over 600 pounds; females are large at 400 pounds.

While the animal does not have large horns or horns fashioned into notable spirals or twists, the nilgai nevertheless is a handsome animal and has trophy value to sport hunters. The dark black coloration of the males with the white throat, stocking feet, and black and white markings in the ears given the animal an elegance. It does not have the graceful carriage of a deer. On the contrary, its bearing and large strong forequarters are attractive features.

Nilgai are not hunted commercially in Texas at this time. Brood stock is available from King Ranch for $750 per head.

Axis Deer

The axis deer or chital, another Indian form, is a very beautiful cervid with a handsome rack highly esteemed by trophy hunters. It has been stocked extensively in the Edwards Plateau, the Rio Grande and Coastal Plains, and in other ranges in the state. It has been established for several decades, and the history of its introduction is not known. Several ranches have populations of over 500 animals and one, the Powderhorn Ranch near Port O'Conner on the coast, has a very beautiful population of over 1, 200 animals. It is on this ranch, the Powderhorn, where our staff and students have studied the species rather intensively. The axis now occurs in feral populations in Bexar and Medina Counties where it has escaped from ranches. It was at one time put on the game list in Bexar Country but since has been taken off.

The most obvious value of the axis deer is its sport hunting qualities. A blocky and marvelously-antlered animal, the axis attracts hunters who pay very handsome prices for taking one. Where they are hunted, prices range up to $500 per head, and for exceptional trophy animals, the price may be even larger. The price of the hunt may also vary according to the services provided by the rancher. The animal has table qualities that are extolled by all who have eaten it. Its meat, like all cervids, is dry but finely textured and flavorful.

It appears that this animal will have a place in sport hunting in commercial hunting systems, but perhaps little value in producing meat in a commercial scheme.

Blackbuck Antelope

The blackbuck antelope is probably the most handsome antelope of all that have been brought from other continents for introductions into wild or semi-wild habitats. The black and white markings and the very long horns set on a black and white head make it a very desirable trophy. It is a small animal, the males rarely exceeding 100 pounds. It has little use in a meat program, but will be extremely valuable in sport hunting. A mature specimen, colored in black pelage and with large horns over 25 inches, will bring $750. The black, mature males are over three years or more of age and thus the problems in producing an exceptional trophy carry through several years. Some suggestion of social hierarchy in producing dark coloration is apparent when one examines the color of males that are harem leaders.

Aoudad or Barbary Sheep

The aoudad sheep is a native of the Atlas Mountains of North Africa. From an original plant of 42 animals in the Palo Duro Canyon in 1957, a herd of about 600 had developed by 1967 (Evans, 1967). Rams may reach 300 pounds or more, and this animal seems to be very popular with ranchers attempting to establish commercial hunting programs in a variety of habitats. They are known to be successful—existing without close husbandry—in semi-arid ranges of western Texas and in high rainfall areas in pine and post oak belts of East Texas.

Because it is seemingly so adaptable, I expect that it will continue to spread throughout the state much the same way as has the now bastardized mouflon sheep. Mouflon stock has interbred with all kinds of domestic sheep, and the result is a great number of crosses which are highly prolific and which have little value in sport hunting or as exotic game meat either.

The aoudad is a desirable trophy animal and in wild populations, as occur on many ranches and in the Palo Duro Canyon, it is a worthy object of hunting. It is wary and inhabits rough terrain and is extremely difficult to stalk. It seems important to say at this point that we should protect our native big horn sheep ranges from importations of this animal.

The sika deer, fallow deer and European wild boar are the remaining three species which are rather widely spread in the state. The sika is often held in close confinement or in company with other fed populations, and has not done as well as other cervids. The fallow is a park animal but can function in wild habitat. The wild boar is considered by many to be a pest because it destroys fences and some maintain that it will kill livestock. In any case, it has crossed with feral hogs and often shows only a small relationship to wild boar stock.

I am not prepared to state that game animals in Texas, or anywhere in highly developed countries, can become commercially important as producers of protein. It seems to me that we have the animals—cattle, sheep, goats—best suited to produce high yields of meat on most of our rangelands. Nonetheless, we should not overlook the very great amount of meat that is harvested by sport hunting each year. Over 22 million pounds of deer meat is taken by sport hunters each year in Texas. While a good part of it is ruined in the care and cooking of the meat, this total of 22 million pounds probably probably presents more than is produced from domestic livestock in many of the larger developing countries of the world. The introduced big game animals such as the nilgai antelope will supplement our production of meat on ranges of common use by livestock and wildlife. But, on the average ranch in Texas, these exotics will likely be more important as objects of sport hunting.

I do not believe that we can say unequivocally that commercial hunting programs with exotic animals are economically successful. Little information is available because the ranchers do not wish to have someone poking around in their business, for proprietary and business reasons. While these programs are questionable at the moment, commercial hunting for white-tailed and mule deer are successful and economically important to the rancher.

On the other hand, if these animals, or others could be successfully established in the arid and semi-arid ranges of the southwestern deserts of the United States and northwestern Mexico, their value as meat producers might be established. As suggested by some range scientists and geographers, fitting the animal to the vegetation might be a better approach than trying to fit the vegetation to the animal especially on some ranges that have been degraded or changed by man. For the time being, however, I see the uses of exotics in the sport hunting context.

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Paper No. 54

The Management of Large Mammals in Natal, with Special Reference to Utilization for Stocking or Restocking Purposes

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ABSTRACT

The major game reserves of Natal, South Africa, fall into two broad life zones—the highveld and the lowveld. Each has its own problems, which are described, and which may be attributed to restrictions imposed by artificial boundaries. Essentially, the numbers of large ungulates in the highveld are limited by environmental factors acting productivity. In the lowveld, however, the reverse is true, and past management has resulted in overpopulations of ungulates. These have been controlled very intensively, and the policy continues although it is a dynamic process and alterations are made from year to year. Methods developed to catch animals alive for redistribution are described, and the numbers controlled by both shooting and capture, together with the revenue accrued from sales, are provided.

INTRODUCTION

In this paper I shall be attempting to relate behaviour to management (which is, after all, the theme of the Conference), laying particular emphasis on the effects that management has had on the behaviour of large ungulates in Natal. Clearly, the problems and consequences are not unique, but have their parallels elsewhere in the world.

May I start by reiterating what is perhaps obvious to any student of wildlife management or to any conservationist ? It is that conservation and consequently management have exhibited a clear evolutionary pattern:

1. A natural ecological balance between primitive man and his environment.
2. A period of ruthless exploitation during which the prime object was economic gain or sport hunting.
3. The recognition of a need to preserve what was left of the natural heritage, and the enforcement of this need, sometimes to almost fanatical lengths, as evidenced by the destruction of predators.
4. A period of ecological enlightenment, in which the natural balance became better understood, and in which numerous management techniques were applied, often quite intensively.
5. Finally, a stage of commercial exploitation on a very rational basis, exhibited by tourism, sport hunting and game ranching.

In South Africa we are very largely in Stage 4 at the present, but are moving slowly into Stage 5. We are therefore vitally concerned with management, part of which of course is a need to understand behavioural aspects of the biology of game animals, as well as the effects which management policies have had, or are having.

Judging from experience gained, in particular, in the game reserves of Natal Province, it is clear that vital changes in behaviour, especially that of populations, have taken place in the 75 odd years of the existence of these reserves.

A brief statement of background is perhaps necessary at this stage. The earliest proclaimed reserves in Natal were established in 1897, at a time when the pressures for land had not yet reached a peak, but only after a great deal of shooting had taken place, resulting in the extinction in the areas chosen for the reserves of several species of large ungulates. After their establishment, pressures from settlers increased rapidly with the opening up of nearby land, and the situation today is that nearly all of the reserves comprise mere 'islands' surrounded by intensive settlement.

The result has been that, whereas before, the large game populations had been able to range extensively (and indeed there is clear evidence that seasonal migrations took place), today they are confined for 12 months of the year to only a remnant of their former range. The future management implications are obvious in that the habitat is subjected to year-round utilization—a situation which has, as we shall soon see, had diametrically opposite effects on ungulate population behaviour in two different habitats in Natal.

Coupled with this fact is that of the destruction of predators, in the belief that it was only by doing this that the herbivorous ungulates could be preserved. So was manifest stage 3 of the evolution of game management, and whilst it was not sound policy in the eyes of modern conservationists, the practice must not be too heavily criticised. This control of predators, embracing not only the large cats such as lion and leopard, but also hunting dog, jackal and baboon, continued until after 1950, before wisdom prevailed.

It is too much to hope that the situation will revert to that pertaining before the interference of man, and it must remain a basic tenet of conservation in almost any area throughout the world that some form of management in the form of habitat manipulation or population control will always be necessary.

This 'nettle' has been firmly grasped by the Natal Parks, Game and Fish Preservation Board, which is the body responsible in the province for the control of all wildlife— not only inside game and nature reserves.

THE PAST AND PRESENT

Firstly, a brief explanation of conditions in Natal is necessary. The altitude varies from over 3000 metres to sea level, with a wide range of habitats from Subalpine to truly tropical. Game reserves are so situated as to embrace these extremes, although regrettably there is little reservation in the intervening life zones. However these conditions, when considered in relation to the fact that game populations are restricted, have led to interesting problems which are far from being properly solved, and a good deal of improvisation has had to be employed with, so far, adequate results.

The Highveld Area. Only one major reserve is situated in this zone, namely Giant's Castle Game Reserve. It consists of very open grassland on rugged terrain, and is subjected to severe winters. During the winter the grass has a very low nutritional value and is unpalatable. Few ungulate species are endemic to the Drakensberg, although of those occurring in Giant's Castle, the blesbok *Damaliscus lunatus,*the black wildebeest *Connochaetes gnou.* and the vaal rhebok *Pelea capreolus* are typically highveld forms.

The first two mentioned are re-introductions to the reserve, whilst the third is a smaller antelope and has always occurred there. Little is known of the past habits of the blesbok and black wildebeest, before they were exterminated from Natal, but because of the nature of the vegetation, it is unlikely that the latter species could successfully have existed in the Giant's Castle area on a permanent basis. Certainly von Richter (1971) has shown that the area is very probably marginal to its distribution, as evidenced by the poor reproductive and survival rates. The same can be said of the blesbok population, which has shown a poor performance since its introduction.

Liebenberg (1964) quotes several early travellers, indicating that migration into the highveld grasslands in summer was a feature of the vast herds of game that inhabited the interior of South Africa. In winter they moved back towards the 'lowveld'.

Another important species which occurs in Giant's Castle is the eland *Taurotragus oryx.* This is a mixed feeder, although in this area it has adapted to an almost purely grazing habit. There are many people alive today who recall the fact that eland migrated to lower altitudes in the winter months, returning to the open plains and grasslands when the grass became palatable. Today this movement is restricted, and the animals can only repair to the lower ground within the reserve where limited browse is available. The results had been that the population has not increased to any extent, having remained very stable since it was first censused by air in 1962. Estimates made by residents prior to this date confirm this fact, as shown in Table 1. It would appear again that the rates of reproduction and survival are severely impaired by this existence—a result of management in the form of artificial restriction.

TABLE 1. ESTIMATES OF NUMBERS, AND CENSUSES OF ELAND IN THE NATAL DRAKENSBERG.

(Figures marked * are estimates, the remainder are results of aerial censuses)

Year	Number
1916	600*
1921	700-800*
1926	1, 000*
1962	703
1963	650
1964	817
1965	709
1966	777
1969	536
1970	682
1971	870

Those smaller ungulates species which occur in the area do not pose problems in management: there is no evidence of any serious decline in numbers or of over-utilisation of the habitat, and it must be concluded that they have achieved a reasonable balance with the habitat. Research is needed to establish whether the stability is due to spatial or nutritional reasons—or both.

Thus it is that highveld conditions impose a restrictive effect on population performances, whilst it will now be shown that the reverse is true of the lowveld.

The Lowveld Area. The vegetation of the lowveld is of the form of woodland of varying density, generally with a grass understorey. Severe winters are not a feature of this biome, and the grasses retain their nutritional value throughout the year, being of a different species composition to that in the highveld. The consistent high level of palatability has lent the general term 'sweetveld' to it, as opposed to the 'sourveld' which is applied to the higher altitude areas.

The presence of both grass and woody plants has meant that a wide range of ungulate species has evolved along with this habitat, to include pure grazers, mixed feeders and browsers. Traditionally, it is the lowveld which has become known as the main game area of Africa, the same—or similar—grass species occurring throughout most of the continent.

Because of the nature of the vegetation, the main problem in management of the lowveld reserves, including Umfolozi, Hluhluwe, Mkuzi and Ndumu Game Reserves, has been one of over-utilisation caused by overpopulations of game.

This fact became very evident in the 1950's after rigid protection had been enforced for some years. It resulted in the introduction of a policy of population control which initially took the form of shooting, although small numbers of impala *Aepyceros melampus* were caught alive for distribution to a few interested farmers. Prior to this time, one of the main reasons for there not having been any such problem was the policy adopted by the veterinary authorities in an effort to eradicate the tsetse fly, which was responsible for the transmission of a disease fatal to domestic stock and carried by game animals. Tremendous numbers of game animals were destroyed, as described by Vincent (1969) and Mentis (1970), particularly in Umfolozi Game Reserve.

Thus it was that in 1954, probably one of the first planned ungulate population control programmes in Africa was put into motion in Hluhluwe Game Reserve—planned that is with the benefit of the habitat as the ulterior motive. During the period August 1954 to May 1955, 729 wildebeest *Connochaetes taurinus* and 494 zebra *Equus burchelli* were shot in the area. Then in 1958 it was resolved that population control in Hluhluwe and Umfolozi Game Reserves should become an established management technique, and efforts were directed initially at wildebeest and zebra, but later also at warthog *Phacochoerus aethiopicus* and impala *Aepyceros melampus.* It was clear at this stage that the step was an essential one if habitat deterioration was not to continue, and the benefits thereof were soon evident. It is interesting to note that there was no real problem in so far as browsers were concerned. Furthermore, the control was based largely on estimated populations, and not on census and calculation of annual increments. The numbers of animals destroyed to date, including those shot specifically for rations are shown in Table 2.

TABLE 2. NUMBERS OF ANIMALS SHOT IN THE HLUHLUWE AND UMFOLOZI GAME RESERVES SINCE THE INCEPTION OF THE POLICY OF NUMERICAL CONTROL OF UNGULATES

Year	Species				
	Warthog	Wildebeest	Impala	Nyala	Zebra
1957	39	309	146	16	
1958	580	199	124	21	
1959	4,353	1,325	1, 330	501	577
1960	2,769	732	566	228	246
1961	1,154	741	441	5	9
1962	2,371	894	455	49	84
1963	2,408	954	456	15	73
1964	3,390	835	427	5	45
1965	1,811	1,209	1,283	176	333
1966	1,059	979	1,153	146	16
1967	827	694	586	1	1
1968	782	332	453	0	21
1969	1,842	274	438	0	18
1970	1,222	267	418	0	0

In Mkuzi Game Reserve, the predominant species has for many years been the impala. In the early 1950's small numbers of these animals were caught alive for redistribution to other reserves and to local farmers, who were already recognizing the advantages of having small herds for sport hunting and domestic use. This in fact was the start of an ever-increasing demand in Natal for live animals, and culminated in 1966 in the establishment of the first game ranch in the province.

The numbers of animals shot in Mkuzi Game Reserve are shown in Table 3. The large numbers controlled in the period 1963-1965 followed the realisation of the need for a drastic reduction in the population. Carcasses were sold on the open market.

TABLE 3. NUMBERS OF ANIMALS SHOT IN MKUZI GAME RESERVE SINCE THE INCEPTION OF THE POLICY OF NUMERICAL CONTROL OF UNGULATES.

	Species		
Year	Warthog	Wildebeest	Impala
1960	5	205	118
1961	17	307	237
1962	38	375	346
1963	32	201	1, 567
1964	7	267	4, 360
1965	138	506	3, 045
1966	159	191	845
1967	26	2	624
1968	109	1	691
1969	140	185	559
1970	103	193	284

In order to provide for the game ranching movement, the Natal Parks Board modified its game control policy to allow for the larger scale capture of ungulates, and to this end employed one man to develop satisfactory methods. Regrettably, the evolution of the capture technique has not been documented, so that it will not go amiss if it is described here very briefly.

At first it was done by means of nets, into which animals were driven, and in which they became entangled. This technique involved a good deal of manhandling of animals, often resulting in injuries to both captors and captives. Variations of this method included driving on foot, on horseback, and by vehicle. A significant breakthrough was the discovery that a blue plastic material provided sufficient of a barrier to the animals' movement to enable them to be trapped in a 'boma' or corral, constructed of the material, and enabling them to be subsequently brought down by sheer force of numbers and manhandled into travelling crates.

This method proved good for wildebeest and zebra, whilst impala continued to be caught by hand at night, with the aid of spotlights. Oelofse (1969) describes the method of catching with the use of blue plastic. Initially it was considered that blue had some 'magical' property, but it was subsequently found that the mere presence of a sufficiently high, opaque barrier, whatever colour—was sufficient to prevent animals from attempting to escape; this despite the fact that any animal could simply walk through the material. Bomas so constructed have been known to contain square-lipped rhinoceros for over 24 hours without water (Oelofse, pers. comm.).

The technique has been further perfected, so that at no stage are the animals handled, but are separated into manageable groups and driven up a ramp into waiting lorries carrying a wooden superstructure. Up to 15 wildebeest or zebra may be transported at once in this way.

The latest major development has been the introduction of a helicopter for use in driving the game into the capture bomas, as described by Oelofse (1970). This has enabled large herds of animals to be captured in a short period, and one of the best operations to date accounted for over 200 wildebeest in 20 minutes of driving. The loading operation of course is a more-time-consuming process. The helicopter technique has been used successfully on most species: wildebeest, zebra, impala, waterbuck *Kobus ellipsiprymnus,* and kudu *Tragelaphus strepsiceros.*

Warthog and Nyala *Tragelaphus angasi* require a specialised capture technique, as neither species is amenable to being driven by any means. The demand for warthog is very limited, although its potential as a meat producing animal is considerable. They are usually caught by placing nets over the sleeping burrows at night and stampedding them very early in the morning. Nyala, being primarily inhabitants of dense bush, have to be caught in small numbers by driving them for short distances into similar traps as are used for larger species.

Specially designed holding pens have been built to obviate handling, where any of the ungulate species may be kept for a period before they are taken by a buyer, who may not be able to collect the animals in the field, or until they are shipped to the overseas market. The latter course, whilst being lucrative, accounts only for a small proportion of the captured game.

The numbers of antelope captured alive for redistribution are shown in Table 4, and the revenue derived therefrom in Table 5.

TABLE 4. NUMBERS OF ANTELOPE CAPTURED ALIVE BY THE METHODS DESCRIBED IN THE TEXT, FOR REDISTRIBUTION.

(H/U = Hluhluwe/Umfolozi, M = Mkuzi

Year	Warthog	Impala		Wildebeest		Nyala	Zebra	Waterbuck
	H/U.	H/U.	M.	H/U.	M.	H/U.	H/U.	H/U.
1960			462					
1961			666					
1962			1,213					
1963			1,352					
1964			849					
1965			671					
1966	50	100	374	15		131	64	16
1967	166	7	592	107		66	129	12
1968	8	308	301	510		5	171	8
1969	6	911	788	527	327	18	344	5
1970	28	1,055	1,353	1,037	251	75	328	72

The capture of square-lipped rhino in Natal has been well documented (Player, 1967), and suffice to say simply that the technique has changed little in the past seven years, other than in the form of slight changes in the drug combinations (Keep, pers. comm.). The operation has proved to be an exemplary success in the re-location of a large species, not only to a large portion of its former range, but also to zoos all over the world.

The problem today with the species is to develop techniques of mass translocation. Capture should pose little difficulty, but the transport of large numbers is an exercise that must be carefully studied, particularly since the taming process is lengthy (up to six weeks), and it is unwise to consider transporting wild-caught animals over very great distances. Rochat and Steele (1968) describe the translocation of 74 white rhino over a distance of over 1600 km (1000 miles), occupying 36 hours and more. It may be possible to extend both time and distance of transportation of untamed rhino

TABLE 5. REVENUE DERIVED FROM LIVE SALES OF ANTELOPE CAPTURED IN NATAL GAME RESERVES

Year	Revenue	
	Rands	Dollars (U.S.)
1961/62	1, 232	1, 720
1962/63	2, 322	3, 242
1963/64	1, 558	2, 172
1964/65	1, 644	2, 298
1965/66	13, 229	18, 490
1966/67	17, 670	23, 200
1967/68	6, 460	9, 000
1968/69	7, 366	10, 305
1969/70	37, 931	52, 820
1970/71	64, 330	89, 580

under sedation, but the logistics of such an operation are enormous. The destinations of square-lipped rhino that have been translocated are shown in Table 6, and the revenue derived from their sale in Table 7. Rhino sent to other conservation authorities in Africa are provided free of charge.

TABLE 6. DESTINATIONS OF RHINO CAPTURED IN UMFOLOZI GAME RESERVE SINCE 1961

Destination	Number		
	Male	Female	Total
Natal Reserves	26	23	49
Natal landowners	13	15	28
Other S. African reserves	133	106	239
Other S. African destinations	23	26	49
Other African reserves	90	109	199
Other African destinations	7	7	14
North America	36	48	84
Europe	34	43	77
Asia	8	7	15
Total	370	384	754

At present the management of large wild ungulates in Natal Game Reserves is a cooperative effort between the scientists and field staff. The latter are responsible for drawing attention to areas that are posing problems, and to the game species concerned. The scientists undertake continual monitoring of the habitat and of the population dynamics of the animals. Annual censuses by helicopter are carried out at the end of the dry season, in August or September, although it is hoped that in the near future sufficient understanding of the population processes will enable such counts to be held only every two years. Consultations between field officers and scientists

TABLE 7. REVENUE DERIVED FROM SALES OF SQUARE-LIPPED RHINO TO ALL BUT GAME CONSERVATION AUTHORITIES

	Revenue	
	Rands	Dollars (U.S.)
1962/63	48, 404	67, 600
1963/64	46, 545	65, 150
1964/65	38, 144	53, 510
1965/66	29, 122	40, 950
1966/67	15, 043	21, 010
1967/68	18, 012	25, 200
1968/69	3, 400	4, 750
1969/70	9, 289	13, 000
1970/71	140, 943	196, 900

result in the formulation of a policy for the ensuing calendar year, detailing the numbers of animals to be removed, and enabling the administrative staff to allocate live game to applicants.

Capture takes place between April and September, due consideration being given to the rutting seasons of the various species, so that reproduction is not disturbed, and animals are already pregnant when captured. The season ends before the animals are too heavily pregnant, as experience has shown that serious losses to adult and unborn animals may take place if stresses are imposed upon the females at too late a stage

THE FUTURE

No major changes in the present policies for the management of large ungulate species in Natal game reserves are envisaged in the foreseeable future, although research into behaviour and population dynamics may result in changes of emphasis.

In the highveld where the habitat is a limiting factor, manipulation thereof may be necessary to improve the 'turnover' of populations. Such manipulation may take the form of artificial 'licks' to supplement the nutritional value of the grasses, or it may involve management to encourage growth of woody species to provide winter browse, particularly for eland.

In the lowveld an increasing population of predators, particularly of lion and cheetah, will influence very significantly the numbers of ungulates to be controlled. This however, will entail merely the modification of an existing policy.

A further technique, which will involve the knowledge of a good deal more of the behaviour of ungulates, and which is well worth more consideration, is the establishment of temporary exclosures—possibly with the use of plastic as a fairly cheap and rapid means of providing a barrier—for the reclamation of areas that are showing signs of over-utilization.

Water is an effective means of moving ungulates from an overgrazed area to one that has not been utilized, and in the Kruger National Park in Transvaal Province, the provision of artificial waterpoints is an established policy. This technique of course depends upon the availability of natural sources of water.

Fire too has proved a useful management tool, although its efficacy extends only for the period that the regenerating grass retains its succulence, before the animals return to their more favoured areas. Used in conjunction with temporary exclosures, there is a good deal of potential for game managers to investigate.

The tendency for herbivores to favour certain areas for grazing seems to depend upon a number of features including cover, soils, grass composition and water. Such areas may be maintained in a state suitable for themselves by suppressing the development of climax grasses and encouraging the often more palatable sub-climax and annual forms. Investigation of all aspects of this phenomenon as a manifestation of behaviour patterns is a necessary development for efficient management.

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Paper No. 55

Behaviour and Domestication of the Musk Ox

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ABSTRACT

Definitions of domestication have traditionally employed criteria such as taming, selective breeding and phenotypic attributes to distinguish 'wild' and 'domesticated' animals. These criteria are often inadequate and obscure the fact that 'domestication' describes patterns of human behaviour rather than attributes of animals. It might be more profitable to distinguish 'harvested' from 'husbanded' animals. In harvesting human populations adapt the necessary aspects of their socio-economic structure to permit the exploitation of populations of particular animals; husbanding involves modifying the behaviour of the animals to integrate their exploitation into an existing economy.

Recent domestication of the musk ox (*Ovibos moschatus*) involves, *inter alia,* taming musk oxen and maintaining them on farms so that their underwool (*qiviut*) can be collected annually and used to establish a textile industry in Arctic villages. The logistics of this process are discussed at length with particular reference to those behavioural attributes of musk oxen which facilitate its husbanding. Finally, some aspects of introducing a new animal and industry into traditional economies in the Arctic are discussed from the viewpoint of human behaviour.

Contemporary civilization arose largely as a result of the ingenuity of our remote ancestors in domesticating certain animals and plants, and its continuation and expansion depend increasingly on the ingenuity of some of our contemporaries in improving traditional domesticates and in finding new candidates for intensive exploitation to feed and clothe the growing population of the world. It is, therefore, disconcerting to realise that so basic a phenomenon as domestication has consistently escaped satisfactory definition. The reason is, of course, obvious: that everyone knows what is meant by domestication, or thinks that he does. Whilst it may be true that most people can distinguish some domesticated animals from some wild animals (although even this distinction becomes increasingly difficult beyond the limits of traditional 'westernised' agriculture), this is not to say that they can define domestication. The antiquity of this strange situation is well illustrated by comparing one of the earliest major treatises on animal and plant domestication (Darwin, 1896) with a recent volume on the behaviour of domesticated animals (Hafez, 1962), for neither troubles to define the phenomenon which it discusses so lengthily and often so well.

Attempts to define domestication have tended to concentrate on three classes of variables: man's control over the animals in question (Zeuner, 1963; Bökönyi, 1969); the physiological, morphological and behavioural attributes of contemporary domesticated animals, which are presumed to have resulted from their domestication (Darwin, 1896; Hafez, 1962); and the services performed by man for his domesticated animals (Loeser, 1969; Rohn, 1972). The following may be taken as a representative zoological definition of domestication: 'I would define the essence of domestication as: the capture and taming by man of animals of a species with particular behavioural characteristics, their removal from their natural living area and breeding community, and their maintenance under controlled breeding conditons for profit' (Bökönyi, 1969: p. 219). The limitations of such definitions have been discussed elsewhere (Higgs and Jarman, 1969; Wilkinson, 1972a) and will not be repeated. The emphasis among many modern authors on the high degree of variability of domesticated animals compared with wild representatives of the same species, which is attributed nowadays to man's preservation of economically or aesthetically valued mutations and to increased gene-recombination resulting from man's interference with natural breeding patterns, is directly attributable to Darwin (1896), although Mayr (1966: pp. 133-4) *inter al.* has emphasised that the supposed distinction is less clear than commonly supposed.

Animal behaviour, including human, has received some attention in studies of domestication. Hahn (1896) and Sauer (1952) suggested that prehistoric animal domestication might have had a ritual or religious motivation. Childe (1952) and Zeuner (1963) adopted the 'propinquity theory', according to which desiccation in the early Postglacial forced men and animals in some parts of the Near East to congregate near watering places and thus provided a stimulus for the initiation of symbiotic relationships, culminating in domestication in its modern form. Behavioural attributes in individual species of animals, notably gregariousness and adaptability, have been considered a limiting factor in establishing close man-animal relationships. Several authors (e.g. Scott, 1962; Jewell, 1969) used these criteria to erect a taxonomy of 'domesticable' and 'non-domesticable' animals, which has been assumed by some (e.g. Chard, 1969) to be equally relevant to modern and prehistoric man.

Whilst the behaviour of animals long since domesticated has been studied in detail (Hafez, 1962), the behavioural aspects of initiating new man-animal relationships have received only superficial attention—largely because there have been so few recent attempts at domesticating new ungulates. A recent experiment in domesticating the musk ox (*Ovibos moschatus*) provides an opportunity to examine the behavioural interactions of men and animals involved in establishing a new form of exploitive relationship.

The process of domesticating the musk ox has been discussed at length elsewhere (Teal, 1958, 1970a; Wilkinson, 1971, 1972a), and some stages of this process will be described in detail below. Experience in domesticating musk oxen serves to support Spurway's (1955) neglected observation that the adjective 'domestic' refers to the behaviour of *man* towards certain animals. Using human behaviour as the chief criterion for defining domestication does not imply that there are no observable phenotypic differences between some domesticated animals and their free-living counterparts, but only that these are inadequate for taxonomic purposes, granted even Johnson's (1970) thesis that perfect taxonomies are unattainable. Defining domestication according to behavioural criteria does, however, pose serious difficulties for prehistorians who must rely for the most part on fragmentary 'cultural' and osteological debris from which to infer patterns of behaviour in past human and animal populations. I have considered some means of resolving this conflict for prehistorians elsewhere (Wilkinson, 1972a).

One major advantage of a behavioural definition of domestication is that it clarifies the often-forgotten fact that the distinction between 'wild' and 'domesticated' animals is in fact a distinction between *human* patterns of exploitation. Whilst at the extremes the difference between these is obvious, and there is a clear and definable difference between, for example, the intensive management of dairy cattle in Britain and the hunting of many African ungulates, both in terms of the patterns of human behaviour involved and their effects upon the animals concerned, there is also an area of 'overlap' in which the distinction is obscure. Ethnographically, this 'grey' area is well instanced by some reindeer-and caribou-based economies. Thus, the Tokma and Ilimpiy Evenks kept and exploited reindeer which were classically domesticated in the sense of being tamed and selectively bred, but they also exploited significant numbers of caribou. The Kamchatka Evenks, on the other hand, kept large herds of domesticated reindeer, but they exploited almost solely caribou, reserving their own herds for social rather than subsistence purposes. Many Chukchi groups kept and exploited only domesticated reindeer, whilst Canadian groups such as the Central Eskimo exploited only wild caribou (Eidlitz, 1969). The distinction between systematically exploited herds of caribou, followed by migratory or semi-nomadic hunters, and systematically exploited herds of reindeer, which differ principally in that the animals are more or less tame, that a proportion of the males may be castrated and that some degree of control is exerted over their breeding patterns, is at best marginal in any other than behavioural terms; certainly, from an economic viewpoint they may be considered equivalent, if not identical.

Instead of thinking in terms of 'wild' and 'domesticated' animals, I believe that it would be more accurate and more profitable to think in terms of husbanding and harvesting economies. Husbanding economies would be those in which the resources (plant or animal) basic to the economy are integrated into the socio-economic structure of the society concerned, which often, but not invariably, implies that they are domesticated in the classical sense of having been tamed and selectively bred. Harvesting economies, on the contrary, would be those in which the relevant social and economic aspects of the life of the society were integrated with the life-cycle or seasonal pattern of the animal species or population(s) on which subsistence was based. Using these criteria, it is clear that all the categories of nomadic reindeer/caribou-based economies described above would fall into the category of harvesting economies, since the annual cycle of the human societies was modified to permit the exploitation of the animal rather than *vice-versa.* The fact that some of the animals were tamed and selectively bred is relegated to secondary taxonomic importance in this scheme of classification, although such criteria might conveniently be adopted to subdivide the larger classes. Such an approach to the classification of economies and of animals themselves has an important bearing on contemporary assumptions and practices in wildlife management and on the present legal status of so-called wild and domesticated animals. Some of these implications will be considered elsewhere (Wilkinson, in preparation).

The domestication of the musk ox is an attempt to transfer the exploitation of this animal from its traditional harvesting pattern to a new form of husbanding. This change is necessitated by the belief that the most rational way in which to exploit musk oxen is to use their underwool, known as *qiviut,* as the basis for a uniquely arctic textile industry, rather than to exploit them in the traditional fashion for their meat and hides. Achieving this transition involves the following steps: capturing and taming wild musk ox calves; transferring these calves to farms and forming them into cohesive social units; accustoming them to their new dietary regime and maintaining them in health until they are mature and can be bred; deliverying, taming, weaning and maintaining the successive crops of selectively bred calves; and collecting their underwool when it is shed annually each spring. The second stage of the experiment, the transfer of domesticated musk oxen from the experimental farms where they are presently maintained, to the social and economic context of Arctic villages, will involve only one important change as far as the animals are concerned: that at least some will be ranged rather than kept on enclosed farms. From the viewpoint of human behaviour, however, this stage will be more important and more interesting, since the associated technology will have to be adapted to the new behavioural contexts represented by Eskimo villages. Human behaviour will not be considered for the experimental stage, since all the participants are either professional farmers or research scientists, in whose culture behavioural patterns appropriate to husbanding economies are so well developed as to excite neither comment nor interest.

The history, present status and objectives of the Musk Ox Project have been reviewed elsewhere (Teal, 1970a, b; Wilkinson, 1971, 1972a) and will not be repeated. Instead, I propose to take each of the steps involved in domesticating the musk ox and to consider some of their behavioural aspects.

There are three ways of capturing wild musk ox calves for domestication, each one of which utilises to advantage a characteristic behavioural trait of the musk ox. The first makes use of the celebrated defensive semi-circle or 'hedgehog' formation adopted by musk oxen threatened by predators, and which was presumably developed as an effective defence against wolves, the only serious non-human predator of musk oxen. When threatened by humans, especially with dogs or on vehicles, musk oxen take up a defensive semi-circle facing their attackers, in which the adult males occupy the most vulnerable positions to the fore and rear and young animals stand safely between the flanks of their mothers. Since it is possible for a man to approach to within a few yards of such a formation with little danger of being charged, it is easy to kill the animals even with primitive weapons and indeed to kill them very selectively. The defensive formation is not broken even when one or more animals are killed, so that it is difficult or impossible to retrieve carcasses or calves without slaughtering entire herds, which was in fact a frequent practice when capturing calves early in the present century (Hone, 1934). Typically, musk ox calves remain with the corpse of their slaughtered mothers, and calf-recovery offers no difficulties once all the adults have been killed. More recently, concern for the survival of musk oxen prompted a search for 'safe' methods of capture which involved neither slaughtering the animals nor endangering their lives by the use of drugs; Teal (1958, 1970a) devised two methods which have been used successfully on several occasions and both of which take advantage of behavioural traits of the musk ox. Upon sighting a potential predator, musk ox herds may run for some distance before adopting their defensive formation. When they do this, their flight follows a consistent pattern: after running for a short distance, the males turn through 180 degress in a sharp anti (= coun ter) -clockwise direction and come to a halt facing the predator. The females and young continue to run a little further and then they too turn and slowly make their way to rejoin the bulls. The purpose of this tactic is presumably to ensure that the adult males are at all times between the predators and the females and young. With a helicopter it is possible to split a single cow and her calf from the main group as they make their turn; once this is done, the separated animals will not attempt to rejoin the herd directly, but will pursue a long, circular course, commonly covering several miles, whilst the herd waits for their return. The adaptive signficance of this strategy is obscure. It may be that if they were to attempt to rejoin the herd directly they would certainly be intercepted by the predators, whereas the tactic adopted gives them a reasonable chance of escaping unobserved, but this is no more than speculation. If pursuit of the separated animals is continued, the cow and her calf will eventually take refuge with their backs against a cliff or large rock, and the pursuers can climb up above them, rope the calf and frighten away the mother by shouting and throwing pieces of earth and stones at her. The second 'safe' capturing method is rather simpler and involves driving entire herds into lakes with the use of aircraft or helicopters and men on the ground. Musk oxen are good swimmers and show little reluctance to enter the water. These two methods have been used on eight capturing expiditions, and only one calf has been accidentally killed during capture.

Wild musk ox calves are normally captured for domestication at the age of five months when large enough to avoid injury during capture yet still small enough to be manhandled with ease by a single person. At this age it is also possible to distinguish the sex of the calves even from an aircraft several hundred feet above the herds, for female calves have a distinctive reddish urine stain on both the hind legs. Once separated from their mothers, many calves show neither fear or nor aggression towards man; others, however, are timid or aggressive, and these animals must be tamed. Taming is accomplished by feeding the calves willow branches (a favourite food) and milk-substitute from cans fitted with rubber nipples, as well as by continuous association between the animals and their handlers for the first days after birth. The first feeding normally occurs some twelve hours after capture and recalcitrant animals are force-fed. By the second or third feeding most calves will take the nipple voluntarily and many will follow their handlers like pet dogs if given the opportunity. Obviously, the process of taming takes advantage of the strong bond between mother and offspring, especially through the use of suckling to reinforce the attachment to and dependence on the handlers, but it may also use to its advantage a behavioural trait limited to slowly developing animals, the major social contacts of which are formed only a long time after birth. Musk ox calves are born in May or early June, and throughout most of their range they continue suckling for at least twelve months, since they are too small and weak to forage for themselves in the first winter of life, although dentally and digestively capable of surviving on a diet of solid food probably by three months of age. During the period of suckling the social bonds of the calves are limited to some or all the members of their peer-group, probably to sporadic encounters with older males and perhaps to contacts with females who act as guards for groups of calves while their mothers graze (this behaviour has been observed among captive musk oxen, although the females in question do not suckle young other than their own; whether or not it occurs in the wild is unknown). It seems probable, therefore, that musk oxen begin to form their most important social contacts as yearlings. If it is correct that young musk oxen remain with their parent-herds (but not with their parents) until the age of three or four years, when the females join breeding harems and the males join bachelor-herds (Pedersen, 1936), it seems probable that they remain 'open' to the formation of new social bonds at least until four or five years of age. The preceding comments apparently have a bearing on the ease with which young musk oxen can be tamed. The upper age-limit for taming is undetermined, although Palmer and Rouse (1963) reported that animals captured as yearlings in East Greenland in 1930 and transported to a farm at College, Alaska became quite tame and tractable, although less so than calves captured at the same time.

The preceding discussion is also relevant to the next stage in the process of domesticating the musk ox: creating new social units from the captured animals after they have been transferred to the experimental farms. No difficulties have been encountered at this stage, despite the fact that the calves have been taken from distinct social units in the wild. Dominance hierarchies are developed in both young and mature musk oxen; in the former they appear to be related to size rather than to sex. Interestingly, preliminary observations suggest that, within the distinct age- and sex-groups which are kept separate on the farms, the dominance hierarchy will depend on where within the confines of the farm the animals are. Thus in the large summer pastures there may be a given order of ranking, but his may vary in the smaller night-pens, again in the holding-pen outside the barn, and again in the small pen in which the animals congregate after they have passed through the barn for weighing and physical inspection. It must be emphasised, however, that more detailed observations are required to confirm this suggestion. From the viewpoint of the domesticator, however, the most relevant point is that there appears to be no incompatibility between animals from different social units in the wild. This may be related to the fact that immature males, and perhaps also certain females, have to leave the protection of the herds during the rutting season. Since single musk oxen are very vulnerable to predation, selective pressures must have operated in favour of a high degree of tolerance towards unknown individuals, so that temporary protective social units could be formed. Nonetheless, it seems that the time factor may be critical, for Lent (1971) reported that groups of wild musk oxen transplanted from Nunivak Island to the Alaskan mainland have frequently fragmented upon release, thus rendering the individuals, who are almost entirely immature animals, very vulnerable to predators and decreasing the chances of males and females meeting and breeding once they are mature. One explanation for this observation suggests itself: that the animals, which came from many different social units on Nunivak Island, were given insufficient time or opportunity to become acquainted with one another prior to their release. If future transplants are undertaken, it would seem to be desirable to construct corrals at the proposed points of release and to leave the animals undisturbed in these for several weeks before liberating them.

Close contact with humans does not seem to prejudice the social status of musk oxen, unlike the situation reported by Tankerville (1948) for the 'wild' park cattle of Chillingham, England: 'If a young animal is ... handled by man, the others will immediately kill it unless it is removed from the herd.' The importance of gregariousness in creating and maintaining new social units in captive animals has been alluded to frequently. Russian experiments in domesticating the elk or moose (Knorre, 1961) have shown, however, that this aspect of the behaviour of wild animals is more plastic than commonly supposed. The Russian studies suggested that gregariousness can be enqouraged by training and by providing a sufficient abundance and density of fodder to permit or stimulate the maintenance of large population aggregates at all seasons.

Adaptability to new surroundings is obviously important if an animal is to be domesticated and it has been facilitated in the case of the musk ox by the apparent unimportance of territoriality. Although many musk ox groups and individuals appear to occupy comparatively restricted areas for long periods, the length of their stay and the size of the area exploited seem to be a function of the availability of forage rather than any strong 'social' attachments to such areas. Maintaining musk oxen on farms is also facilitated by the sedentary nature of musk ox social groups, none of which have been reliably reported to undertake seasonal migrations, although some groups do move short distances from winter to summer feeding quarters. In the case of musk oxen on the experimental farms movements of any sort are impossible, for the farms are enclosed by fences. If open-range farms are ever established, the tendency towards seasonal movements can probably be reduced or even eliminated by locating the farms in areas with an abundance of food at all seasons, as well as by 'attaching' the animals as calves to the location of farms through the provision of salt-licks and small quantities of supplemetal winter fodder. The success with which this can be accomplished was strikingly illustrated by the Russian experiments with the moose, in which such training eradicated even the inclination to migrate seasonally (Knorre, 1961).

No difficulties have been encountered in accustoming captive musk ox calves to their diet of milk-substitute and hay during their first winter and to the diet of hay in winter and natural browse and grazing in summer as they mature. The captive musk oxen in Alaska and Quebec receive long hays such as timothy and brome, but Oeming (1965) reported that musk oxen can deal equally successfully with short hays such as clover and alfalfa. There is some dispute concerning grain feeding, for Teal (pers. comm.) found that large quantities of grain could not be digested by the captive musk oxen in Alsaka, whereas the Alberta Game Farm (Oeming, 1965) and the Copenhagen Zoo (Andersen and Poulsen, 1958) both report successfully feeding significant quantities of grain as part of the staple diet of their animals. Nonetheless, the important point is that young musk oxen at least appear to be receptive to a large variety of foods. It is uncertain whether this is because they are too young to have developed strong preferences or whether older musk oxen would display a similar catholicity of taste if they were to be captured. Palmer and Rouse (1963) conducted feed-tests on a group of captive musk oxen at College, Alaska, in the early 1930's, and they found that the following foods were accepted: alfalfa hay, alfalfa meal, alfalfa molasses meal, brome hay, oat hay, pea hay, vetch hay, vetch-oat hay, native redtop hay, native sedge hay, native marsh-grass hay, oats, barley and potato peelings; and Teal (pers. comm.) reported that captive musk oxen in Vermont developed a strong preference for apples.

The food-intake of musk oxen is very conservative, which is an obvious advantage if the animals are to be raised either commercially or for subsistence. Early records (Palmer and Rouse, 1963) estimated food intake at 1. 8 lbs per 100 lbs live-weight for maintenance and 2. 5 lbs per 100 lbs live-weight for fattening. These estimates are in reasonable agreement with figures recorded at College, Alaska, in January, 1970 (Wilkinson, unpublished) as follows:

calves: 2.63 lbs hay per 100 lbs live-weight

cows: 1.41 lbs hay per 100 lbs live-weight

yearlings: 2.31 lbs hay per 100 lbs live-weight

bulls: 1.67 lbs hay per 100 lbs live-weight

Unfortunately, these figures are not for air-dried fodder and do not include an estimate of the amount of food wasted, which may be as high as 20% and is probably greater for calves and yearlings than for older animals. Weight records from this period indicate that the consumption represents an intake intermediate between that for maintenance and that for fattening. These data are important from a behavioural viewpoint, since there is reason to believe that some sheep, for example, show a behaviourally conditioned reduction of food consumption in winter even when unlimited food is available, and weight records from the College musk oxen suggest that the same may be true for the musk ox.

Although musk oxen are not generally believed to select reindeer lichen (*Cladonia rangiferina*) as a preferred food, it is interesting to note that it forms an important part of their diet at the Copenhagen Zoo (Andersen and Poulsen, 1958). It is clear that the catholic taste of wild musk oxen, recorded, for example, by Tener (1965: p. 45), is an obvious advantage to their domesticators, although it is little more than an unsupported assumption that herbivores with more specialised tastes cannot be domesticated. Nonetheless, it seems improbable that such animals, or those involved in complex vegetational or grazing successions (Bell, 1971), would be obvious candidates for domestication in the traditional sense, since they can be exploited more efficiently by strategies such as game farming or simple hunting. Clark (1972) and I (Wilkinson, 1972b) have discussed this point with reference to African prehistory, for it offers one explanation for the apparent absence (or failure) of large-scale animal domestication in sub-Saharan Africa.

Breeding captive musk oxen in zoos has been relatively unsuccessful, although calves have recently been born in Whipsnade Zoo (Polar Record, 1971) and at Calgary Zoo

(W. McKay, pers. comm.). Few difficulties have been reported, however, when the animals have been raised under conditions approximating more closely those of their natural environment (Palmer and Rouse, 1963; Oeming, 1965, 1966; Wilkinson, 1971). Breeding captive musk oxen is facilitated by the fact that any bull will breed with any cow. It cannot be inferred from this that permanent or semi-permananent partnerships are not formed in the wild, but simply that that they are not mandatory for successful copulation to occur. Hale (1962) implied that such behaviour, which he termed 'promiscuous', might be essential before an animal could be domesticated. It seems probable, however, that this aspect of behaviour is flexible.

In the wild, musk oxen breed between mid-August and early October. The precise time of the rut is probably controlled by a combination of photoperiodic, temperature and perhaps nutritional factors. On the experimental farms breeding is strictly controlled, both with respect to which bulls mate with which females and to the timing of the breeding. Selective breeding is designed to increase the quality and quantity of the annual *qiviut* yield, to promote docility and to reduce the size of the musk ox. Mature males and females are kept apart throughout the year and the breeding groups are formed only in early September, to ensure that no calves arrive before the beginning of May, by which time the weather is normally mild. Parturition involves few difficulties and all births occur in the open. Musk ox cows show no tendency to seek isolation, although a few may move a short distance away from the herd shortly before the calf is dropped; nor are they disturbed by the presence of observers, although Lent (pers. comm.) reported that wild cows on Nunivak Island are very prone to such disturbance and may even abandon their calves occasionally, even when the observers do not approach very closely and act with caution. Although most births occur without complications, captive cows react well when assistance is required, and it has proved possible to reposition several calves to facilitate delivery without bringing the cows to the barn or restraining them in any way.

The relationship between female musk oxen and their offspring has been discussed elsewhere in these Proceedings (Lent; Vol. 1, Paper No. 1: pp. 16ff.). With few exceptions musk ox cows are excellent mothers but they also permit their herdsmen to handle their calves within a few days of birth. There has been only one instance when a calf was rejected after incautious handling, and it was in fact accepted once again some six hours later. There has also been only a single instance in which a female rejected her calf at birth, and this involved a primiparous cow at College, Alaska, in 1971. In fact, calves are rarely handled before they are weaned, except to give them a protective injection of bovine serum at the age of three or four days or in the event that they are injured or fall sick. Weaning takes place in early September, when the calves are three to four months old. The animals show signs of stress for some 36 hours after the young are separated from their mothers and bellow incessantly at one another and at their herdsmen. The process of taming is identical to that described earlier for wild calves; in some respects it is more difficult for calves born on the farm than for those captured in the wild, for the former can hear and sometimes see and smell their mothers after separation. Despite this, most calves are tame and accustomed to close contact with humans a few days after weaning, although a small proportion remains timid for several months after weaning. There is only one instance in which a calf was weaned at birth (by Female no. 58 at College), the calf who was rejected by her mother in 1971. For some time the mother was milked daily and the milk fed to the calf, supplemented by milk-substitute. Later the calf was fed solely on milk-substitute and hay. This animal has consistently shown a much higher degree of tameness than any of her contemporaries; even at the time of writing, after she has been with her peer-group for over two months, she still displays a preference for human company to that of other musk oxen. It has been stated frequently (e.g. Zeuner, 1963; Grigson, 1969, 1969) that prehistoric pastoralists are likely to have reduced the size of their animals through conscious or unconscious selection since smaller animals would have been more docile than large. Whilst it is difficult to make accurate assessments of 'personality' in animals, there is no apparent correlation in musk oxen between small size and increased docility or tractability; on the contrary, in the case of the bulls it seems more common that the tamest animals within each age class are also the largest.

The purpose of domesticating the musk ox is to use its underwool or *qiviut,* which is the finest and the rarest natural fibre in the world, to establish an Arctic textile industry, which will contribute to alleviating the poverty of many villagers of the region and permit them an alternative to welfare payments as a source of income. Musk oxen shed their *qiviut* annually in spring and the bulk of it is normally collected during the final two weeks of May, although the entire collection period may extend from mid-April until mid-July. When the idea of domesticating the musk ox was first proposed, sceptics believed that it would be impossible to collect the wool. Some believed that it would be impossible to tame musk oxen, whilst others thought that it would be necessary to shear the guard hairs forming the outer coat with the wool and that the two would become intextricably mixed. In practice, the animals can be tamed easily and permanently, and there is no necessity to shear the guard hairs since only the underwool is shed and this can easily be collected by hand. Plucking the underwool is greatly facilitated by the fact that, at least at this season, musk oxen have no aversion to being touched by man, except in the anal and genital regions. Musk oxen are a 'contact species' in that their defensive formation and the closely packed units formed during severe winter storms bring them into frequent body-contact with one another—a factor which doubtless makes *qiviut* collection easier; on the other hand it is interesting that at other seasons musk oxen do not like humans to touch them anywhere except on the face, especially near the pre-orbital gland.

The preceding observations have concerned musk oxen at present on the experimental farms at College, Alaska, Fort Chimo, Quebec, and Bardu, Norway. The next stage of the experiment will be to establish commercial musk ox farms in the villages of the Arctic. These will be under the direction of specially established co-operative organisations, the first of which has already been incorporated in Alaska. Procedures on the commercial farms will be similar to those already described but the musk oxen will have less frequent and intensive contact with humans, and it is hoped that, at least in some cases, the animals will be ranged rather than maintained on enclosed farms. Two points of behavioural interest arise: whether the musk oxen will become feral as a result of the decreased frequency and intensity of human contact; and whether it will be practicable to range them. Since no commercial farms have yet been established, speculation must be limited, although evidence from other experiments may offer useful guidelines. In the case of newly domesticated moose (Knorre, 1961), it proved possible to range the animals and even to overcome their tendency to migrate annually. The moose were 'attached' as fawns to the farms by teaching them to associate them with food and salt blocks, and also by bringing oestrous females to the farms, where they conceived and calved. Posselt (1963) reported that tamed African elands which were permitted to range freely returned frequently, and even daily, to the corrals in which they had been raised. Another danger frequently cited is that domesticated animals are said to show a strong tendency to run with their wild counterparts when these co-exist in the same areas, and such appears to have been the case with reindeer and caribou (Leeds, 1965). On the other hand, neither the moose nor the eland discussed above seem to have shown this tendency and the former seem even to have attracted their wild counterparts. The same may well hold true for tamed and selectively bred musk oxen; on the rare occasions when musk oxen have escaped from the enclosed portion of the farms by accident, they have shown no tendency to wander. Comparisons with transplanted wild musk oxen, which have dispersed rapidly over large areas upon release, cannot be adduced with confidence, since these animals were not tamed and had undergone the multiple traumas of capture, holding in small crates, often for prolonged periods, and transport by air.

The process of feralisation is poorly understood, but is frequently described as the loss of certain behavioural patterns, notably tameness, and the reversion to 'wild' patterns of behaviour. However, even where the moose or the eland has no significant contact with humans, both appear to remain tame and docile, and the same is true for cattle and sheep, for instance, in many parts of the world. Several musk oxen in Vermont were isolated for a prolonged period, after which all were as tame as previously and participated willingly and with good memory in the farm routine of weighing and physical examination. It is anticipated that on the commercial farms the musk oxen will be checked at least weekly by their herders, that they will be rounded up for calving and wool collection and for the breeding season, and that calves born on the farm will be weaned and tamed in the same manner as calves born at the experimental stations. The evidence cited above suggests very strongly that this will be sufficient to maintain their tractability and docility. The problem of contact with wild musk oxen does not exist in Quebec or in Norway, and in Alaska it is unlikely to exist for many years, assuming that the wild musk oxen transplanted to the mainland survive and increase their numbers. Should the problem arise, it seems difficult to predict whether the wild musk oxen will attract the domesticated or *vice-versa.* The evidence cited above suggests that the probabilities are about evenly balanced.

The role of human behaviour in domesticating the musk ox will be considered only briefly, and the discussion will be limited to the second, as yet only anticipated, stage of the project—the establishment of village musk ox farms.

The chief prerequisite for the successful transfer of domesticated musk oxen to the socio-economic context of Arctic villages is obviously a social perception among the proposed recipients of the value and desirability of the new pattern of economic activity. Formal statements from official organisations in Alaska (e.g. Arctic Slope Native Association, Resolution 67-1, 1967), from individual communities (e.g. Nunivak Island, Nelson Island, Povungnituk), and from individual village residents, provide a good quarantee that the required perception does exist. It seems safe to say that at any given time existing patterns of economic and social activity will not be abandoned or modified in favour of innovations unless the real or imagined benefits to be derived from such innovations are overwhelming. In the case of prehistoric animal domestication, the evidence suggests that this was in fact the case at some point in time after the first domestication (although this may have been many millennia), since the wide spread of domesticated animals beyond the range of their wild progenitors, together with the rise of the first urban civilizations, are well evidenced in the archaeological and historical records. The situation regarding the modern domestication of the musk ox, seen from the viewpoint of the present and the immediate future, is less dramatic, since it seems improbable that herding domesticated musk oxen and producing textiles from their underwool will revolutionise either the social or the economic basis of life in the Arctic, although they will provide a very considerable supplement to existing forms of economic activity. Some of the economic aspects of musk ox domestication have been discussed elsewhere (Wilkinson, 1971). Briefly, it is anticipated that in the immediate future a relatively small number of families will make a large annual income as herdsmen, but that most of the earned income will be derived from a 'cottage' industry producing textiles from the *qiviut.* Such an industry is already operating in eight Alaskan villages and individual women are earning up to $1, 500 p.a., compared with an average per capita income in 1966 of $800 p.a. in rural Alaska (Arnold, 1968). Since the work involved is lucrative and is not restricted to particular age- or sex-classes (there are already a few men producing knitted textiles), and since it does not involve leaving homes, families and villages, it is easy to see why the value of the domesticated musk ox has won social acceptance.

Granted this situation, it is clear that the objective of transferring domesticated musk oxen to the villages of the Arctic must be to minimise the associated change in existing patterns of social and economic behaviour. Present indications are that such congruence can be achieved. Firstly, the sedentary nature of musk oxen permits their being herded on a year-round basis within the framework of the existing pattern of settled life in villages. Modern methods of transport, especially snowmobiles, make it easy to check and control herds within a several-mile radius of a village, and the distance to be travelled will normally be less than that travelled to check traplines in many villages (in some cases it may be possible to combine the two activities). The lack of such congruence was, in my opinion, one of the major factors responsible for the failure of the reindeer industry in Alaska earlier in the present century. This industry could not be pursued effectively without adopting a nomadic or semi-nomadic way of life, but the economic benefits and social status attached to reindeer herding were insufficient to stimulate such a drastic change in existing economic and social behaviour. Within the annual cycle of subsistence activities and cash-employment in Arctic villages, there is also no clash between musk ox husbandry and other activities. There are two busy periods associated with herding musk oxen: the period in spring when calving must be supervised and the *qiviut* collected; and a period in September and early October when selective breeding has to be organised and supervised and when the calves must be weaned and tamed. In both cases, most of the work will be carried out by the chief herdsman and his assistant, who will be paid a sufficiently large salary to make them independent of most subsistence activities except for the prestige and pleasure associated with participation: since two herdsmen will be employed, one will be free at most times to participate in three activities. This system has been applied very successfully at the Fort Chimo musk ox farm, where it was found that both herdsmen had ample time for hunting, fishing, sealing and visiting. In the case of *qiviut* collection, additional labour will have to be employed as herds increase in size. This labour force will require little training, and women and children can safely be employed for these tasks if either necessary or desirable.

The textile industry will also involve no conflict with other activities, for the *qiviut* is cleaned and processed commercially (mainly to avoid undue expense), and the finished yarn is distributed to villages or to individuals as they require it. Each woman (or man) knits in her own time as subsistence and household activities permit, and it is already clear that variations in subsistence activities account for seasonal fluctuations in the volume of finished products submitted to the Alaskan Musk Ox Producers' Cooperative. Since knitters are paid by the Cooperative as soon as finished garments have been received and checked, and not when the products have been sold, an immediate cash return for work—a prime requisite of most village residents in the Arctic and an interesting behavioural analogy to traditional activities such as hunting, in which there is an immediate return for energy expended—is achieved.

Whilst it is difficult and dangerous to make predictions in a situation as fluid as that which pertains in the modern Arctic, the preceding discussion suggests very strongly that the behaviour of men and musk oxen can be integrated into a new and mutually profitable form and one which falls into the category of husbanding rather than harvesting.

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Paper No. 56

Management Implications of Behaviour in the Large Herbivorous Mammals

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INTRODUCTION

Since man first pursued animals he has been a student of animal behaviour. In all hunting cultures the reputation that arose from success in the hunt and the survival value this brought to the individual, his family or his social unit has been of social and selective importance. The more intimate relationship between man and animals associated with captive rearing and animal husbandry required even more detailed knowledge of animal behaviour.

Thus a substantial part of the knowledge of feral and rural man has concerned itself with such aspects of animal biology as the nature of the foods sought by different species, the daily and seasonal movements of important animals, their response to the presence of man, the ways that their peculiar characteristics could be turned to man's advantage as a hunter. Interest in the roots of wildness and the ways in which the animals' capacity for adaptive behaviour and learning could be used to train animals to man's use required much more detailed understanding of health and disease, of nutrition and nurture, of response to impoundment and many other features of the behaviour of the relatively small group of animals that were domesticated.

Understanding of these attributes of animals, empirically gained by early man, was adequate to the needs of human density at that time. The application of the methodology of science, however, has greatly expanded the sophistication of our understanding and has distributed it over a much wider spectrum of animals. This increased understanding has been accompanied by a growing concern for the plight of many species whose survival is threatened by burgeoning human population.

Despite rapid extension of our knowledge of animal behaviour over the last thirty years, our understanding is still fragmentary and still involves only a small fraction of the larger mammals.

Central themes are now discernible, but the extension of our inquiry to a wider group of species is revealing an increasingly complex series of variations upon these themes.

The purpose of this review is to focus attention on the many behavioural features of ungulate mammals, reported to this Symposium, that have direct or indirect potential for improving our management of large wild herbivores.

I will review these under the following headings:

1. Strategies of range occupancy
   (a) Variations on the themes of territoriality, home range and nomadism
   (b) Special requirements and their influence on distribution
   (c) Social constraints upon density
2. Behaviour of neonates in relation to dam and physical environment
3. Feed selection and interspecies compatibility
4. Response to physical alteration of the environment by man
5. Tameability and controlability
6. Social constraints upon harvest and management
   (a) The role of the aged in the maintenance of tradition
   (b) The role of the separate senses in establishing critical distance

(c) Structure and dependence relationships within groups

(d) Sex ratios and reproductive efficiency

7. Behaviour and techniques of research

8. Behavioural constraints upon non-consumptive use.

While it is obvious that understanding of the finest details of the behaviour of animals we seek to manage may be the key to success in our efforts, one must nevertheless recognize the limitations of this knowledge. The order of priority for large mammal conservation must recognize as fundamental a place to live that provides the specific needs in food, water, shelter and special facilities, and, as well, protection from overkill.

As long as agriculture removes living space, war destroys habitat and decimates wild stock, as well described by Mendelssohn (Vol. 2 of these Proceedings, Paper 40, p. 722 ff.) referring to gazelles in Israel, or the developers have free run of natural areas, behavioural data have little to contribute to conservation.

If, however, societal affairs are orderly, if peace prevails; if we recognize the important place of these creatures in the human environment and have as our goals to optimize production, to restore species locally extinct, to ensure that viable populations exist even if only on small refuges, then behavioural information is most useful.

1. STRATEGIES OF RANGE OCCUPANCY

(a) Variations on the themes of territoriality, home range and nomadism

The least formalized strategy of range use would be random movement throughout the year by both sexes and all ages. However, few ranges are sufficiently homogeneous or few species sufficiently adaptable to make this type of strategy a useful one in their adaptive repertoire. Some populations of African elephants, as described by Laws (Vol. 2, Paper 26, p. 9), come close to this pattern but only where water is widely distributed and feed is evenly dispersed. Here the nomadic unit is of two types: the lone male or small group; and the matriarchal family unit of five or more individuals probably related to the senior female.

The difference between herd nomadism and migration are important in several respects. Both are probably strategies designed to make use of regions where the adequacy of resources varies seasonally or from year to year, in ways which make possible the survival of a larger population by a moving pattern of use rather than a sedentary one under which maximum population would be determined by capacity at the time when the limiting resource is minimal.

Many northern ungulates are seasonally migratory—most wild sheep populations, wapiti (*Cervus elaphus*), moose (*Alces*) and odocoileine deer in mountainous terrain, as well as pronghorn (*Antilocapra*) and saiga (*Saiga*). In most of these, population units have well-defined seasonal ranges and move between them in a predictable way. In all of them the winter range is the scarce resource and all that have access to mountains evince acrophilia, which leads them to remain at the highest possible altitude on the winter range slopes. This behaviour is most strongly evinced by the males and in them is one feature leading to a higher mortality rate.

The caribou and reindeer (*Rangifer*) populations of the tundra and subtundra areas also are migratory, but the degree of attachment to the same winter ranges appears to be less precise. It might be said that some Arctic *Rangifer* populations are nomadic within vast but discrete ranges, each serving one or more panmictic herds but with little interchange between herds on adjacent ranges (Bergerud, Vol. 2, Paper 29, p. 552; Kelsall, 1968). This pattern of herd definition and range use can lead to great differences in age structure, turnover rate and population trend on adjacent areas of approximately identical carrying capacity. There is nothing in the behaviour of the caribou to suggest that it has ever departed from this pattern.

The arid lands of Africa also have nomadic components, as for instance the oryx (*oryx spp.*), wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), the plains zebra (*Equus burchelli*) and the Thomson's gazelle (*Gazella thomsoni*). On the plains of East Africa where these species abound, rains while seasonably predictable are local (Bell, 1971). This feature has led the migratory plains game to follow the rains, moving with the seasons from grassy plains to open savannah and forest edge by traditional routes modified to make use of precise localities where rain has fallen in amounts sufficient to stimulate new plant growth. There are features in the behaviour of both wildebeest and Thomson's gazelle that suggest that these species descended from more sedentary ancestors. I refer, in particular, to the transitory male territories set up quickly whenever the herd pauses. In all of the species mentioned there are sedentary populations where conditions permit.

Comparable seasonal influences in Ceylon have produced a similar pattern of movement in the Asian elephant (*Elephas maximus*), as shown by McKay and Eisenberg (Vol. 2, Paper 39, p. 708).

The oryx and eland are probably more truly nomadic than the other species mentioned, as they are less dependent upon free water. The latter indeed is probably the most highly evolved socially of the African antelopes, in that it is alone in substituting male rank hierarchy for territoriality in any of its forms (Estes, Vol. 1, Paper 8, p. 183). This gives the eland unique advantages in game ranching, as it more nearly corresponds to cattle in behaviour and thus presents opportunity for somewhat similar management.

Obviously, species with migratory-cum-nomadic habits require ranges of very large size. In addition, the area must include the seasonal components and opportunities without which the herds cannot survive. Management of such species therefore imposes unique demands that require new patterns of range allocation such as the preservation of migration corridors connecting areas of seasonal importance.

The American bison (*Bison bison*) is an example of a species that has been totally displaced from its former range by man. It survives only as protected 'specimen' herds.

The zebras (*Equus burchelli* and *E. zebra*) are probably unique in being nomadic but harem forming.

A number of species are described as evincing male territoriality closely similar to that characteristic of many species of passeriform birds. The territory is breeding ground and feeding ground for the incumbent male either through the breeding season, if there is such, or throughout the year.

The white rhinoceros (*Ceratotherium simum*) (Owen-Smith, Vol. 1, Paper 15, p. 341), Defassa Waterbuck (*Kobus defassa*) (Spinage, Vol. 2, Paper 33, p. 635), Grévy's (*Equus grevyi*), dik-dik (*Madoqua kirki*), are all in this category. In each of these only the adult males are territorial while the rest of the population roams over the territories of a number of males within a herd home range. In most of these species the subadult males leave the female herd and form groups of their own. Where such occurs the bachelor herds are usually excluded from the male territories and if these represent the choicest environment two consequences arise. First, the bachelor herds are forced into less suitable areas and are likely to experience increased mortality from a number of sources. Secondly, the nursery herds of female and young gain less competitive access to the choicer range areas defended by the territorial males.

Vicuna (*Vicugna vicugna*) and several of the harnessed antelopes form harem groups that occupy territories throughout the year. In all these the young males, and in the vicuna the young of both sexes, are ejected from the territory to become nomadic. The young females either remain with the harem or join another.

The forest-inhabiting duikers (*Cephalophus*) of Africa (Rails, Vol. 1, Paper 4, p. 114), the small Asian cervids *Muntiacus* and *Tragulus*, and probably the neotropical cervid *Mazama*, have the extreme of territoriality, in which one male and one female occupy and defend an area, or each sex occupies and defends a territory against others of its own sex (Eisenberg and McKay, Vol. 2, Paper 30, p. 158). From this the young of both sexes are ejected shortly after weaning.

Estes (Vol. 1, Paper 8, p. 183) states that 29 species (i.e. 42% of the African bovids) are solitary and apparently monogamous. If the territories are larger than the food resource would permit, species in this category may not be as productive under game ranching circumstances as are herding, polygamous species.

The final variation is the 'lek' form of territoriality discovered and elucidated by the Buechner (Vol. 2, Paper 49, p. 853) in the Uganda kob (*Adenota kob*). In this species only a small proportion of the males are at any one time holders of the small leks that are densely clustered upon traditional breeding grounds. Large herds of mixed age and sex inhabit rangelands centred upon the lek areas. Each of these herds appear to constitute a deme, probably the offspring of the males of that breeding ground. The leks are breeding grounds only, as they are in such lek-holding birds as sharp-tailed grouse (*Perioecetes phasianellus*) and sage grouse (*Centrocercus urophasianus*). All breeding takes place on the leks.

This strategy gives rise to a very select fraction of the males holding leks and from these the females tend to favour only a few as mates. Thus this pattern may provide for highly selected male genetic input.

It has been suggested that the confinement of males within relatively small and sharply-defined territories serves to protect the proestrus females from too much disturbance by over-zealous courting males, (e.g. in *Antilocapra.* see Bromley and Kitchen, Vol. 1, p. 356). This is certainly one of the consequences of territoriality but there is no demonstration of its importance to the species. The ewes in the non-territorial bighorn sheep (*Ovis canadensis*) are herded and harrassed constantly during the day or so prior to estrus, frequently by groups of males. During estrus they are served repeatedly, usually by more than one male, up to as many as 50 times in a 24-hour period (Geist, 1971a), but there is no indication that these are forced services, nor that there is a relationship between amount of disturbance experienced by the female and her subsequent well-being or fecundity.

A number of management constraints arise from each of these strategies of range use. The requirement for male territories or for harem territories appear to be reasonably precise; the boundaries tend to persist over many years in those species that have been studied in this way. Thus if management is directed toward encouraging a maximum density it can probably only succeed when the requirements of a territory are understood and can be manipulated. An important item of information concerns the features that govern minimum area of a territory and this in the long run will govern the predictable attainment.

In general the male territories, because their special requirements are more precise than those of the herd range, are likely to be limiting in the management sense. This will be particularly true of lek-breeders. Thus the male territories will require special protection against take-over for other uses by man, also against frequent disturbance as by hunting, highways or low flying air traffic, or even by tourists. Furthermore it is usually territorial males that fall victim to hunting and poaching.

In the horned ungulates, males approaching senility will possess horns of maximum size. From the standpoint of trophy hunting therefore, the old males, no longer capable of maintaining a territory, will be available and select. Their removal will be of no consequence to the maintenance of the population. It many species, e.g. waterbuck, giant sable, kudu, etc., they are likely to be solitary. Sinclair's finding (Vol. 2, Paper 36, p. 676) that male African buffalo may have a long post-reproductive life, during which they are frequently solitary, indicates that here is a surplus class in the population that can be removed without reducing the productive capacity of the herd. Their removal by hunting will therefore present added recreational challenge and may be done with minimum disturbance to the herd. Removal of a surplus of females will require a different strategy.

Within the ungulate species it is possible to recognize two categories upon the basis of the pattern of dispersal of young. Some species, usually solitary or territorial species, disperse their young. In these the young are vulnerable to many forms of mortality arising from this displacement into habitat that is unsuited to the species or exposed to unusual hazards, such as hunting, poaching, predation or seasonal shortage of feed or water. Even so, the 'dispersers' are constantly providing young to colonize new habitat or to re-enter former range now restored to usefulness. In other words, these species are equipped to respond quickly to new opportunities.

On the other hand, the social species which conserve their young present a more difficult management situation. Re-created range will be slow to re-colonize and the task of re-introduction will bear behavioural limitations peculiar to these species (Geist, 1971a).

(b) Special requirements and their influence on distribution

Not too much has been reported upon the special requirements of some ungulate species that will to some extent influence distribution and perhaps abundance. Each species has its food preferences, water requirements, its response to the presence or absence of cover. Some species, as the Cape buffalo, are relatively non-specific in their demands for facilities. They are therefore adaptable to many kinds of environments and broadly distributed. The African elephant also has a wide range of tolerance.

Of the rather special requirements only water is amenable to management within the limits of economic strictures. Small springs can be successfully developed to produce large amounts of water through many months or year round. Thus, where a water source is limiting range occupancy, it may be possible to provide it.

At the other extreme, some species such as the red and black lechwes (*Kobus leche*) and reedbuck (*Redunca arundinum*) are closely tied to the reed beds associated with permanent wet land, as are the klipspringer (*Oreotragus*), the mountain goat (*Oreamnos americanus*) and others to rocky terrain. The extent of these special habitat types will serve to set limits on distribution and abundance of such species.

Many migratory herds of barren ground caribou return annually to about the same areas to give birth (Kelsall, 1968). These have been described as having distinctive attributes that apparently attract the parous females. We do not know how essential these areas are to the maintenance of the herd; whether indeed they could as readily give birth somewhere else and are merely following a tradition which has lost its importance. Bergerud (Vol. 1, Paper 20, p. 395) makes no mention of special birth facilities required by caribou in Newfoundland. But you do have them for mountain caribou.

Estes (pers. comm.) refers to the important role of termite hills in the feeding regime of the giant sable antelope in Angola. Here the critical element is apparently grass of unusual nutritive content growing in these highly fertilized areas. If this is so, such circumstances could be artificially provided in an area of intensive management, or in an area such as a park or reserve especially dedicated to maintaining the species.

(c) Social Constraints upon Density

I have already commented upon some of the obvious implications of social organization upon the density achieved by ungulates of different social types.

It is axiomatic that highly territorial species in which males and females acquire and defend fairly large territories will be able to achieve relatively lower densities than species tolerant of crowding. This will not be true if the species has evolved so as to defend a territory only large enough to provide a safe amount of feed for the territory-holder and his family group during years of scarce food. It will be particularly restrictive if the basis of the territory is a scarce resource, such as water, which would provide more than is needed by the territory owner. However, water is usually a common property resource, even among ungulates, and is seldom included in a territory restricted to the exclusive use of the resident male.

Apart from distribution patterns that limit overall density, there are other social influences that are well known in some species of mammals.

Mutual avoidance reaction may be operative in non-territorial ungulates as it is in certain carnivores such as *Felis concolor* (Hornocker, 1969). It may well be involved at the group level in undisturbed African elephants. Feeding behaviour that leads to the avoidance of ground contaminated by urine and excrement reduces the carrying capacity of an area. The extent to which this is operative between species rather than within species has not been reported. If it is usually an intra-species repugnance, we have here another sound reason for mixed species populations, rather than the encouragement of single species, if high density with maximum utilization of range resources is an objective (Kiley,Vol. 2, Paper 31, p. 606).

A number of unrelated concomitants of population density have emerged. Thus Estes (Vol. 1, Paper 8, p. 183) comments upon the amount of time spent by social species on the 'alert' rather than feeding. In such species, lone animals or those in small groups spend a significantly greater proportion of their time watching and listening for danger than do those in large groups. This could have importance in the nutrition of the animals in low density, dispersed populations.

Markgren (Vol. 2, Paper 42, p. 756) finds that in moose, where the sex ratio is normally closer to 1 : 1 than in deer of the general *Cervus* or *Odocoileus* or *Rangifer* types, only where densities are high can very low proportions of males to females be tolerated without reduced birth rate. In this species the amount of time spent in courtship and pair bonding, along with the highly synchronized estrus, makes wide searching for a mate by either sex impossible. There is, however, suggestive evidence that the North American moose may be more effective in mate search than the moose of Scandinavia. In North America both sexes use advertising calls to extend their contact orbit—a behaviour not found in Scandinavia.

Several behavioural features may act in antagonistic fashion. Thus increased density in social species finds increase in the time spent relaxed rather than alert. On the other hand, there may be an increase in antagonistic behaviour. Beyond an unspecified critical density, numbers may interfere with effective mother-offspring bonding and give rise to ineffective mothering. At the same time the individual young in a large group may be less conspicuous and less subject to predation loss than if alone with its mother or in a small group.

Populations of low density may also suffer the loss of important genetic material and of traditions essential to the effective use of the habitat.

2. BEHAVIOUR OF NEONATES IN RELATION TO DAM AND PHYSICAL ENVIRONMENT

In general the newborn young of the large herbivores can be divided roughly into those species which follow the mother very soon after they are born (followers, or *nachfolgen* type) and those that secrete themselves and are visited periodically by their mother (hiders, or *abliegen* type: Walther, 1961, see also Lent, Vol. 1, Paper l,p. 31). Among the North American species *Odocoileus virginianus* and *hemionus*, *Cervus canadensis*, *Alces*, and *Antilocapra* are among the *abliegen*, while *Bison*, *Ovibos*, *Rangifer*, *Ovis* and *Oreamnos* are follower species.

Lent (Vol. 1, Paper 1, p. 19), in his extensive review of the behaviour associated with birth and the subsequent period of mother-young bonding, has indicated a number of aspects that can have significance to those who seek to manage ungulates in the wild, on game ranches or in captivity.

The need for privacy at time of birth varies, and its significance even to those social species that usually seek it is not well known. In general it can be expected that privacy at birth is probably most important among solitary or semi-solitary species and least in such highly-mobile dense-herding kinds as American bison, wildebeest or barren ground caribou. The critical issue is the amount of time needed to establish a firm bond between the mother and her newborn. The establishment of mutual recognition, the initiation of appropriate following or joining behaviour, nursing and other forms of mutual response, involves the full catalogue of sensory input and steady reinforcement through a critical period. If this opportunity is denied through overcrowding with loss of privacy, through harrassment by predators, tourists, air or ground traffic, there is likely to be an increased incidence of desertion, of inadequate recognition by either mother or newborn of the other, inappropriate nursing behaviour, inhibited milk flow or other forms of maladjustment, the end product of which will be increased loss of the young. The bond is more rapidly formed by the mother than her offspring, and more effectively by the experienced female than by the primiparous one. However, it is the time required by the slower partner of the learner pair that must govern the conditions provided.

There is a possibility also that a female which has failed to establish a satisfactory bond with her newborn on 2 or 3 successive births may be permanently impaired and thus removed from the production pool of the population (Kiley, Vol. 2, Paper 31, p. 603). All these considerations point to the importance of constraints when one plans for situations in which ungulates are exposed to man-made disturbance. If the births are usually concentrated in special time and places, as they are in caribou, protection can be focused appropriately. Where there is a diffuse season of birth, though the danger of major interference with the reproductive input of an entire herd as a consequence of local and time concentrated disturbance is less, the problem of how to provide adequate privacy will extend over a longer time and may require some restriction of access on the part of tourists, to provide for a planned sequence or ' ribbon of sanctuary areas' available throughout the entire period of birth.

The essential period of private contact between mother and young (the 'critical period') may be as short as 5 minutes (goat) or 45 minutes (Grant's gazelle), one hour in caribou (Lent, Vol. 1, Paper 1, p. 38), or as long as six hours in *Antilocapra* (Prenzlow, 1964); thus detailed information on the species specific characteristics of the neonate period can be important to intensive management. Musk ox seem particularly vulnerable to disturbance at this time of birth, as a consequence of their prolonged critical period.

The amount of disturbance tolerable after the critical period but during the hiding period, of species with this habit, has not been studied but could be important. This may be of special concern in species with a very long period before the young begin following their mothers. This may extend over three or four months in some of the antelopes (Lent, Vol. 1, Paper 1, p. 25).

3. FEED SELECTION AND INTERSPECIES COMPATIBILITY

Few of the presentations to this symposium deal with the feed selection of different species co-inhabiting the same ranges. Selection of feed plants and parts of plants has been the subject of several other studies. Cowan (1943) has referred to the degree of feed separation evinced by bighorn, Rocky Mountain goat, caribou, moose and black-tailed deer in the Rocky Mountains of Alberta and British Columbia. He revealed essential compatibility on joint use of large areas. At the same time the elk or wapiti is known to have extensive overlap in feed selection and habitat occupancy with all these species.

The ungulates of Africa, by virtue of their very long period of evolution in multi-species associations, are more specialists in their feed selection (Casebeer and Ross, 1970), and consequently lend themselves to a greater variety of compatible co-occupancy of given areas of rangeland. At the same time, designing for efficient range use in the African region requires more detailed information and more refined planning, in terms of the species mix and the relative number of each component, than in more youthful biomes.

As an example of the successful application of the species mix technique in the operation of a game ranch, Johnstone (Vol. 2, paper 52, p. 890) lists 17 species of big game managed for meat and trophy production on a 57, 000-acre ranch in Rhodesia. It is anticipated that 10% cropping per annum will be the sustaining rate. That should yield about 21 lbs of meat per acre, a yield well in excess of the production when the same area was managed for cattle.

Deane and Feely (Vol. 2, Paper 51, p. 882) describe a similar strategy of multi-species stock on a 2, 700-acre ranch. Here 14 big-game species are used to provide a dramatic example of the potential compatibility of many species on even small areas. It is doubtful whether the selection of species was done on the basis of information upon plant food selection by the wild species to be used. However, the mix is stated to be more productive than the usual monoculture of domestic livestock. The total yield of game meat after 5 years of management is 12-14 lbs per acre. This is the product of a biomass of just over 100, 000 lbs per square mile, where 60, 000 lbs is sought as a long-term average.

4. RESPONSE TO PHYSICAL ALTERATION OF THE ENVIRONMENT BY MAN

Bergerud (Vol. 2, Paper 29, p. 559) with specific reference to free-ranging caribou, suggests that the behavioural repertoire contains elements that are relatively fixed responses to such stimuli as the arrival of a hunting man or of a traditional predator (wolves). Such responses he regards as of ontogenetic origin and relatively automatic. Other elements of behaviour are generalized responses to environmental stimuli that are changeable and demand an adaptable response mechanism. The latter involves learning and provides for behavioural adaptation to new situations. Examined against this hypothesis most species appear to possess components of their environmentally induced responses falling into both of these categories.

Bergerud further suggests that appreciation of the category of the response can provide a basis for predicting the probable reaction of a species to the presence of man and such artifacts as roads, railroads, aircraft and automobiles. As stated by him: 'The seriousness of human disturbance should be considered in the light of the perceptive and escape adaptations caribou have evolved in association with wolves. For example, a road or a building are not factors that have been prior phylogenic contingencies'. He points out that caribou have no aversion to roads, respond by temporary alert to the noise of a car, but flee from the motion of a car. Similarly low-flying aircraft and helicopters provide alarming motion but the noise of high-flying aircraft does not. Klein (1971) also comments on the response of caribou to unusual stimuli. In addition to motion he found caribou to evince alarm in the presence of overhead electric power lines and to avoid crossing bridges. In the latter instance it may be that the hollow sound may be similar to that of thin ice and thus elicits the avoidance response appropriate.

Tourists in the African National Parks will have noted the lack of response to automobiles by most large wildlife. I suggest that this results from the similarity between size and shape of the automobile and their evolutionary companion, the rhinoceros. Where cars are used by hunters to approach game, a learned response is developed.

Johnstone and Deane and Feely (Vol. 2, Papers 52 and 51) have commented upon the problem of shooting game for butchering on game ranches and suggest that night shooting with powerful lights prevents the development of a learned flight response to the presence of automobiles.

There are few species that do not learn to flee at long distance from man where shooting of large mammals is prevalent. Bergerud (Vol. 2, Paper 29, p. 579) suggests that caribou are vulnerable to hunting because of their innate curiosity and of a failure to detect and to flee from a stationary man any more than from a stationary wolf. They do learn quickly to respond to human odour.

Few, if any, wild ungulates learn to respond appropriately to altered natural features that have acquired dangerous characteristics in the alteration. Thus deer and other species attempt to swim irrigation ditches as they would rivers and drown when unable to climb out; moose populations confronted with a newly-flooded reservoir across their migration route will attempt to swim it and drown, due to the debris that litters the shoreline. Where such modified natural features are entered into an environment, care should be exercised to include also recognizable signals of the hazard: drift fences to direct moving animals away from the danger area, or escape facilities incorporating clues designed to lead the animals into the appropriate recognition and response.

The expanding search for fossil fuels and the resulting demand for the construction of pipelines through the wilderness range of barren ground caribou in Alaska and Canada, are already demonstrating the need for meticulous studies of the behaviour of this species. Child (Vol. 2, Paper 46; p. 805) reports preliminary observations of caribou and reindeer in contact with various types of simulated pipelines. It is not unexpected that these animals avoid the strange artifacts and often refuse to go either over or under them despite the provision of apparently suitable opportunity.

More recently, I have seen individual caribou and small groups that have become accustomed to these pipelines and use underpasses freely. They seem to cross over only if they can see over. It is tempting to suggest that ways can be devised to train, or lead caribou herds to pass both over and under pipelines without delay, but the techniques have not yet been devised. Perhaps the restoration of main caribou trails across the disturbed area, the scattering of dung or urine or the scent from the leg glands might serve to allay fears. Identification of the criteria that identify caribou travelways to the animals and the introduction of these into the disturbed area, all offer potential solutions.

I have seen no references to the role of such major artifacts as pipelines in the reduction of populations of large mammals of the desert areas of the Middle East.

In considering the impact of major artifacts (highways, pipelines, electric power lines) into the range of the large wild ungulates of open landscapes, one is concerned not only with the outright obstruction of normal movement of the population, deflection away from important resources or denial of access to part of the normal range. Of equal concern is delay, induced even where the animals sooner or later negotiate the obstruction. Delay and disturbance can have an important effect upon the energy budget of animals (Geist, 1971a).

Some of the real but subtle consequences of disturbance are to be seen in the observations of Baskin (Vol. 2, Paper 27, p. 530), Kiley (Vol. 2, Paper 603) and Gauthier-Pilters (Vol. 2, Paper 28, p. 542) that unguarded herds of reindeer, sheep and camels respectively are in better 'condition' than herds under the direct control of men. Herding apparently causes disruption of feeding, resting and ruminating. It may increase the intake of poisonous plants and reduce grazing selectivity (Kiley, Vol. 2, Paper 31, p. 607. Furthermore, this author observes that even mild harassment in domestic herds increases fighting, hypersexual mounting and wounding, and depresses milk production. She emphasizes that an occasional loud noise is more disturbing than frequent predictable loud noises.

Vincent (Vol. 2, Paper 54, p. 907) reports from South Africa that stress imposed on wild adult females during late pregnancy led to serious losses of adult and newborn animals. The stress was associated with live capturing.

All these studies point to the general principle that optimum utilization of a habitat, and optimum production from a population, can only be realized in a known and predictable social and physical environment. The introduction of a wide variety of surprises induces avoidance reactions and excitability. These lead to greater energy demands and inefficient use of habitat (Geist, 1970b).

From this viewpoint certain management objectives for National Parks become obvious. For instance, it is important to habituate the animals to people, to normal transportation vehicles and other potentially disturbing things. To encourage wilderness is to arrange for inefficient range use.

It is equally important not to introduce new sources of disturbance. This is of particular concern during periods of the year when food is scarce and energy demands high as they may be during northern winters. One thinks of snowmobiles or other O.R.V's in National Park or game refuges, as a case in point, even if used only by wardens.

5. TAMEABILTTY AND CONTROLABILTTY

Even though wildness is known in some species to be a heritable characteristic (Leopold, 1944), many if not all species of big game can learn to accept man as a harmless associate. Indeed, Parker and Graham (1971) make the point that wild ungulates can live in proximity to man, if man permits. The problem then is one of human behaviour. There is no comment upon this feature by any of those contributing to the present symposium, but Geist (1971b) dwells on the point at length.

Hand-reared young of most species, if not all, learn to 'imprint' upon man and to evince no fear of him; they may indeed become highly aggressive toward him, or court him. This capacity to learn to accept the near presence of man without alarm is different from the capacity to adapt to the close contact situations of domestication, including herding, haltering, harnessing, saddling, packing or milking. There must be a wealth of experience with this feature of African ungulates that is unrecorded. It is well-known that the Indian elephant quickly adapts to domestication, while the African elephant is reputed to be less amenable. Eland are reported to domesticate fully, permitting haltering and milking. Plains zebra have been trained to harness. I have no success in persuading, Odocoileine deer to accept the halter and to be led by it; on the other hand, *Rangifer* responds quickly and *Alces* (Heptner and Nasimovic, 1968) may do so but only in experienced hands.

Gilbert (Vol. 1, Paper 11, p. 247), in his account of the influence of foster rearing of young fallow deer (*Dama*) upon the behaviour of these individuals as adults, remarks that young foster-reared or completely domestic goats were still wild toward man. My experiments with the rearing of newborn wild-taken, black-tail and white-tail deer support this finding. Young raised by hand-reared and completely docile females remained almost as wild as wild deer, whereas fresh caught young, hand-reared, became docile, though with marked individual and racial differences. Clearly there is, in some species, a major element of inherited wildness which is modified by experience.

Another aspect of this topic is the extent to which the young of different species will submit quietly to physical restraint—such as being carried. From experience with a limited variety of species, I am tempted to suggest that the 'hider' species will permit restraint during the hiding phase but not after that, even when imprinted on man. I would expect the 'follower' species to resist handling from birth.

Early in human history, man discovered that certain species could be easily impounded or directed toward traps or slaughter areas. Mendelssohn (Vol. 2, Paper 40, p. 725) reports this as part of the Bedouin attack on the gazelles (*Gazella dorcas, G. subgutterosa.* and *G. gazella*). Similar techniques were used in parts of arctic North America with the barren ground caribou and doubtless by other peoples to capture a variety of species. This may well have been one beginning of paddock rearing.

It may be that domesticability, as with zoo breeding, rests upon the selection of rare behavioural genotypes from within a population heterozygous for wildness, and cultivating these for man's use. Research on this aspect of wild-living large ungulates merits further attention, in view of the growing interest in cultivating wild species for the more efficient use of rangelands.

Apart from tameability,the response of wild species to fences or other means of directing or confining populations is important at some levels of management. This aspect of behaviour is still largely known at the empirical level. Jumpers, such as Odocoileine deer and impala, are more difficult to confine than caribou, muskox, pronghorn antelope and other species which seldom jump. The response of various species to such abnormal experiences as electric fences has been recorded for few large mammals, though there is a wealth of zoo experience.

6. SOCIAL CONSTRAINTS UPON HARVEST AND MANAGEMENT

In parks and reserves, as in game farms, it is important that surplus members in a population be removed with as little disturbance as possible to those that are to remain. It is frequently desirable to be selective in the harvest as for instance to take predominantly young males, in polygamous species, or old males no longer able to maintain a position in the breeding hierarchy.

The behaviour studies reported here contain a number of features that can be used to accomplish these ends of management. There are also behavioural features that must be given serious consideration in the drafting of harvesting plans.

Owen-Smith (Vol. 1, Paper 15, p. 351) suggests maintaining 'vacuum' areas into which the displaced sub-adult white rhinoceros would move and from which they could be removed without disturbing the resident adult animals.

The bachelor herds of oryx, giant sable and other species of similar behaviour offer opportunity for removal of the desired portion of that category, unless they are merely temporary resting herds of otherwise reproductive males. The exact composition of bachelor herds in each species must be known, if the behaviour is of possible use in accomplishing removal of surplus animals.

(a) The role of the aged in the maintenance of tradition

The general desirability of harvesting predominantly from males where a population experiences heavy predator pressure, should not overlook the need to maintain a proportion of adult males adequate to support the breeding pattern of the species and to assure the preservation of the traditions of the species. Geist (1971a) has indicated the importance of the older members of both sexes as the essential custodians of such traditions as the location of winter and summer ranges, fawning grounds, escape terrain and specially secure areas where infrequent severe weather threatens survival. This is of particular significance in species such as bighorn sheep in which the older males are the preferred trophy.

Bergerud (Vol. 2, Paper 29, p. 570) has documented the importance of tradition in the Newfoundland caribou when he reports that groups of captive reared animals, or of animals captured elsewhere and released into suitable habitat, failed to establish essential patterns of migration.

Another matter of importance that has a behavioural input concerns the design of harvest routines so as to remove animals from each of the harvestable demes or geographical units of the population. Thus in a species such as the Uganda kob, where each male breeding ground has its satellite herd or herds of mixed age and sex (Buechner, Vol. 2, Paper 49, p. 865), if effective reduction of the population is the objective then each of these demes should be included.

Elephant populations present unique constraints. Laws (Vol. 2, Paper 26, p. 520) maintains that the most effective technique to be used in a reduction programme is one that concentrates on the killing of entire matriarchal groups. In this way there is no dissemination of 'wildness' through the remaining population which would arise if there were experienced survivors of these family parties. He points out that where indiscriminate shooting of elephant has been practised, the results can be seen in the development of large herds of very wild animals which are difficult to control and can cause damage disproportionate to the size of the population.

Yet another constraint is the previously mentioned requirement to protect the female with a newborn young from disturbance that will impair the bonding between the two. Furthermore, we have little evidence to reveal the success of orphans in growing up and establishing themselves as fully-equipped members of their 'society'.

Learning and tradition are inescapable when a species enters a new range and, if it is to survive, it must weave together the seasonally-changing feed resources and the alterations in temperature, rainfall and snow accumulation into a viable life style. This becomes of particular importance in the re-introduction of species to areas formerly inhabited successfully. Choice of the genotype to be reintroduced, and careful selection of the most appropriate time of the year and the segment of the range upon which the animals are to be released, are important derivations of this acknowledgment.

One of the areas where behaviour can make a real contribution is in developing species-specific techniques for the reintroduction of species. An excellent illustration of this approach is the experiments reported by Bergerud (Vol. 2, Paper 29, p. 581). In introducing caribou to a new range he used fawns which were led through the area they were to inhabit. Later he added wild fawns which learned the habitat from those already 'introduced' to it. In short, he not only introduced caribou to the area but also introduced the area to the caribou, thus re-creating home range knowledge.

This becomes particularly demanding where the newly transplanted animals must learn to find and to know both a summer range and a winter range in widely separate places. Failure in this is the reason so many re-introductions of bighorn are unsuccessful in establishing new centres of dispersal.

Spinage (Vol. 2, Paper 33), Gauthiers-Pilters (Vol. 2, Paper 28) and Baskin (Vol. 2, Paper 27) write that female Waterbuck and camels form a permanent attachment to the birth place of their first calf. Mendelssohn (Vol. 2, Paper 40, p. 736) states that in gazelles it is the gravid females that appear to be the colonizers of new terrain. They go there to fawn and return thereafter. This may be a widespread principle and if so could be made use of in increasing the predictable results of re-introduction or introduction.

Geist (Vol. 1, Paper 10, p. 238) draws an important contrast between species of northern and southern origin in their conversion of vegetation. He points out that the species from areas with great seasonal fluctuation in feed supply will tend to concentrate such biological events as rutting and birth into short periods and to store energy as fat. On the other hand, species from areas of relatively constant carrying capacity will have a more diffuse biological calender and convert feed more generally into protein than to fat. This would be a consideration in the choice of species for game ranching.

(b) The role of the separate senses in establishing critical distance

Critical distance, the distance at which animals will flee from stimuli recognized as dangerous, certainly differs between species and upon competing stimuli. A classic example is the strong inherited behaviour of muskox toward wolf-like creatures, including sled dogs, that so many hunters have used to permit themselves to get close to the animals while hunting them.

Deane and Feely (Vol. 2, Paper 51, p. 885) comment on the importance of presenting the automobile and man to ranched game in circumstances that will not increase the critical distance. Here reference to the important paper of Parker and Graham (1971) provides many useful data and ideas. If the automobile-man combination becomes a source of alarm, hunting becomes so difficult as to be uneconomical. This thus becomes a limiting factor in the economics of game ranching.

Dean and Feely emphasize that it is important to restrict hunting to short, well spaced intervals. It should be compensated for by harmless activity by day and night. A further concern is the reduced carcass quality caused by fear of man at the time of killing.

In most of the open-ground ungulates discussed in this symposium, it is inferred that vision is the primary initiator of alarm reactioa There are no studies specifically directed to exploration of the relative importance of sight, hearing and olfaction in modifying behaviour. The successful management of a variety of species can be influenced importantly by such information adapted to management procedures.

(c) Structure and dependence relationships within groups

All the major constraints in this category have been referred to already in other contexts. The need to protect the mother and neonate from disturbance; the uncertain survival status of the orphan; the role of the territorial male in the orderly distribution of the population over its range and the effective reproduction of the herd; the possible role of the male in inducing ovulation at times appropriate to the seasonal cycle in food supply (demonstrated in hogs but perhaps operative in other species also); the role of the harem male plains zebra in defending all members of his harem from attack by predators, are all in this category.

(d) Sex ratios and reproductive efficiency

The traditional hunting patterns in North America, more than in most parts of the world, concentrate upon removal of the males. Where trophy hunting is important as a recreational pursuit, the pressure is further concentrated upon the mature or old males. In territorial species these are critical to effective maintenance of the breeding pattern. Furthermore, as stated above, the older animals are the custodians of important traditions. Where males and females occupy different ranges seasonally, as is the case in many northern and mountain species, the loss of tradition by either sex could lead to the failure of the population.

In species such as the moose, where there is prolonged courtship and pair association prior to breeding, the sex ratio required to assure full reproductive participation of the females depends upon density of the populatioa

Obviously in pair forming monogamous species an even harvest of the two sexes is important and techniques that lead to a differential pressure on either sex should be avoided.

7. BEHAVIOUR AND THE TECHNIQUES OF RESEARCH

The researcher must be fully aware of all behavioural characteristics of the species he is studying that may contribute to or bias his results. Thus the daily activity of animals, seasonal or local movements and differential distribution of the sexes can bias census or facilitate it. Sex- or age-specific behaviour can alter death rates, as can patterns of territoriality. This can involve displacement of young into vulnerable peripheral habitats and exposure of territorial males to increased predation or greatly increased energy demands.

Many studies now require the marking of individual animals for later recognition. Plainly marking of newborn young can have two possible consequences that may endanger survival. One is the inhibition of appropriate bonding between mother and young, both by the disturbance itself and by the introduction of man odour and a strange device (the tag) into the sensitive relationship. Such considerations should enter into the decisions concerning when, during the critical period, the operation should take place. Ideally it should be postponed until this period is complete and the bond likely to be well established.

Elsewhere in this review I have commented upon the great differences between different wild ungulates in their amenability to restraint and handling. These differences can be important in the selection of a species for a specific research study.

8. BEHAVIOURAL CONSTRAINTS UPON NON-CONSUMPTIVE USE

One of the most rapidly increasing uses of wildlife is tourism or the study of wild creatures as a hobby. Inasmuch as all such man-animal contacts are potential sources of disturbance, some cautions can be derived from the studies reported here. Of first importance is protection of the mother with newborn young from disturbance (Lent, Vol. 1, Paper l, p.44).

Another constraint arises from the desirability of protecting the traditional breeding grounds of such lek-species as the Uganda kob, that may be easily accessible, from frequent disturbance by tourists that could lead to its abandonment and the loss of the satellite population.

Similarly, the searching out of the concealed young of *abliegen* species can lead to their exposure to added predation dangers. Such problems suggest a need to proscribe some areas where young are traditionally born and concealed, and even to limit the territory of automobile use in park areas to the roadways or to buses operated by the unit rather that private or hire vehicles. Intensive use of some areas by car-driving tourists is inducing erosion and reducing carrying capacity of the ranges.

I refer again to my remarks earlier in this paper about the need to habituate animals to people and the artifacts that normally accompany people. It is equally urgent to introduce people to animals in park areas. Where animals are accustomed to people it is important that people behave so as to be readily recognizable as such. The quadrupedal sneak attempted by some observers and would-be photographers makes the individual more like a predator than a man and introduces disturbance, to the detriment of both participants.

In general the papers presented to this symposium reconfirm the principle that animals strive to live in a predictable habitat and when this is altered in any way react in a manner likely to restore predictability. A thorough knowledge of species-specific behaviour allows the manager to adjust management practices to fit his objectives. Unfortunately these objectives are seldom stated in precise terms. Only when there are clearly stated objectives for conservation of wildlife in National Parks, for sport hunting, for game ranching or in the search for solutions to the conflict between wildlife and industry, can full advantage be taken of existing knowledge of animal behaviour. Only then, also, can the research be designed to extract new knowledge.

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Index of Ungulate Species

The International Union for Conservation of Nature and Natural Resources (IUCN) is an independent international body, formed in 1948, which has its headquarters in Morges, Switzerland. It is a Union of sovereign states, government agencies and non-governmental organizations concerned with the initiation and promotion of scientifically-based action that will ensure perpetuation of the living world—man's natural environment—and the natural resources on which all living things depend, not only for their intrinsic cultural or scientific values but also for the long-term economic and social welfare of mankind.

This objective can be achieved through active conservation programmes for the wise use of natural resources based on scientific principles. IUCN believes that its aims can be achieved most effectively by international effort in cooperation with other international agencies, such as Unesco and FAO.

The World Wildlife Fund (WWF) is an international charitable organization dedicated to saving the world's wildlife and wild places, carrying out the wide variety of programmes and actions that this entails. WWF was established in 1961 under Swiss law, with headquarters also in Morges.

Since 1961, IUCN has enjoyed a symbiotic relationship with its sister organization, the World Wildlife Fund, with which it works closely throughout the world on projects of mutual interest. IUCN and WWF now jointly operate the various projects originated by, or submitted to them.

The projects cover a very wide range from environmental policy and planning, environmental law, education, ecological studies and surveys, to the establishment and management of areas as national parks and reserves and emergency programmes for the safeguarding of animal and plant species threatened with extinction as well as support for certain key international conservation bodies.

WWF fund-raising and publicity activities are mainly carried out by National Appeals in a number of countries, and its international governing body is made up of prominent personalities in many fields.