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SOCIAL BEHAVIOUR OF THE ELAND
(TAUROTRAGUS ORYX) ON LOSKOP DAM
NATURE RESERVE

by

Roderick Underwood

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R. UNDERWOOD

Supervisor: Dr. J.A.J. Nel,
Dept. of Zoology,
University of Pretoria,
Pretoria.

ABSTRACT

Despite its game ranching potential, little is known of eland ecology or ethology. This study aims to systematise basic knowledge of these, providing a basis for future research. Cape eland were observed in captivity and free ranging; giant eland were observed in captivity.

Sightings of various age classes in the wild indicate a high calf mortality, possibly affecting males more than females. Basic activities vary seasonally, particularly feeding - always the main activity. Feeding style and plant selection were seasonally variable, as were movements, and were probably greatly affected by the limited range of the population and the heterogeneous vegetation. Groups formed and broke up easily, giving great seasonal variability in size and composition - also probably linked with vegetation changes.

Apart from calves, dominance rank ruled access to all resources. It was reinforced by characteristic threats and contact activities. Challenges were distinct from these and occurred mainly

between bulls. Aggressive and dominance behaviours were the main forms of social interaction.

Visual signals depended on context for their meaning: this is illustrated by an analysis of grooming actions in various situations. Calls could be assigned to three basic continua, only one of which, contact calling, was often heard. Olfactory communication was probably mainly through facial apocrine and false hoof secretions, and self marking with urine.

The mother-infant bond was loose but exclusive. For the dam, it was probably established 30 minutes postpartum, but in calves this could take several days. The first twelve hours, the lying out period and the first six months were the major phases in the development and integration of behaviour.

The basic social organization is discussed in terms of feeding and breeding strategies. Management implications are indicated.

Key words. Elands. Socioecology. Ontogeny. Social signalling. Dominance hierarchy. Africa.



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CHAPTER I

INTRODUCTION

THE ELAND

The eland is the largest African antelope, having a maximum shoulder height of 1,7 m. While its maximum mass is uncertain, owing to extreme variation in male size, it is more comparable with buffalo (Syncerus caffer) than other antelope, maximum recorded weights in both eland species being up to 900 kg (Dorst & Dandelot 1970). This resemblance to buffalo extends to the animals general appearance - in fact the Masai hunt buffalo and eland for food on the basis of their cow-like appearance (Grzimek & Grzimek 1960a). The lack of resemblance to other antelope is reflected in its various names - "eland" itself being derived from the Dutch "eland" (elk). Similar names are: Elenantilope (German), and Elan du Cap (French).

The elands are distinguished from the other members of the Tragelaphini in having axially straight horns with a corkscrew twist, ox-like feet, and no inguinal glands (Ansell 1971). Their taxonomic status is uncertain, since they will hybridise with greater kudu (Tragelaphus strepisceros), but their general habits and habitat preferences are very different to those of other living tragelaphines and they are classified in a separate genus: Taurotragus (Ansell 1971). This consists of a single superspecies formed by the common eland, T. oryx (Pallas), and the giant eland, T. derbianus (Gray).

T. derbianus: longer horns (up to twice the head length); a large white cheek spot; ears broad and rounded with a dark bar inside; the sides of the neck are darker with a posterior white throat bar; the dewlap begins just behind the chin.

T. oryx: horns shorter; no cheek spots; ears narrow and pointed, without the dark bar; neck coloured as the body; dewlap commencing on the throat (From Ansell 1971 - see Fig 2).

Both species carry body stripes, but going south from Kenya, T. oryx loses these progressively, the Cape eland lacking stripes

A



B



Figure 2. Eland bulls.

A. Common eland adult, Loskop Dam.

B. Giant eland yearling bull, National Zoological Gardens, Pretoria.

completely in the adult (in younger animals, stripes and even cheek-spots and facial chevrons are sometimes visible, although soon lost). Apart from the Cape eland (T. oryx oryx Pallas 1766), Ansell (1971) recognises T. o. livingstonei (P.L. Sclater 1864 and T. o. pattersonianus (Lydekker 1906), although previously many intergrades between the southern forms and the more fully marked northern ones were recognised as races.

According to Ansell (1971) T. oryx were found originally in the South West Cape zone; most of the South West Arid zone; virtually throughout the Southern Savanna, except for the area beyond the Lower Congo River; it extended into the Somali Arid zone west as far as the Albert Nile, while its northern extreme touches on the borders of Ethiopia.

T. derbianus continues the superspecies range westward into the Northern Savanna zone, although it was apparently always more discontinuously distributed than T. oryx. Ansell (1971) suggests an eastern population (from Nigeria eastwards), an isolated population in eastern Ghana and western Toga, and a larger population west of 9°W as the historical distribution. In this, he differs with Sidney (1965) who suggests that a more continuous distribution was disturbed in recent times by rinderpest and overhunting.

In either event, the eland would seem to have been very successful in terms of distribution until fairly recently. The introduction of European hunting methods, tsetse control and similar factors preventing nomadism, and rinderpest, have broken up this distribution. Protection, reintroduction and ranching have partially restored the T. oryx range. Game farming is particularly important in South Africa: of a maximum of 3209 animals within South Africa but outside the Kalahari Gemsbok National Park, 1080 were on farms (Skinner 1971). The Kalahari animals migrate between South Africa and Botswana; their numbers, although high, are uncertain. Outside farms and reserves, the status of this animal is sometimes precarious: for example, only about ten naturally occurring eland remain in the Transvaal: Lambrechts (1974), while the whole T. derbianus species - whose range contains few game farms or suitable reserves - is scarce, and the western race is regarded as highly endangered (Simon 1966).

The eland has long been known as an easily tamed, very manageable antelope - Woodhouse (1971) describes cave-drawings which indicate that it may have been domesticated by bushmen at one time. Thus it is not surprising that, when the possibility of farming African game commercially was seriously explored, the eland should be one of the first animals considered. In fact isolated instances of taming and experiments in domestication go back to the end of the last century, when a small herd was established in Askaniya-Nova (Treus & Kravchenko 1968); Stevenson-Hamilton (1947) reports a tame eland which was regularly ridden by its owner, while Haagner (1955 In Sidney 1965) reports eland being used as draught animals.

Much of the present information on eland comes from work on semi-domesticated or tamed animals, in particular the Askaniya-Nova herd and a semi-domesticated herd established by Mr J. Posselt in Rhodesia. Such studies have shown that the eland can be managed under intensive or semi-intensive conditions, along much the same lines as domestic cattle. If, however, the animal is to be successful in large-scale commercial ranches, or even if it is to be managed efficiently on reserves, its behaviour under more natural conditions must be understood.

Despite its history of utilisation by man (reviews in Skinner 1967, 1971), little is known about the basic behaviour or ecology of the eland. This is partly because of its low numbers in the wild, and also because it is usually timid and wanders over large distances. What information that is available on free ranging populations has usually been collected incidentally in the course of more general studies (e.g. Lamprey 1963). Even serious studies of basic behaviour are limited to those made by Walther (summarised in Walther, 1974) and Kirschoffer (1963), and to management oriented studies (e.g. Posselt 1963; Roth, Kerr & Posselt 1972). Since the eland may be a valuable meat producer, and farming is certainly important to the eland, it was felt that a basic general study was necessary. This would organise the present data about eland, outline their behaviour in a more general way than to date, and provide a basis for later, more specific studies.

STUDY ANIMALS

In all, eland were observed under three sets of conditions. Firstly, free-ranging common eland (Taurotragus oryx Pallas) at Loskop Dam Nature Reserve were observed in the wild for about 1,000 observation hours over a period of two years from June 1972 till May 1974. Secondly, tame cows from the Loskop Dam population were observed in captivity prior to, during and after parturition, and the subsequent development of their calves was recorded until these were between six months and a year old; about 400 hours of observation were spent on this. Finally, a pair of giant eland (Taurotragus derbianus Gray) were observed between July 1974 and March 1975 for 60 observation hours.

FREE RANGING ELAND

These consisted of 70 - 80 individuals, all descended from an original herd of 16 animals introduced to the Loskop Dam Nature Reserve in 1963, together with the offspring of a young bull brought in to sire the first calves in 1965. The herd founders were brought as calves of one to four weeks old from Giants' Castle Nature Reserve in the Drakensberg Mountains in Natal. They were reared on cow's milk and became very tame. The first generations at Loskop were born in captivity, but were later released into the wild. By May 1972, an aerial survey showed a population of 70 eland on the reserve. Apart from the animals raised in captivity, the population was quite shy and did not often accept my presence at close quarters. Groups containing some of the tame animals were much more approachable, and the most detailed observations are on these individuals.

CAPTIVE ELAND

The original cows retained their tameness and could be lured into a large paddock by food. When the calving season was about to begin (August), these individuals were brought into the paddock and kept there until they had calved. They were then released but returned every night to nurse. This continued until January or

February, when the cow visits became very infrequent, after which the calves were considered weaned and the cow were not admitted. The calves were kept in captivity for various lengths of time.

GIANT ELAND

These were brought to the National Zoological Gardens in Pretoria in early 1974 from Amsterdam. They were both quite young, the bull being about one year old when observations began in mid-1974, while the cow was about six months older. By the time observations began, they had become very tame and usually ignored people except to watch or, occasionally, to approach and investigate them.

STUDY AREA

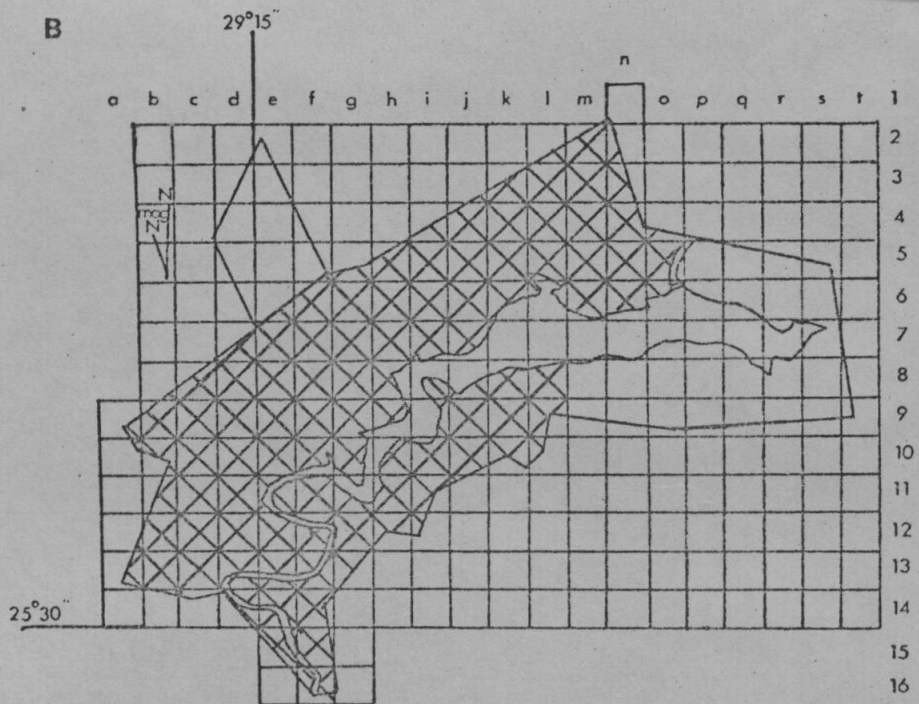
Loskop Dam Nature Reserve is situated approximately 160 km north east of Pretoria at latitude 25° 30"S and longitude 29° 15". The dam giving its name was built from 1934 - 1938 (Officers of the Department of Water Affairs 1960) and formed an irrigation reservoir of up to 1700 ha surface area (Irby 1973). The reserve itself was proclaimed in 1940 and consists of an area of 12,762 ha surrounding the main body of the reservoir. The reserve includes some sections of the highveld plateau, a series of hills descending to the Olifants River valley and a few flats alongside the river (Fig 3). The major part of the terrain consists of very broken ground, with an extensive network of dongas. Slopes are usually steep and rock-littered. Erosion of the Karroo system sediments has resulted in the exposure of felsite and sandstone hills, which line the Olifants river in this area, soils are usually thin except in the valley itself (van Biljon 1960).

Although the area had been farmed prior to being made a reserve, there had been little damage to the veld, which is probably much the same now as it was forty years ago (Theron pers. comm.). There are, however, some areas around the old encampments and homesteads which still present a lawn-like appearance and which are preferred grazing for several species. The vegetation has been

A



B



Scale: 1 2 3 4 5
km

Figure 3. Loskop Dam Nature Reserve.

A. Aerial view with black lines delineating reserve

classified by Acocks (1953) as "Mixed Bushveld" and "Sourish Mixed Bushveld". Theron (1974) finds three major characteristics (aspect, soil depth and altitude) governing the distribution of plant species at Loskop, and the heterogeneous nature of the vegetation types reflects the broken and variable nature of the terrain. Theron (1974) distinguishes 24 communities at Loskop, eight of which made up the major part of the vegetation available to the eland and were used by them; only one major plant community (the Protea caffra - Tristachya biseriata tree savanna) was apparently avoided.

From local place-names it is probable that eland were found in the immediate locality at one stage (e.g. Elandsberg, Elandsdoorn), but they had disappeared from the area when the reserve was proclaimed (there were, in fact only nine ungulate species present at that time - du Plessis, In: Irby 1973). Other ungulate species, either originally present or introduced, include Chapman's zebra (Equus burchelli antiquorum Gray); hippopotamus (Hippopotamus amphibius, L.); grey duiker (Silvicarpra grimmia, L.); steenbok (Raphicerus campestris Thunberg); oribi (Ourebia ourebi Zimmermann); klip-springer (Oreotragus oreotragus Zimmermann); mountain reedbuck (Redunca fulvorufula Afzelius); reedbuck (Redunca arundinum Boddaert); waterbuck (Kobus ellipsiprymnus Ogilby); impala (Aepyceros melampus Lichtenstein); sable (Hippotragus niger Harris); blesbok (Damaliscus dorcas phillipsii Pallas); blue wildebeeste (Connochaetes taurinus Burchell); bushbuck (Tragelaphus scriptus Pallas); nyala (Tragelaphus angasi Gray); greater kudu (Tragelaphus streptoceros Pallas); buffalo (Syncerus caffer Sparrman); giraffe (Giraffa camelopardalis, L.) and white rhinoceros (Ceratotherium simium Burchell). Other large animals present include leopard (Panthera pardus L.) and brown hyaena (Hyaena brunnea Thunberg) while there are large numbers of black-backed jackal (Canis mesomelas Schreber). In May 1972, just prior to the study, a game census was made. Table 1 shows the results for most of the larger ungulates.

Until 1969, the large game on the northern side of the reserve was confined to an area of 22 km² on the eastern end by a fence. This was removed in 1969 and the animals began to move into the rest of the reserve. The eland did this very quickly and during the ^{study period} they seemed to move freely over the whole reserve, although concentra-



ting in the northern half. Other species moved into the new area more slowly e.g. impala in 1972 - 1974 were concentrated in the area north-east of the line of "F" squares in Figure 3b, with occasional small groups and territorial males elsewhere.

Table 1 : Large ungulate species at Loskop Dam Nature Reserve, May 1972.

	<u>Animals sighted</u>
White rhinoceros	25
Zebra	93
Mountain reedbuck	325
Reedbuck	50
Waterbuck	42
Impala	450
Sable	46
Blesbok	178
Blue wildebeeste	67
Nyala	28
Kudu	182
Eland	70
Buffalo	6
Giraffe	28

From the nutritional point of view, the grasses in the Loskop area vary greatly throughout the year (Fig 4), depending on rainfall (Fig 5) which is itself variable from year to year. The seasonal rains fall as showers and intense thunderstorms during the mild/hot summer months. The dry winters are mild, with light frosts occurring in midwinter. Water is well distributed over the reserve, both in the form of permanent or temporary streams and storage dams; the main body of the reservoir is also available to the animals. A few salt and aurea licks were distributed at intervals over the re-

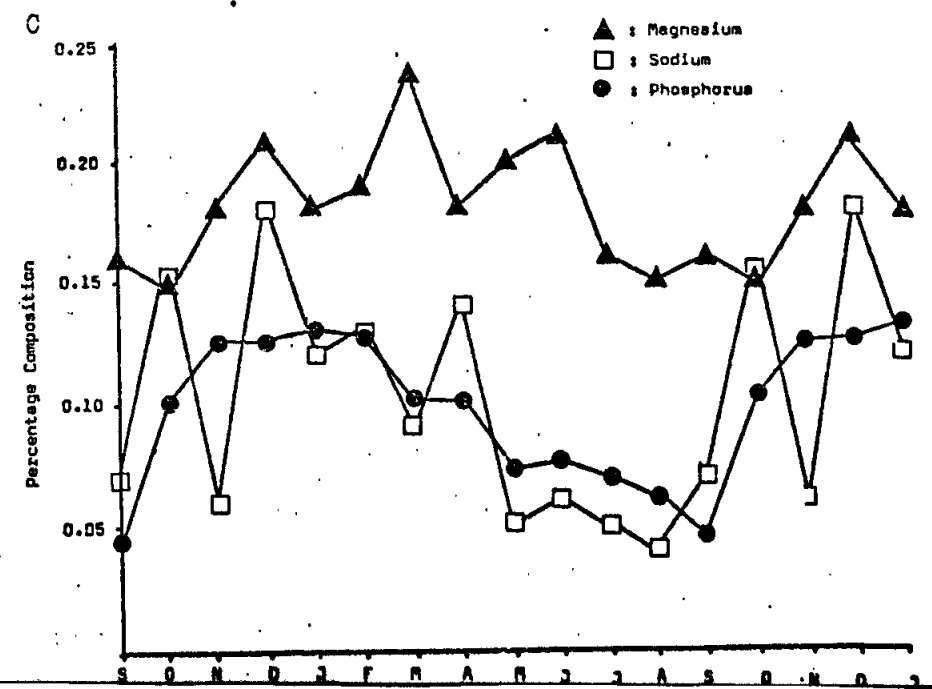
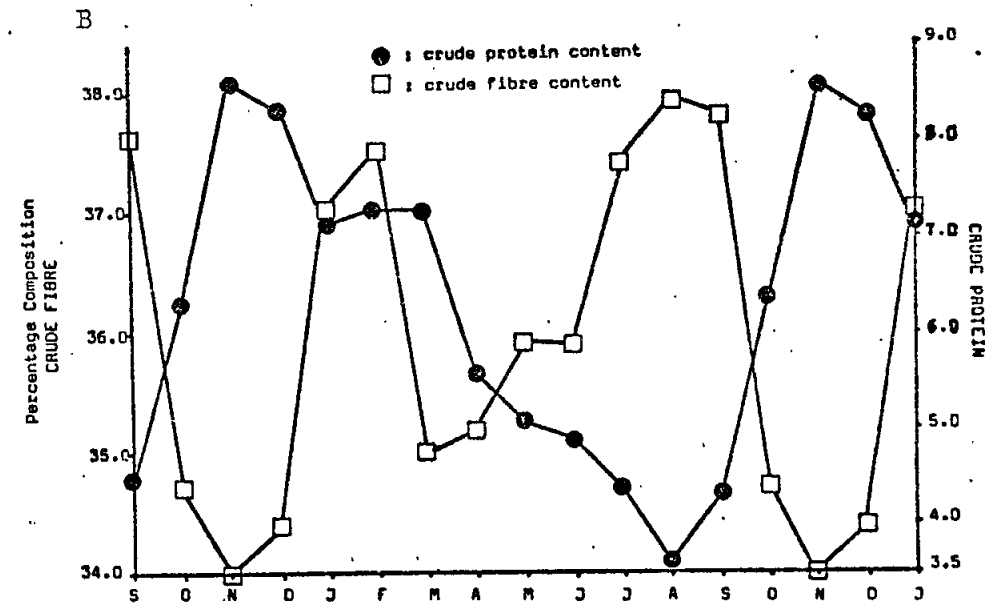
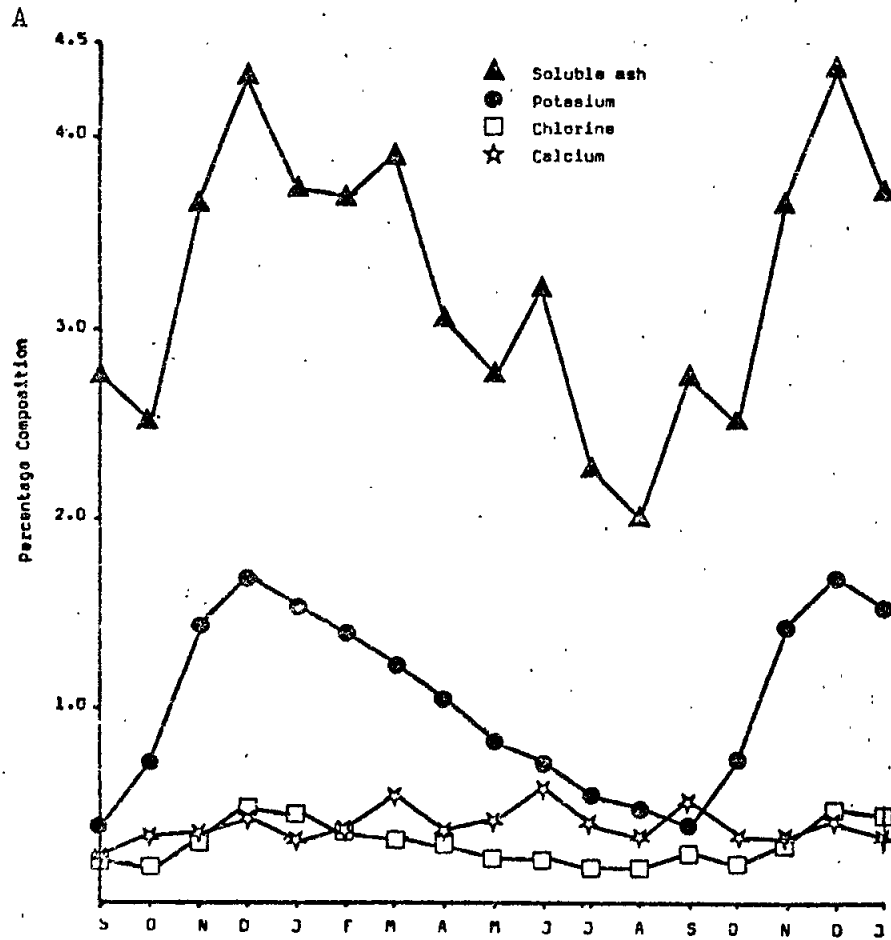


Figure 4. Nutrient contents of graze species in the Loskop Dam area. From Du Toit, Louw and Malan 1940.

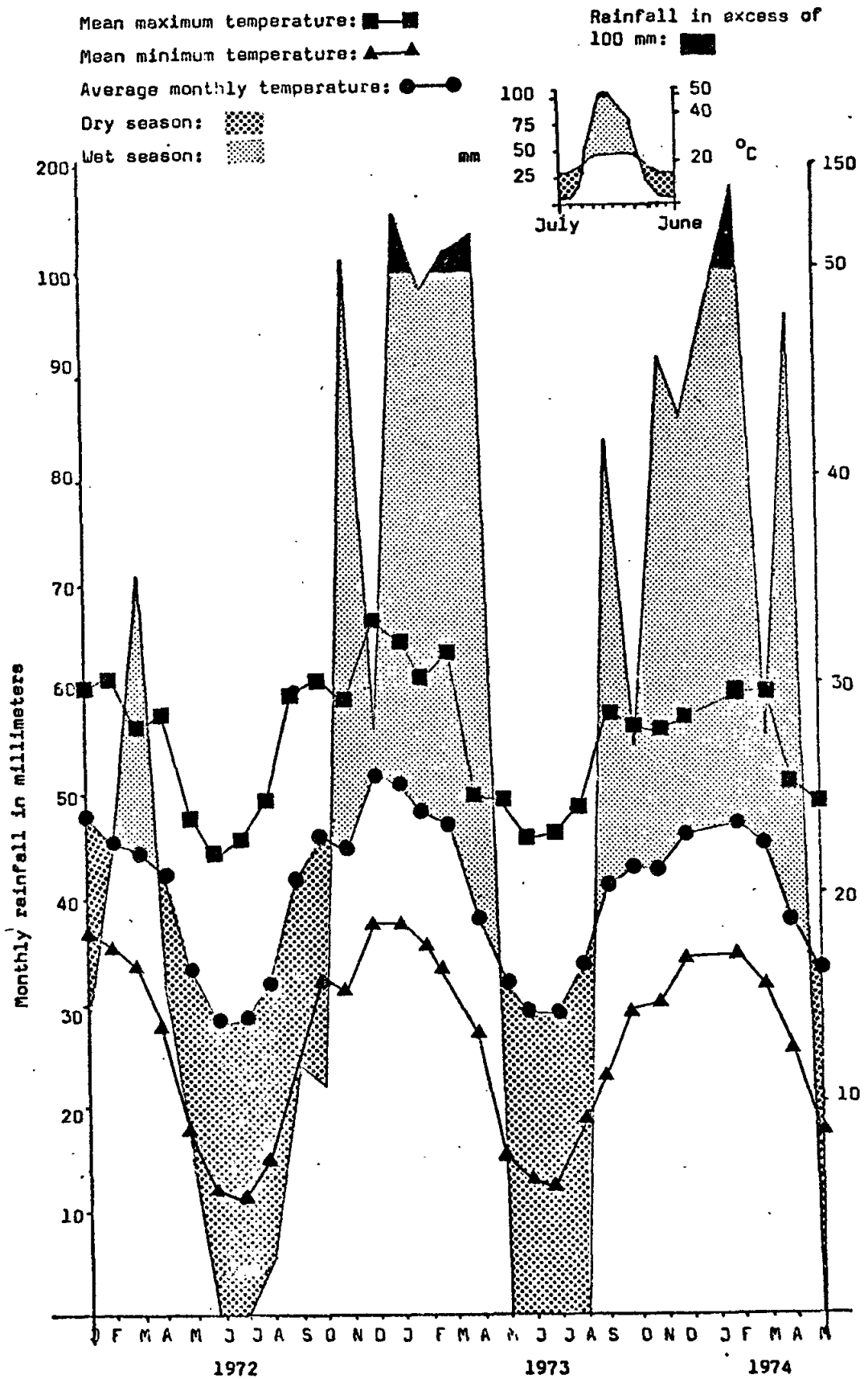


Figure 5. Climate at Loskop Dam Nature Reserve during the study period (June 1972 - May 1974). Inset is a 35 year average (1935 - 1970).

serve in winter. Main fodder trees on the reserve are Combretum apiculatum, Diplorhynchus condylocarpon, Burkea africana, Acacia spp., Faurea saligna, although eland (as in Hofmeyr 1970) took almost all available plant species at some time. Important grasses in the main communities available to eland are: Themeda triandra, Heteropogon contortus, Setaria perennis, Loudetia simplex, Enneapogon scoparius, Tristachya biseriata, Andropogon spp, Eragrostis spp, Aristidia spp and Panicum maximum.

The captive eland were kept in an otherwise unused paddock enclosing about 12,000 m² of Combretum apiculatum, Acacia caffra, Themeda triandra tree savanna (Theron 1974). Adjoining this were a set of stalls, where very young eland calves were kept during the day, and a smaller paddock (about 1500 m²) where the animals were fed and the calves nursed at night.

EQUIPMENT AND METHODS

A 100 c.c. cross-country motorcycle was used for transport, which limited the amount of equipment normally carried (see Appendix 1). A 35 mm camera with a 200 mm lens was carried at all times, as were binoculars (20 x 50). Notes were taken on file cards, which were cross-referenced together with additional information the same day. On some occasions, a Bauer super -8 cine camera was used to record interactions. A stop-watch in the form of a wrist chronograph was used for timing. The recordings shown in chapter 6 were made on a Uher 2002 tape recorder and were analysed on a Kay sonograph by Mr. N. Passmore of the University of the Witwatersrand.

Studies of the free-ranging population consisted of locating the groups and observing them. They were located by a variety of methods, since eland are notoriously elusive and mobile. To begin with, I made a general tour of the roads on the reserve at 10 - 15 kph on the motorcycle. If, as happened quite frequently, no groups suitable for observation were seen, the less accessible parts of the reserve were surveyed using several of the highest hills on the reserve as vantage points. Where this failed, areas known to occa-



sionally harbour eland but which could not be examined from a distance (e.g. dongas, hillsides facing straight onto the lake, concealed valleys) were covered on foot. Such a detailed search usually took two days and if unsuccessful, the whole process was repeated, usually with results. If such a detailed search had not already been necessary, it was performed in any event once a week as a survey of eland positions. These surveys rarely gave the positions of more than a third of the population and were only useful in the most general way, since the eland were extremely mobile (see chapter 3). The positions of kudu sighted during these surveys were also recorded, which gave some standard for comparison. This was necessary because of the non-standard search procedure and visibility conditions. All plots of eland positions given, therefore, are only valid for comparison with other plots and do not represent actual dispersions. The mobility of the animals (up to 12 km/day) invalidated any prolonged search procedure on such a (relatively) small area.

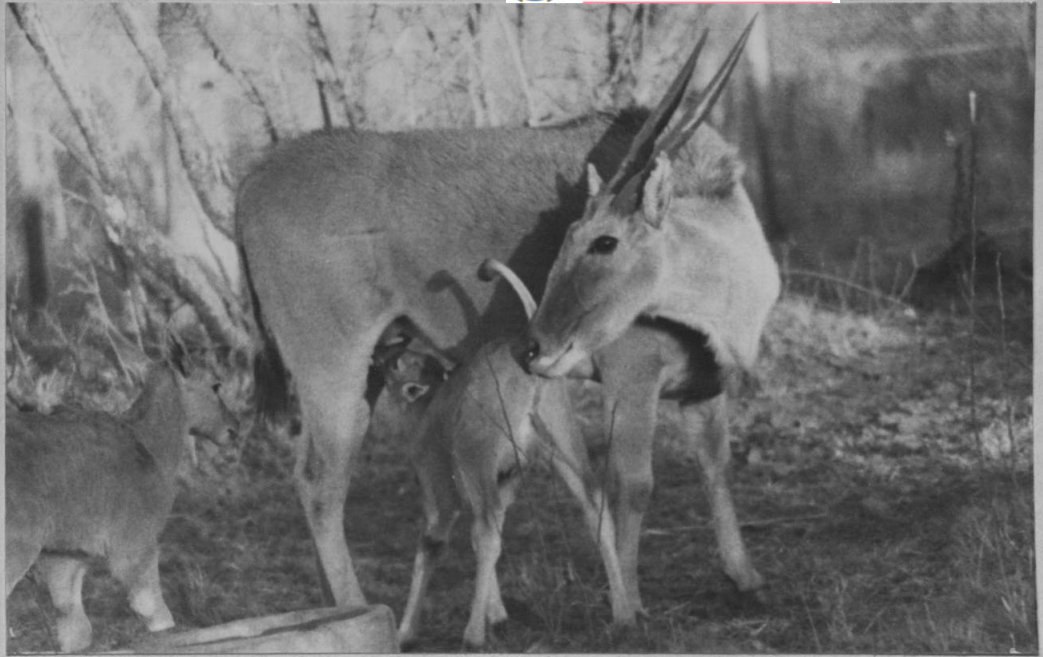
Once animals were located, group size and composition was recorded, as was the position relative to local landmarks. Position was later plotted on a 1km grid. Where possible, individually known animals were noted. Age/sex classification was based originally on Kerr & Roth's, 1970, measurements of horn length vs. ear and skull length. This was later confirmed by a series of photographs of developing captive calves, covering growth from 0 - 18 months. For the purposes of general analysis, animals were divided into six classes (Figs 6 and 7): unweaned calves; juveniles; subadult males; subadult females; adult males and adult females. Unweaned calves were those under six months of age when horn length was halfway between head and ear length. "Juveniles" were animals from six to thirty months of age, when the horn length was up to half again the head length and the first two whorls on the horns were visible. Subadults were animals of 30 - 42 months, where the horns and body were still growing, but cows might be carrying calves. Adult animals were those with fully developed horns (4 - 5 whorls in females, 3 - 4 whorls in males) and a general adult conformation, aged $3\frac{1}{2}$ years or more. This latter is a compromise

Figure 6. Age classes of eland at Loskop Dam Nature Reserve.
June 1972 - May 1974.

- A. A one to two week old calf - horns still undeveloped, shoulder height approximately the same as its dam's ventral surface - suckles. A calf of approximately the same age is in the left foreground, showing traces of body stripes which will disappear after the first month of life.
- B. From left to right: a 15 - 18 month heifer, a young adult bull, another 15 - 18 month heifer, a 6 - 8 month calf, a group of calves 4 - 6 months, with an adult cow in the background, an adult cow.
- C. A cow (left) and a bull (right) both about to enter the subadult class, i.e. 27 - 30 months.



A



B



C

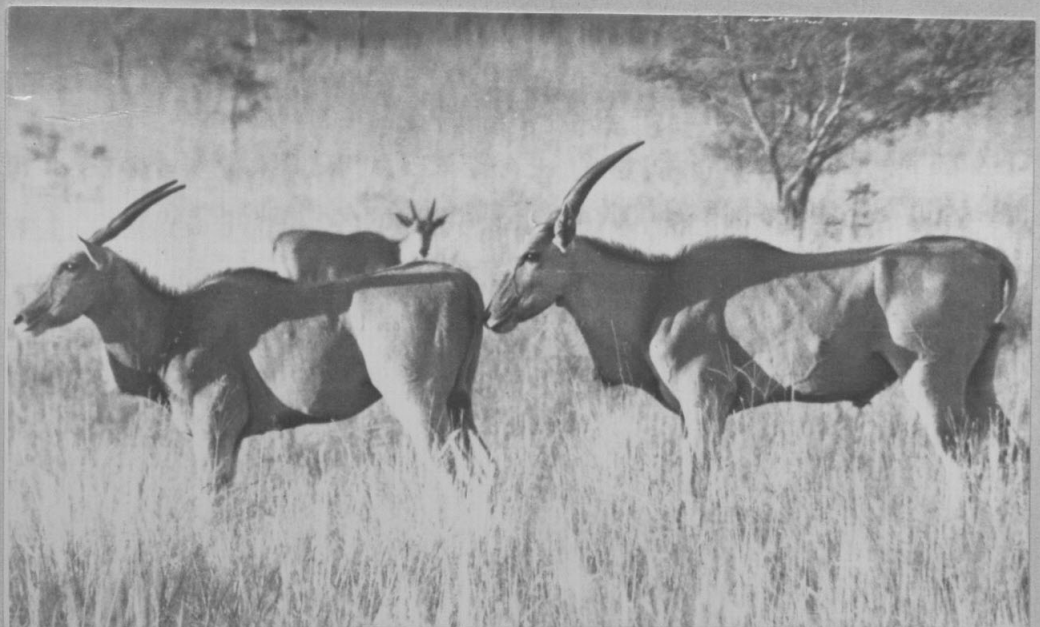


Figure 7. Age classes of eland bulls at Loskop Dam Nature Reserve.
June 1972 - May 1974.

- A. A young ($3\frac{1}{2}$ - 4 years) adult bull and an older (9 - 10 years) grey bull.
- B. The same, to show the difference in dewlap and general bodily development.
- C. A year after entering the "grey" phase 6 - 7 years. This photograph was taken towards the end of summer, while A and B were taken in early spring, showing the difference in condition seen at these times of the year.



A



B



C



figure, since some subadult cows might be indistinguishable from adults at 36 months. It was however, difficult to draw the line for bull maturity because males continued to grow throughout life. The "subadult" classification was therefore made by analogy with females. It was also possible to recognize a subdivision between young adult males, who had probably achieved full bone growth but were less bulky and lighter in colour than the older, grey bulls, whose hair was very sparse, allowing the darker skin to show through.

Individuals were identified by various characteristics - usually natural markings, although some of the older animals had steel ear-tags or the holes left from tags which had been lost. Unlike the more northern populations, adults at Loskop (T. oryx oryx) lacked most of the typical tragelaphine markings - stripes, cheek spots, forehead chevrons - at least, as far as field identification was concerned. There was, however, variation in horn shape, facial structure, size and colouration, which was enough to distinguish the more approachable animals. Over long distances, the only useful characteristics were horn shape and colouration, neither of which was reliable over $\frac{1}{2}$ km. Male horns were more uniform than females, and fewer males could be identified with certainty. Calves changed so rapidly that recognition was doubtful if they had not been seen for more than a few weeks, and no serious attempts was made to identify most of them. After about 18 months, characteristic horn shapes were recognisable. Towards the end of the study, a few captive calves were marked with coloured plastic ear tags and small ear streamers and were released.

Once a group was located and classified, it was followed on foot for as long as possible. This might be for several hours or a few minutes, depending on the general visibility, rate of movement of the eland and their timidity. It was rarely possible to stalk them unaware and I had to rely on keeping outside their flight distance to observe them. While groups were being watched, the activities of the group was recorded every 15 minutes by noting the number of animals performing each of ten categories of non social behaviour. These categories accounted for 98% of the activities seen. Observable interactions were very scarce and quickly over; they were therefore recorded on an Ad Lib basis (see Altmann 1974).

Animals/.....



Animals were also observed at licks, where the majority of aggressive interactions took place. This allowed me to determine the dominance hierarchy for females and calves in terms of priority of access to a limited resource (the lick).

The captive cows and calves provided information on three main aspects of behaviour: the cow/cow relationship: parturition and the mother/infant relationship: ontogeny and calf/calf relations.

Cow/cow interactions were observed as at the licks and a similar hierarchical system emerged (chapter 5). Dominance and aggressive actions were frequent (chapter 5) and easily recorded. I would sit in the small paddock, watching the animals feeding from a distance of 5 - 10 m and could record almost all interactions. For the most part, I was ignored, especially when food had just been put into the troughs. Observations were made on cows during the day in the large paddock, but few interactions occurred. All captive group statistics in chapter 5 refer to the 1 - 1½ hours during and after feeding in the small paddock.

Behavioural and physical changes associated with parturition were recorded in both captive and wild animals. Changes in the external genitalia, the udder and in the general appearance of the cow were recorded systematically for the captive cows. Observations covered a period of up to two months prior to parturition in some individuals. Behavioural changes were also recorded.

All observations presented in numerical form in chapters 7 and 8 were derived from the group of captive calves; these consisted of these calves born in captivity, totalling twelve individuals which were observed at some stage, together with two bull calves from outside the reserve, temporarily kept with the others. Fourteen animals were therefore included in the quantitative observations but at least two other calves contributed to qualitative results obtained from the captive group.

For the purposes of calculating captive group frequencies of interactions, the total number of hours a particular animal was present when the group was observed formed the basis of calculations based on the individual. Where age groups (e.g. 1 - 2 months) were used, the total number of animal-hours of observation for that age formed the basis of frequency calculations. This

worked/.....

worked well enough at low densities, especially as calves mainly slept during the first months of life, but the effect of higher densities is rather complex and is discussed more fully in chapter 5.

Observations were made as nearly continuously as possible for the first day of life, at least until the first lying out period began. After this, the animals were observed on being released to their dams at night and for one to one and a half hours following (depending on the light available). Since the observations were incidental to those on calving and to the taming of the calves, they were not systematically planned with reference to ontogeny and the low levels of some observations reflect this. The observations were, however, made under as uniform conditions as possible and may be taken as being representative of the changes which occurred within the captive group.

The giant eland observations were intended merely to get a preliminary idea of the behavioural repertoire of the species. Little else could be achieved because of the youth of the animals and the fact that there were only two of them. They were observed for an hour or so in the evenings, when they would be most likely to interact, at intervals of one to two weeks. Some observations were, however, made at other times of the day.

Where annual cycles of behaviour were recorded, averaged each month's results in 1972 - 3 with the same month in 1973 - 4, to give an average annual cycle. This was necessary because of the variation in the numbers of animals sighted under observable conditions in any single month. Productive observation hours were much lower than the time spent watching animals, and were sometimes patchy because of e.g. transport difficulties. I have partly repeated the annual cycles shown in graphs, to remove emphasis from months in the middle of the cycle (see e.g. Fig 4).

Often I found that my photographs and records for giant eland illustrated particular points better than my records from Loskop. Where figures include giant eland, they may be taken as illustrating both species, except where a difference is actually mentioned.

CHAPTER 2

GENERAL BEHAVIOUR PATTERNS

The division of behaviour into social and non-social forms is arbitrary. Adapting Altmann's (1968a) definition of meaningful communicatory behaviour, I have here included all activity which, by itself, seems to have no significance to other free-ranging eland. However, some activities which have both social and non-social functions are also included.

Non-social behaviours are of interest on their own, and also because they are often adapted to social functions. Phylogenetically this may have happened either because the behaviour was unrelated to the original social repertoire, and has therefore good "neutral" material for new signals, e.g. grooming activities, or, paradoxically, because it contained potential social information. Once these activities begin to serve a signalling function as well as their original one, they may become adapted to serve as signals i.e. ritualised (Huxley, 1923 In: Tembrock 1968, for reviews see Tinbergen 1952, Huxley et al. 1966, Cullen 1972). The actions themselves may remain unchanged, their informative value being in the context of the activity (W.J. Smith 1965, 1968) e.g. grooming actions during aggressive interactions; and "aggressive" grazing in many ungulates. The eland shows such modification of its non-social behaviour, particularly its grooming activities (see chapter 6). For this reason, some facets of "non social" activities are described more fully than others, since they are of importance in the interpretation of overt social behaviour and will be referred to in later sections.

LOCOMOTION

GAITS

These are classified as by Bullock (1974) for pronghorn since his descriptions of the relevant gaits fit very well those of the eland.

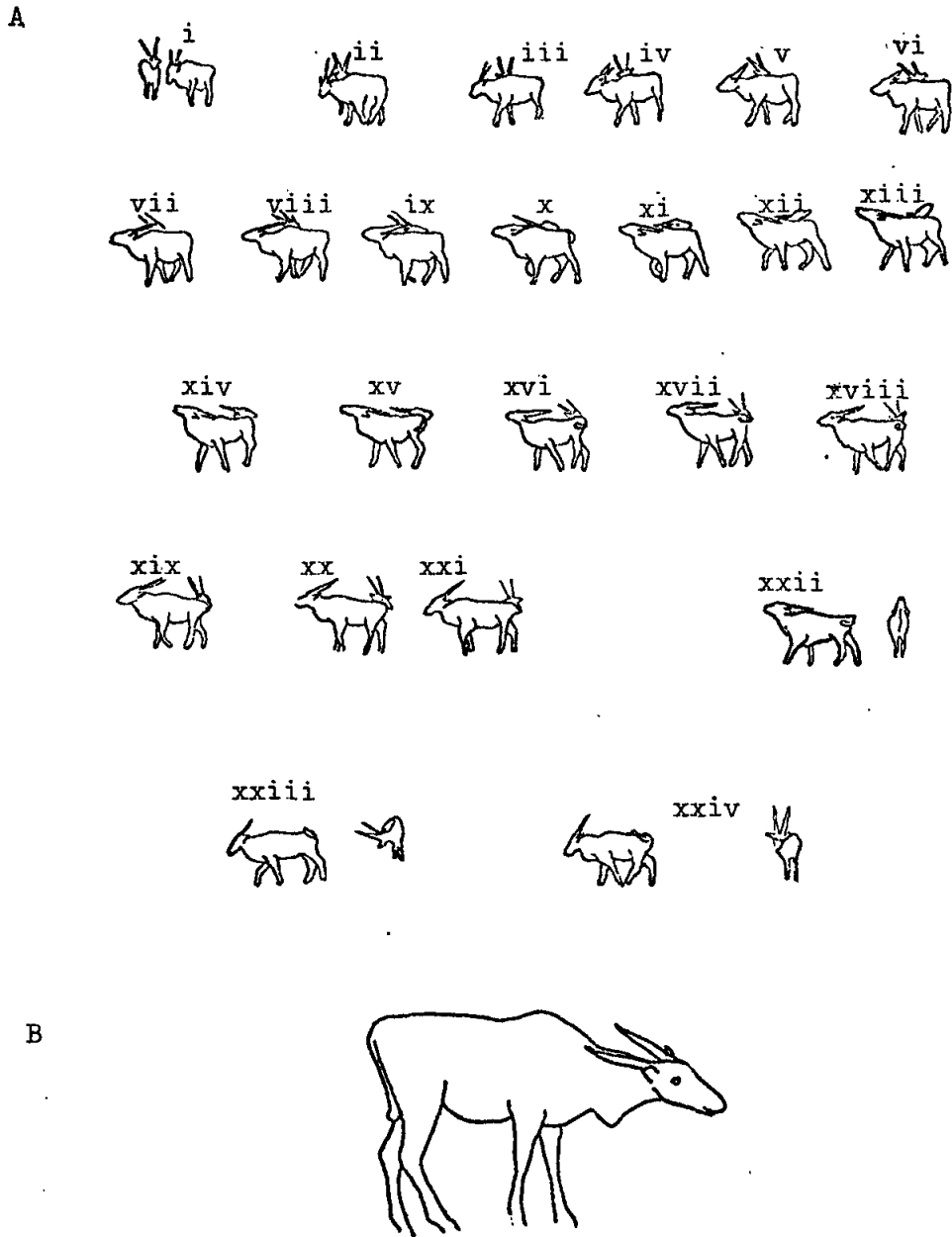


Figure 8. Walking and Grooming in eland at Loskop Dam Nature Reserve June 1972 - May 1974.

- A.(i - xxv) Diagonal walk
 (iii - xxii) Head tossing from both cows
 (xxii) Repeat head toss
 (xxiii) Ducking grooming from furthest cow.

All drawn from super 8 cine film at 18 frames per second. There is a gap of 20 frames between (i) and (ii), (ii - xxii) is continuous, while (xxii - xxiii) and (xxiii - xxiv) are approximately 30 frames apart.

- B. Back scratching.

Crawl

The animal moves very slowly with at least three feet on the ground at all times. There is a transverse sequence of footfalls. Used mainly in grazing.

Diagonal Walk

(Includes Bullocks' "fast" and "slow" walks). There are never more than two feet off the ground. The sequence is transverse. The slower forms are used for movements when within a small stationary group, while the faster forms are typical of animals avoiding aggression, of animals moving between groups, and of groups moving from one focal point in their home range to another (see Fig 8).

Trot

Without formal analysis, the various forms of the trot cannot be distinguished clearly, but there seem to be two forms normally employed. These correspond roughly with the equestrian's "trot" and "extended trot". The first of these was seen during some group movements, during aggression and by calves at play. The "extended" version of the trot is very distinctive and was seen during flight and again during calf play. Eland can move quite quickly at the trot and for considerable distances. Abbott (1968a) reports a cow trotting at an estimated 20 miles per hour (32 kph) for at least one mile (one and a half km), while Hofmeyr and Lensen (1975) record herds being driven 10 - 25 km, trotting at 8 - 15 kph. Dagg and de Voss (1968) note that trotting is the usual pace in eland migrations.

Canter and Gallop

These gaits were never seen except in extreme panic flight or else in playing calves. Both canter and gallop are assymmetric paces involving periods of suspension and periods when the animal has all of its weight on one foot; this makes these paces inconvenient and tiring for large ungulates (Dagg and de Voss 1968). Because of their rarity and the situations involved, I cannot compare them accurately with descriptions from other species.

LEAPS

When in flight, eland may perform leaps which are similar to the "arched jump" of gazelles (Walther 1969). It is performed in the open (rather than in tall grass as in gazelles), and looks very much as if the animal is leaping over some invisible object. In play, this jump sometimes appears to be elicited by unevenness in the ground.

On two occasions a stiff legged leap was seen in young animals starting flight from a standing position. The animal landed in almost exactly the same place as it started from and then trotted off. No other animal appeared to pay any attention to this.

On two occasions during group flights, and twice when two groups of calves and females were converging to meet each other, I saw bounds from several members of the group which resembled the stiff legged jump mentioned above, except that the animals were moving, the body was less arched, and that the legs were slightly flexed, especially at the beginning and end of the bound.

Leaps "in vacuo" such as those described above, were rarely very high, and they covered no great distance. When the eland were faced with an obstruction, especially when in panic, they would sometimes attempt to jump e.g. fallen trees. Hofmeyr and Lenssen (1975) record animals clearing a 2,1 m fence, while Posselt (1963 : 82) reports that even bulls are "capable of clearing a six foot fence with little effort". At Loskop, two yearlings scraped over a two to two and a half metre fence when driven. When a curtain in the same boma fell to about 1 m in height, however, only about half the animals in a group of 13 jumped it of their own accord. It seems, therefore, that some individuals jumped more readily than others. The sight of one animal jumping successfully seemed to stimulate others to follow.

POSTURES

NORMAL

Walther (1964a) describes the "Normalhaltung" of Tragelaphus species as "..... the neck held easily upright and forward. The head would be somewhat higher than the withers. The nose points

straight/.....

straight ahead or forward and down. The tail is laid along the curve of the hindquarters. The ears point to the rear and are erect, the pinna outward. The forelegs are vertical, the hind-legs rather bent at the hocks". (My translation). This description also fits the giant eland, but the common eland holds the head on the level of or slightly below the withers. This slightly lower head position probably accounts for the fact that the term "majestic", often used with reference to the kudu and the giant eland (e.g. Skinner 1967) is rarely applied to the common eland (see Fig 9A and B).

ALERT AND INVESTIGATORY

The neck is held steeply upwards, and eyes, ears and nose are usually directed towards some stimulus. This posture is similar to the Tragelaphine "Sichern" position (Walther 1964a). In situations involving mild watchfulness, e.g. at the end of a group movement and before settling down to a bout of rumination, this posture is often seen. If there is a particular stimulus, e.g. a sound, causing alertness, the posture is more distinctive and corresponds to Walther's (1964a) "angespannt Sichern". This would be the eland version of "concentrated attention" (Andrew 1972). If the animal is uncertain as to the source of the stimulus, or if it is extremely uneasy, the head is held slightly further back and the ears are rotated rapidly or held pointing to either side, pricked. This would be the equivalent of Andrew's (1972) "scanning". In all cases, the feet are kept still and the animal's weight is evenly distributed over them.

The "concentrated attention" and "scanning postures" give the animal its best field of view and allow almost any other activity to begin immediately, e.g. flight, resume grazing, or approach. They are therefore a combination of investigatory actions with preparation for the next activity, the strength of the two components depending on the results of the initial investigation. There is apparently a continuum between the "concentrated form of alertness" and a pure "investigatory" posture ("Untersuchungstellung" in Walther 1964a). The stronger the "investigatory" component, the more commitment the animal has towards the stimulus,

since/.....

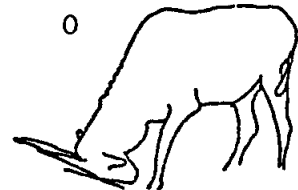
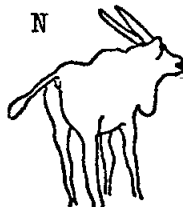
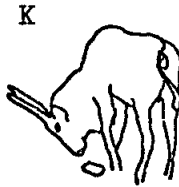
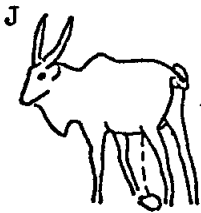
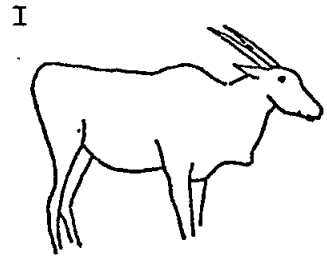
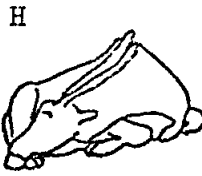
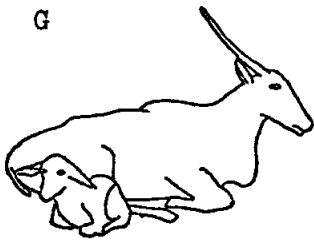
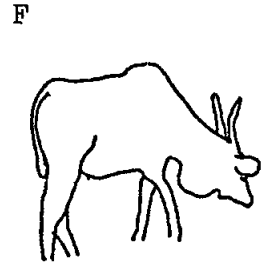
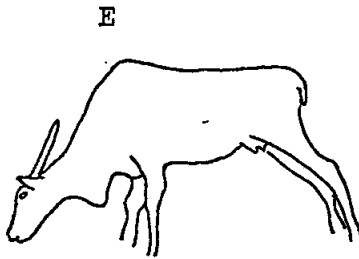
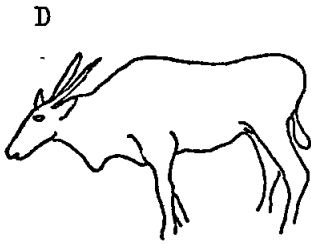
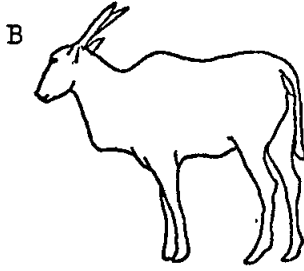
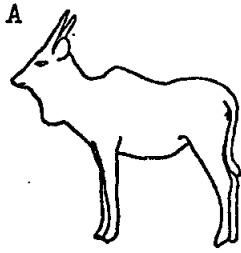


Figure 9. Basic postures and activities in eland at Loskop Dam Nature Reserve and the National Zoological Gardens, Pretoria. June 1972 - May 1974.

- A. "Normal" posture in T. derbianus.
- B. "Normal" posture in T. oryx.
- C. A calf shows rapid "scanning" while a cow in the background shows "fixed attention".
- D. Balanced investigatory posture - the most extreme normally seen.
- E. A cow investigates with unusually strong flight components.
- F. T. derbianus casually sniffing the ground while walking.
- G. A neonate calf lies in "star" formation with its dam.
- H. Sleeping in an adult.
- I. Ruminating posture - assumed after the animal has settled down to its ruminating bout.
- J, K, L, M, N. Forehead rubbing in a yearling T. derbianus bull.
J: the bull urinates while looking around. K: the bull sniffs the urine. L: he laps it briefly. M: he places his forehead in the urine. N: he flehmens.
- O. Forehead rubbing in a T. oryx cow.

since the sense organs are brought as close to this as possible. In cases of great interest, this commitment may involve a shift of balance onto the forelegs, rendering the animal unable to react quickly to any change. When this shift occurs the animal usually takes a step forward, thus restoring a more balanced posture.

The "balanced investigation" (Fig 9D) represents the most extreme posture assumed in normal, non-social investigation. The body is held in balance and the animal can follow with a variety of gross body movements without any further preparation. The question of bodily balance versus investigation also is of interest in the interpretation of visual signals (chapter 6).

Both alert and investigatory head positions may also be assumed while walking. The alert posture causes the head to move in time with the paces, as Walther (1964a) notes for Tragelaphus spp, but the head movement is not as prominent as it is in e.g. the kudu (pers. ob.), probably because of the eland's less slender neck. Eland may freeze in the alert position in mid-step, with one hoof in the air as do kudu (Walther 1964a), but normally they will complete the step and gather themselves into the stationary "alert" posture.

With respect to the investigatory posture "Untersuchungsstellung" Walther (1964a) states that: "The more uneasy the animal is, the lower the nose sinks". This attitude was never seen in an "uneasy" non-social situation in eland, but a rather similar posture was seen when one young animal was given medical treatment. After fighting against the attendants holding it, it relaxed and allowed itself to be handled, but when it was released it lowered its head with ears forward and stood with legs splayed for several minutes before moving. This position corresponds with the very low "postural tonus" of Andrew (1972 : 199) and might be the result of extreme fatigue or else temporary loss of all confidence. The posture illustrated by Walther (1964a : 396) was, however, shown by eland when seen investigating objects at ground level or in social interactions when it functioned as a submissive posture.

LYING

"Lying/.....

"Lying Down"

The actual process of lying is very similar to that in other tragelaphines (Walther 1964a). Adults sniff the ground, sometimes in several places, gather their legs inwards slightly, and arch their backs. One foreleg is bent up at the carpal joint ("Carpalgelenk") and the animal lowers its body onto this joint. The other foreleg is then bent in the same way and the animal allows its hindquarters to collapse slowly. The forequarters are lowered slightly later so that they touch the ground after the hindlegs have fully collapsed. The animal lies with its concave side as the side of the first foreleg to be bent.

"Normal" Lying and Associated Behaviour

The animal lies with the neck held loosely upward and forward from the body. The head is held with the nose forward or with the nose tip slightly lower than the rest of the head. The head itself is slightly above the level of the body. Ears are held back, folded back to the side of the head, or downwards and outwards (Sitzen - Walther 1964a).

The animal may engage in several activities when in the lying position, normally grooming, ruminating, sleeping or doing nothing. Grooming and sleeping involve changes in head position, with the head being brought round to the side for sleeping and placed along the outside of the hindleg (Fig 9H). All grooming actions mentioned in "grooming" as not requiring a specific posture may be seen but "ducking groom", Shoulder and side grooming, and "incomplete grooming" are the actions most often seen. Ruminating does not require any change in posture or head position, but the animal seems to relax slightly so that the head is lower than normal, and the ears are normally in the downwards and outwards or rear-pointing positions.

Although the giant eland were frequently seen to rub their chin and necks on the ground, resulting in a position similar to "Kinnstütze" (Walther 1964a) the common eland were never seen to do this. Giant eland were not, however, seen to sleep in this position.

Occasionally/.....

Occasionally, animals would stretch out one of the fore- or hindlegs, usually the ones on the concave side when lying.

No animal was ever seen to throw itself into the "Schreckliegen" position, unlike the Tragelaphus spp., ("Die Vorderbein nach vorn, die Hinterbein nach hinten weggestreckt"), nor were they ever seen to assume a position that I might consider derived from it.

Very young calves (less than three days) sometimes gathered their legs underneath them when lying, so that the body itself was straight and vertical rather than curved and resting on one side, although there was a tendency to lean slightly sideways (Fig 9G). This posture was seen in calves which were also known to use the more normal lying position.

"Demuthaltung", as a submissive posture when lying, was never seen. This may have been the result of other behaviours obscuring it, since lying calves turned to point their nose to an approaching animal or else to lower their horns to meet a play attack. More serious attacks were rarely seen amongst calves, while amongst adults, the response to a threat from a standing animal was always to rise and move away.

Since rank was uncertain in the calves, I was unable to tell whether lying involved temporary loss of rank, although lying calves frequently received apparently unwelcome attentions from other calves. In adults, the few interactions seen between lying and standing animals were always in the direction of the normal dominance relationship between the two, although lying adults were apparently approached more closely than usual by calves and sub-adults. This situation is rather different to that found by Walther for the Tragelaphus spp, probably because the dominance hierarchy is a more important part of the social organization in eland and is therefore more stable.

Calves slept for long periods, especially when lying out, and seemed able to maintain the sleeping position indefinitely at that time. Adults and calves older than a few weeks, however, rarely maintained the sleeping position for more than a few minutes, the longest recorded continuous sleeping period being six minutes for adults. Prior to sleeping, all age classes sometimes groomed the hindquarters and the area where the head was to lie. This grooming

sometimes merged imperceptibly into the sleeping position proper. Animals were seen to assume the position without sleeping, but rarely maintained it for more than a few seconds unless they were lying out calves.

URINATION AND DEFECATION

The adult female urination posture is the typical bovid "arched back" position with the tail held rigidly out (see e.g. Hafez and Schein 1962, Walther 1964a), although the position is not usually as marked as that in smaller antelope (e.g. gazelles). The adult male posture may involve no more than a brief period of standing in an "normal" position, although the hind legs may be slightly straddled. Female calves may adopt a more extreme position than their elders, especially in the first weeks of life, but even the youngest bull rarely assumes a posture noticeably different to the "normal" stance. As with other tragelaphines (Walther 1964a, pers. obs.), the bull urinates in a slow, weak stream while the cow produces a large volume of urine very rapidly and strongly.

All individuals showed an interest in others' urine, drinking it while it flowed, licking and sniffing it when it was on the ground, and sometimes rubbing their faces in it. Flehmen was almost invariably seen on these occasions. This effect was normally only seen with very fresh urine, and from about a minute after elimination urine rarely evoked any interest. This behaviour was very noticeable in the captive group and, unlike Walther's (1964a) eland and lesser kudu, access to the urinating animal was determined by dominance amongst the females, cows frequently being displaced by higher ranking ones. The motivation to this is uncertain and seemed to vary with time and density of animals in the paddock. Such interest was most common in early summer (pre-calving) and was comparatively rarely seen in free-ranging animals at any time.

Walther (1964a, b) describes "bodenforkeln" (ground horning) and mentions (1964a) that it is often directed towards urine and faeces in Tragelaphus spp. Both eland species show a distinct but similar behaviour with reference to their own and other's urine (Fig 9 J - 0). The action never included horning motions, although

these sometimes followed it, but the animal distinctly placed its forehead flat onto the ground and rubbed it. The action was also seen directed to other stimuli, e.g. salt, water, or mud. Once a pool of urine was "rubbed" eland lost interest in it.

Adults would rarely change posture or even interrupt their on-going activity, e.g. grazing, while defecating, merely flicking their tails from side to side, probably to ensure that the pellets did not become attached to their coat. Calves less than a month old were seen to strain in a squatting position similar to that seen in small antelope (e.g. grey duikers, gazelles - pers. obs.), occasionally giving faint grunts, and producing only small amounts of very liquid faeces.

Faeces from older calves and adults were small solid pellets. The water content of these seemed to vary with vegetation and water availability, with moister, more clinging pellets being produced in spring and summer.

There were no preferred places for defecation or urination, but some stimuli seemed to facilitate urination e.g. pressure on the rear and flank from another individual, or the sight or scent of urine. Both urination and defecation often followed rising after a prolonged bout of lying and periods of intense activity (fighting, flight).

COAT AND SKIN CARE

GROOMING

This is taken to involve two activities, scratching and licking. Walther (1964a) mentions gnawing (with the incisors) and nibbling (with the lips) as playing an important part in the grooming activities of Tragelaphus spp., but I rarely saw these in the Loskop eland. As with Walther's (1964a) animals, all accessible areas were apparently groomed by the hind hoof, the horns and the mouth. The front hoof was never used in this way, probably because eland cannot balance properly on two hind legs and one front leg. Animals were often seen to jerk their foreleg upwards and backwards during a grooming bout, but the hoof never touched any other part of the



body. Scratching did, however, involve rubbing on various inanimate objects; the areas rubbed being mainly the face and neck regions, but the flank was also rubbed from time to time and on at least one occasion I saw a cow straddle a fallen tree and rub her chest, stomach and udder. This rubbing is directed mainly towards objects which seem to be suitable as scratching posts, e.g. rough-barked Acacia trees rather than Combretum spp., and I have no doubt that comfort is the main purpose of this activity (but see "chemical communication" in chapter 6).

Motor Patterns Involved in Grooming

These are mainly distinguished by the positions of the head relative to the body, by the speed of the movements involved and by the basic posture.

Grooming the Foreleg

One foreleg is extended forward and placed on the ground about 25 cm in front of the other. The animal lowers its head and licks at the area just above the hoof, although it may then extend its licking further up the foreleg in the same position. In this, as in other licking, the incisors appear to come into contact with the fur and may therefore aid grooming. In this position, the horns are pointed forward and upward at an angle of from 45° - 90° to the horizontal.

Grooming the Shoulder and Side

The animal turns its head to one side and licks at the coat without any sharp movements or changes in posture. This activity is frequently seen in various situations.

Grooming the Hindquarters

The animal reaches round to the rear and licks at its flanks and haunches, sometimes reaching as far back as the base of its tail and the anus. In performing this action, there is an increasing tendency to arch the body outwards from the side being groomed and in the process the tail is curved around towards the inside of

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the arc. At the extreme, most of the animal's weight seems to be over the two outermost legs (i.e. away from the side being groomed). This activity appears to be characteristic of intensive bouts of grooming.

Ducking Groom

The animal swings its head round rapidly from the front to the hindquarters, usually resulting in the nose and mouth hitting the side at just about the top of the hindleg. There is sometimes an audible "smack". The action may precede a bout of inguinal grooming, but will also occur in a variety of other contexts. It appears to be aimed at driving away flies or relieving local irritations.

Grooming the Udder or Penis

This action again involves bending to the rear and arching the back laterally, but in this case the inside rear leg is frequently lifted, so that the animal is tripodally balanced. The nose is thrust into the inguinal region and the udder or penis is licked. As with the more extreme forms of hindquarter grooming, the action is typical of intensive grooming bouts, probably because of the special posture and balance involved.

Scratching the Ear

The head is lowered, nose forward, horns tilted back, and the hind hoof is brought forward outside the foreleg and is used to scratch the base of the ear, the ear itself being held slightly below the horizontal and to the front of the head. The side of the face and the horn bases may also be scratched, but there seems to be little control over the exact area being scratched away from the ear itself. I never saw an animal scratch any area away from the head and the very top of the neck using this method. The hoof is often sniffed after scratching.

Scratching the Back

The horns are lowered onto the back and used to scratch the

dorsal ridge and all other areas accessible without a change in the basic posture (Fig 8). These areas include a large portion of the forequarters, and the head may be tilted so far back that the throat is almost vertical.

Scratching the Anal Region

The head is twisted to the side so that one horn tip can be brought upwards to meet the base of the tail. This again may involve a special balancing posture, although some animals seem able to scratch without any great difficulty.

Headshake

The head is twisted sharply in one direction and then the other, around the axis of the neck. This action may be superimposed on a head lowering movement, usually with the horns either vertical or pointing slightly to the front. The speed of the action is often enough to cause the ears to flap audibly. The headshake is often combined with, or superimposed on, non-grooming activities.

Incomplete Grooming Movements

These are often performed very quickly and represent the initial stages of the movements listed above. They often appear along with skin tremors and may be directed toward flies rather than to any particular part of the body. They are also very typical of disturbance behaviour, and frequently appear after the animal has been startled into trotting a short distance.

Head Toss

This may be regarded as a special case of an incomplete grooming movement. The head is swung rapidly upwards and the horns both pass on one side of the neck. The action may be superimposed on a head-lower motion, so that the nose is forward and almost horizontal and below the level of the body, or it may involve throwing the head right up so that again the throat forms an almost vertical line. This action is also characteristic of disturbance situations although it often occurs in undisturbed grooming (Fig 8).

OTHER SKIN CARE ACTIVITIES

Foreleg jerking has already been mentioned briefly, but it is of further interest because it is involved in several non-grooming situations. It is often seen in combination with skin tremors in the chest region and during bouts of grooming, but it sometimes occurs (both with and without skin tremors) when the animal is slightly disturbed or alert. This action may represent the only response to sudden cutaneous irritation that the animal is capable of making when its senses and therefore its head orientation are fixed on something else. There is a similar action of the hindleg in such situations, but in its extreme form, the foreleg jerk suggests pawing the ground, and this is even more noticeable in T. derbianus.

Eland seem capable of controlling skin tremors in various parts of the body, but the main areas where these were seen were the chest, the base of the dorsal ridge and the haunches. The tail is frequently swished during bouts of grooming especially those following disturbance, and it may be used almost continually during late summer, probably to drive flies away. It does, however, also play a part in agonistic situations. As with most ungulates, the ears are very mobile and are frequently flicked during grooming bouts, either unilaterally or bilaterally, otherwise they are either held downwards and outwards or else oriented towards the part being groomed. The T. derbianus couple often rubbed their necks and chins at full extension on the ground while lying, but this very rarely happened in the common eland.

OTHER COMFORT ACTIVITIES

Yawning, shaking the whole body and stretching were most often seen when eland stood up after a long period of lying. There were two basic "stretching" positions: firstly with the feet gathered inwards slightly and the back arched ("Katzenbüchel" of Walther 1964a), and secondly with the forelegs upright, the hindlegs extended back and the whole back sloping towards the rear. In both positions the tail was curled around the one side, often with the tip reaching up to the level of the backbone.

Yawns were silent and rare. They were performed with the mouth wide open and the tongue extruded and curled at the tip. Coughs and sneezes were rarely seen or heard in the field, but were sometimes stimulated in the captive eland by finely ground lucerne. Sneezes were much the commoner and caused the animal to thrust its head forward in a low, flat position and arch its back slightly in the more violent cases. Both coughs and sneezes were fairly quiet.

Fresh wounds or scratches were rarely seen, except for the most superficial types, but it seems that the eland has no way of caring for them except to lick them. Open wounds stimulated investigation from others, who sometimes gave a flehmen after sniffing the blood. When the population suffered severe ear infections, probably tick mediated, I repeatedly saw one cow scratch the inside of her ear with her hind hoof, sniff the hoof, lick it, then flehmen.

FEEDING

While feeding preferences and other ecological aspects of the eland's behaviour are considered elsewhere, the actual postures and some of the motor patterns involved are described here, since they are of importance in understanding the interactions and displays described later.

GRAZING

When grazing, the eland may show two forms of behaviour: "intensive" grazing and "casual" grazing. In intensive grazing, the animal remains in approximately the same spot for several minutes, occasionally stepping forward to another feeding station. In this position the animal's head is normally held down at ground level for long periods, although it may lift its head from time to time in the "alert" posture as it chews some large plant part.

In "casual" grazing, the animal is continually moving. It lowers its nose in investigation of the ground after which it may or may not take one or two bites. There is, in fact, a continuum between "intensive" grazing and normal walking, but the grazing activities described above are "typical forms" (Tinbergen 1964)

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which occur much more frequently than intermediates. "Casual grazing" often occurs in transitions between grazing and other activities; it is also seen during most slow walking activities, where an animal is continually sniffing towards the ground as it walks, sometimes taking a bite of some herb or grass as it passes.

The eland uses both activities in feeding on the herb level of the vegetation.

BROWSING

In feeding off shrubs and trees, the animal shows two distinctive behaviour patterns: firstly fixation of attention on the plant, approach and feeding from the available leaves; secondly, hooking the horns into the branches of the taller trees and breaking off otherwise inaccessible foliage. The latter activity may involve branches or saplings up to two inches thick, and the animals are very persistent in their attempts. Both of these behaviour patterns are very conspicuous to other eland in the group, especially when a particularly large branch is being broken (Fig 10).

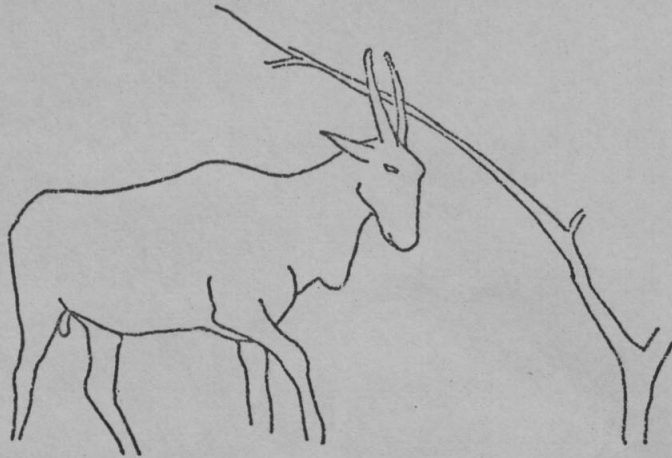
ORIENTATION TO OBJECTS

Walther (1964a) extensively catalogues the lying orientation of Tragelaphus spp. with respect to the objects in the environment, particularly to other individuals. His "Ster" formation of lying animals was only infrequently seen in either wild or captive eland (Fig 8). The ground at Loskop was very broken and normally on a slope, therefore substrate preferences may have prevented this behaviour from appearing by limiting the number of places available for lying. Animals did, however, lie together when ruminating and I saw many instances of eland seeking out other animals to lie with. Among other things which governed orientation were: slope (animals lay with their convex side facing uphill), shadows (which were sought out mainly in summer), large, solid objects, (which the eland kept their backs towards) and objects of interest or fear (which the animals would face).

These factors also governed orientation when standing, especially the presence of objects of interest or fear, which would be

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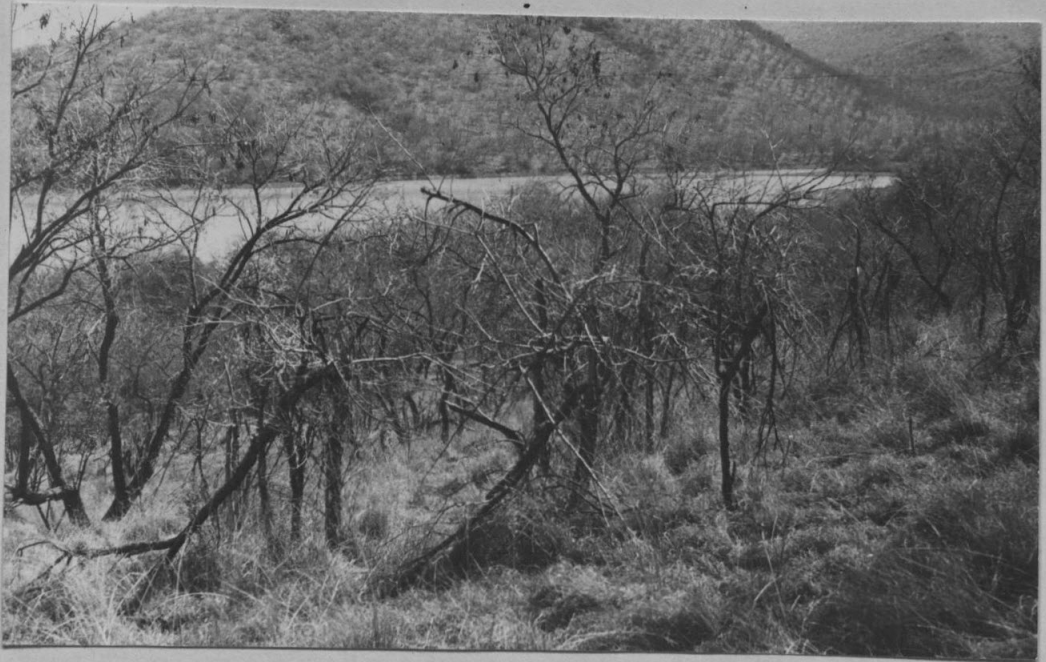


Figure 10. Branch breaking in eland at Loskop Dam Nature Reserve,
June 1972 - May 1974.

A. A cow breaking down a sapling.

B. The results in an intensively used area.



continually examined with groups larger than three or four individuals. This resulted from the individual members of the group watching the object from time to time, in such a way that there was usually at least one watchful animal. This sounds like a "guard" system, but I did not see a particular sequence of guards or particularly alert animals, so I conclude that the situation results from the unease of individuals who reassure themselves from time to time and only coincidentally is there continual wariness. The unease may, of course, be facilitated or diminished by the reactions of others.

CHAPTER 3

GENERAL ECOLOGY

Aspects of eland ecology are included in several general studies of areas or ecosystems (e.g. Vesey-Fitzgerald 1960, Lamprey 1963, van Zyl 1965, Wilson 1969a, Hendrichs 1970, 1972). As eland are usually timid and difficult to observe when free-ranging, they are often only mentioned in passing even when constituting a major part of the herbivore biomass (e.g. Mason 1973). Although population structure and feeding habits are known in some areas for semi-domesticated or restricted populations (van Zyl 1965, Kerr, Wilson & Roth 1970, Hofmeyr 1970), field observations are limited (e.g. Lamprey 1963, Abbott 1968a, b) except where animals are being shot or captured (Wilson 1969b).

Feeding habits and population structure are important in determining the social organisation of species (see e.g. Crook 1970, Jarman 1974) and the organisation of eland activities through the year reflect changes in the influences of these factors on their social behaviour.

POPULATION STRUCTURE

Due to the nature of the terrain and the mobility of the animals, I was unable to survey the population systematically. The ratio of animals in sightings of fully classified groups away from the camp area (i.e. squares L5, L6 Fig 3) was:

0.66 bulls : 1 adult cow : 0.13 subadult bulls : 0.12 subadult cows : 0.42 juveniles : 0.59 unweaned calves in June 1972 - May 1973, and 0.44 bulls : 1 adult cow : 0.15 subadult bulls : 0.16 subadult cows : 0.54 juveniles : 0.49 calves in June 1973 - May 1974. Since all unweaned calves in the population may be assumed to be in the central nursery herd at some time during October - January, the maximum count of calves in this period should represent the number of calves in the unweaned class. Using the above ratios and the unweaned calf maximum gives a population of 69.23 animals in 1972 -

73 and 74.56 in 1973 - 74. These figures are supported by a 1972 aerial count of 70 individuals.

Eland females kept on a high plane of nutrition may bear calves while in the "subadult" class (i.e. $2\frac{1}{2}$ - $3\frac{1}{2}$ years old - Skinner 1967, Roth et al. 1972). However, this seems unlikely at Loskop, and calves may therefore be assumed to have adult dams. Contrary to early reports (e.g. Lydekker 1894), most eland cows apparently calve at approximately yearly intervals. This, for Loskop, gives a potential from the ratios of 24 calves in 1972 and of 27 calves in 1973 (Table 2). The fact that calf numbers were lower than this in both years reflects both mortality in this class and the fact that the dams of the captive calves were included in the sightings while their calves were not. Taking known mortality, miscarriages and captive calves into account, the actual calf production was nearly the same as the potential calculated from sighting ratios. This correspondence is, however, suspect, since calves dying in the field are unlikely to be traced and included in the mortality count. The maximum sightings of calves were in December/January for both years, so that the majority of calves were in the four to five month age class, but the sightings contributing to the ratios include many in the one to four month age class during the previous months. From studies of other antelope (e.g. Joubert 1970, 1974) mortality in calves appears to be concentrated in the first month of life, which would result in an error, since these calf sightings are included in the calf ratio which is then divided into the December/January maximum to give an estimate of the population size. This would result in an underestimate of the overall population size and of the proportions of the other classes within the population. These figures are therefore minimum estimates. My own impression is that they underestimate the actual eland population, but probably by less than ten percent.

The structure of the population (from sightings) is represented in Fig 11. The numbers of animals in the younger classes were probably seriously affected by the practice of removing calves from the population. Sometime prior to the study a dozen calves were removed, which presumably reduced the proportions of animals in the juvenile and subadult classes. In addition, four calves were kept

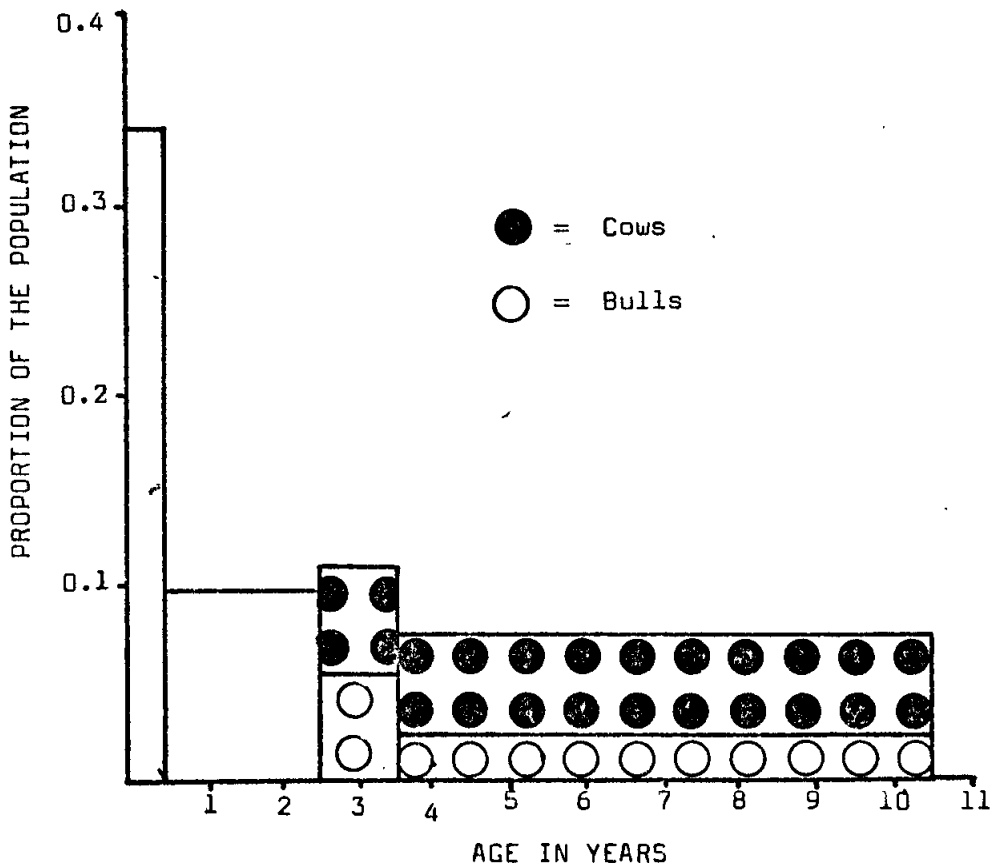
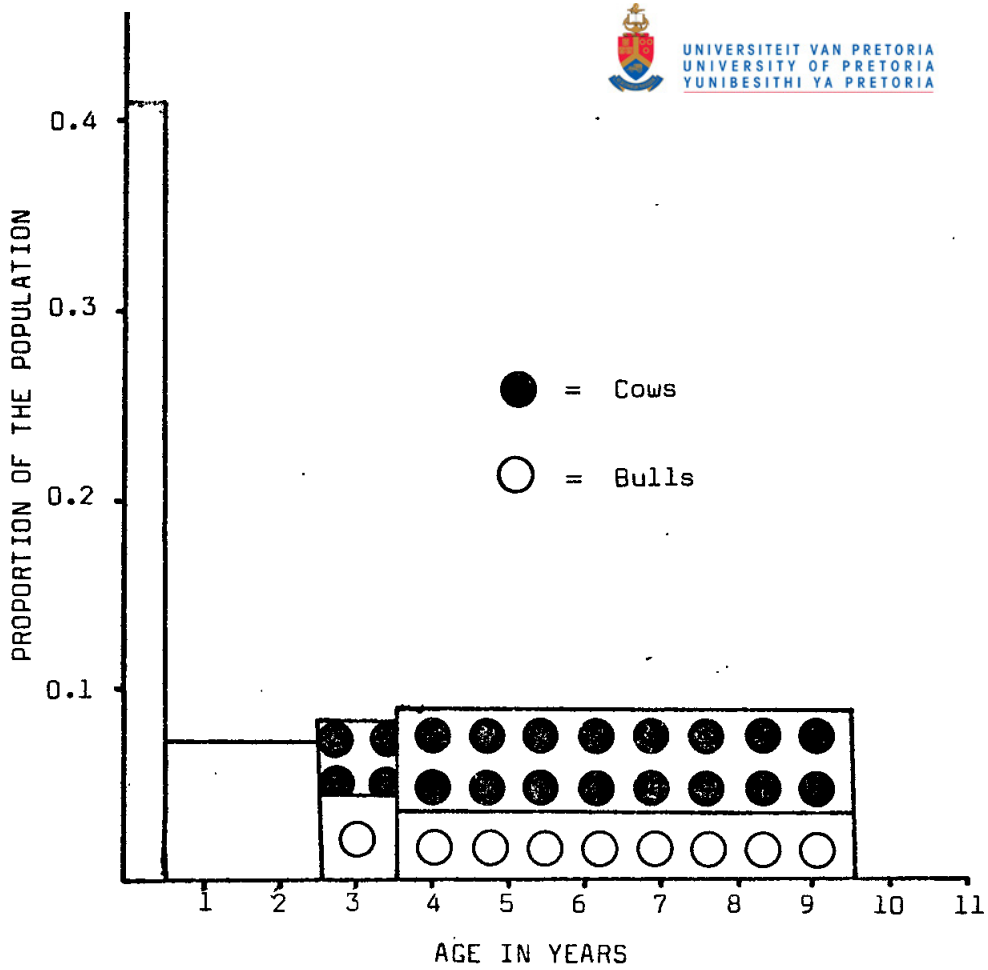


Figure 11. Calculated population structure of eland at Loskop Dam Nature Reserve.

A. June 1972 - May 1973.

B. June 1973 - May 1974.

in captivity in 1972 - 73 and up to nine in 1973 - 74. This also probably affected the population structure (compare proportion of calves in 1972 - 3 with that in 1973 - 4).

Table 2 : Potential calf production of eland at Loskop Dam Nature Reserve, June 1972 - May 1974. Calculated from the proportion of adult cows in the population

Calculated calf crop	June 1972 - May 1973	24
Maximum calves sighted	June 1972 - May 1973	14
Calves in captivity		4
Known mortality prior to maximum sighting		3
Miscarriages		1
Calculated calf crop	June 1973 - May 1974	27
Maximum calves sighted	June 1973 - May 1974	13
Calves in captivity		9
Known mortality prior to maximum sighting		0
Miscarriages		2

There is a significant difference in the overall distribution of age classes in 1972 - 73 and 1973 - 74. ($\chi^2 = 14.28$, $df = 5$, $P = 0.02$). The adult male and juvenile classes are the main contribution to this difference ($\chi^2 = 7.95$, $df = 1$, $P < 0.01$; $\chi^2 = 3.43$, $df = 1$, $P < 0.02$ respectively). The juvenile increase is to be expected, since the large removal of calves prior to the study was not repeated in 1972 - 73, giving a higher recruitment to the juvenile class in 1973 - 74. The more significant change in the proportion of adult males represents a decrease in their numbers (16 in 1972 - 73, 12 in 1973 - 74), despite recruitment from the subadult class. This was probably due to several factors e.g. in December 1972, an old eland bull was shot, having become dangerously aggressive; in winter 1973, two bulls and a cow

were reported outside the main fence on the south side of the reserve, and as they remained there during the spring and early summer at least they were never recorded during sighting surveys; in the same winter at least one adult bull died, possibly from snakebite.

Even if the calf count was a gross underestimate, which seems highly unlikely, the proportion of herd founders and of second generation calves (protected for the first year or so of life) contributing to the female reproductive pool was very high considering the length of time that the herd had been established. At least nine of the original cows were calving every year, while many of the remaining cows had ear tags (or holes from tags), indicating that they were born in captivity during 1966 - 1967.

DAILY ACTIVITY PATTERNS

Figure 12 shows that the main difference in daily activity patterns of eland in the dry and rainy seasons is in the distribution of time spent on diurnal feeding activities. In winter, there are periods of grazing alternating with rumination, while browsing tends to occur in the early morning and evening. In summer, on the other hand, there is a distinct tendency for animals to ruminate during the afternoon, while browsing has a three to four hourly cycle throughout the day, usually at the expense of grazing (the records from 06h00 till 08h00 are limited, since I was looking for rather than at animals at that time). The distribution of activities throughout the day reflects habitat utilisation. Phases of walking punctuate the other activities, but are underemphasised here since walking bouts were too short for the original sampling period - walking bouts were from ten to twenty minutes long, concentrating around ten minutes and the original sampling periods were fifteen minutes. In addition, once groups had started to move, it was rarely possible to record their subsequent activities because I often lost sight of them for up to an hour while reaching a new vantage point.

During winter there were four main phases of activity during daylight in the "typical" group. The earliest was a sequence of intensive feeding, then ruminating followed by walking; this often

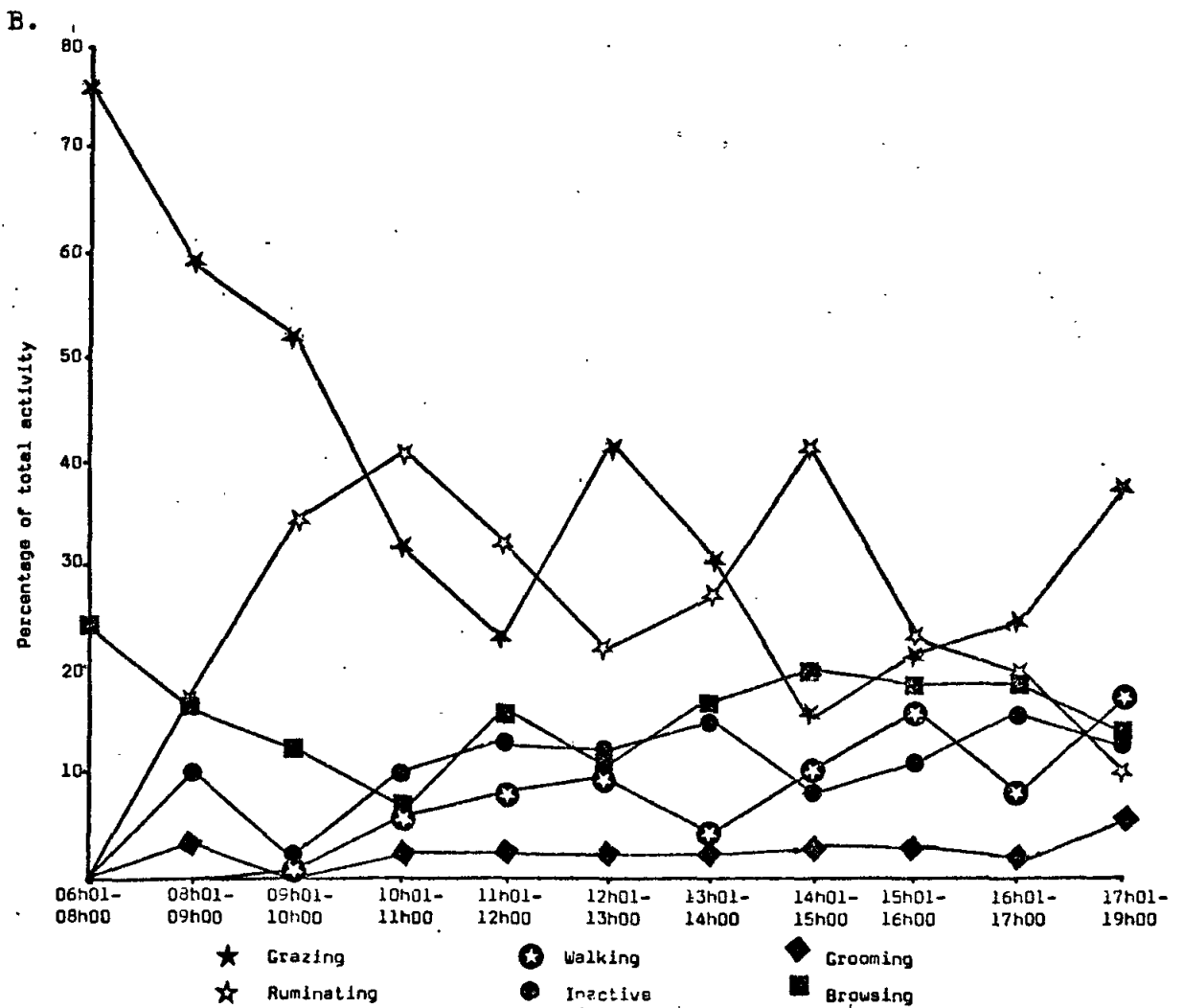
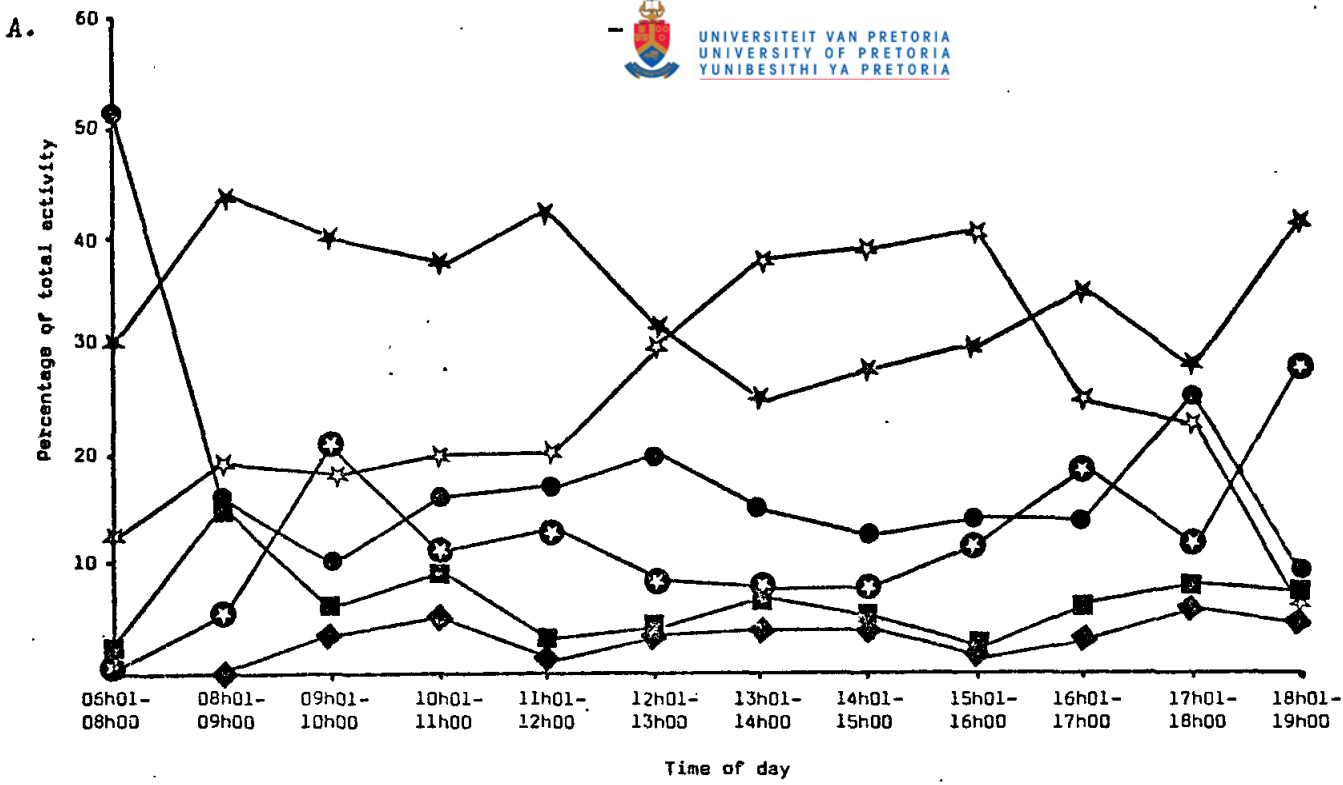


Figure 12. Daily activity cycle in eland at Loskop Dam Nature Reserve June 1972 - May 1974.

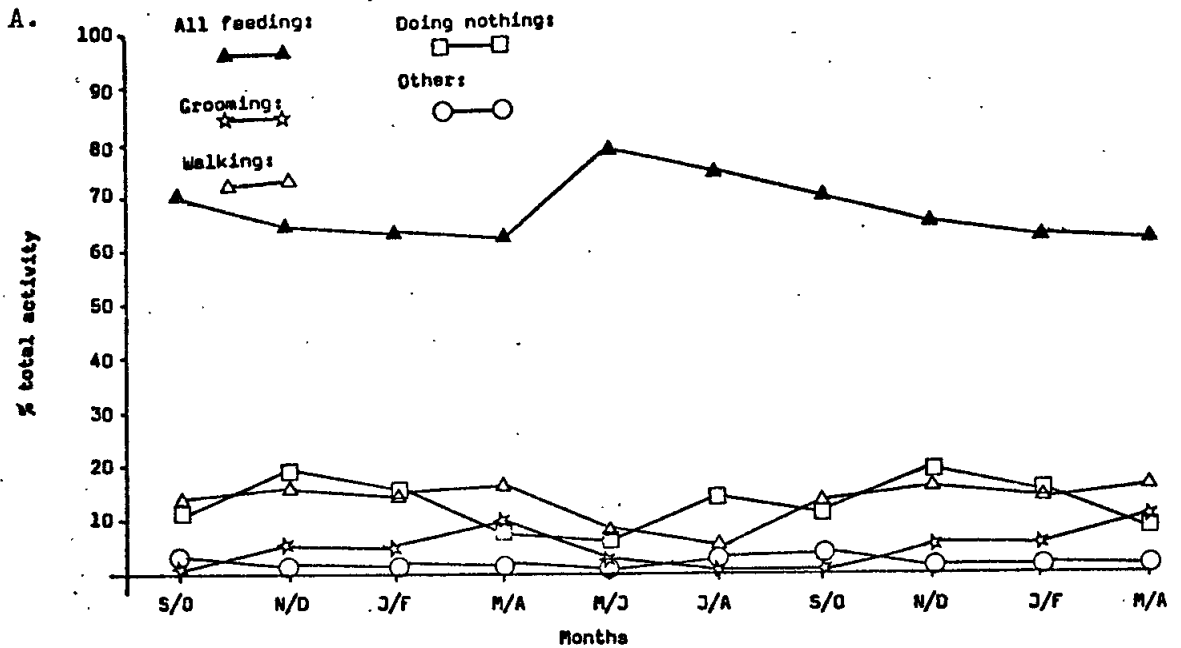
A. Time spent on activities during rainy season.

B. Time spent on activities during dry season.

involved a move from one vegetation type to another and was frequently either uphill or out into the open flats from the lowland woodland areas. At noon and in the early afternoon, the groups would feed and ruminate in approximately the same spot for two hours or more, then begin a walking/browsing bout, usually moving into the wind. Later the animals may turn about after a brief, stationary period and move downwind again (see Chapter 4). The various halts were usually in distinct vegetation types, but no pattern of movement was very obvious; in fact, the behaviour of the "typical" group is best expressed in terms of tendencies rather than distinct bouts.

These tendencies describe the typical winter groups behaviour, but there was considerable variation from one day to the next. The areas utilised were rarely identical two days running, and the actual sequence of movement and activities was never repeated exactly - even by the dams of the captive group, who were limited to the area around the camp and were kept to a fixed feeding timetable. For this reason, I could never be sure how much the daily activity pattern was governed by the area and the elands' knowledge of it, how much by internal cycles, and how much by opportunism. Each of these presumably plays a part: no activity ever occurred exclusively at any particular time, but there were distinct peaks, suggesting that an internal clock partly governs the activities; opportunism was seen in the concentration of animals around food supplements regardless of the time of day; knowledge of the area was indicated by the direct movements of animals to and from stands of vegetation and similar resources - trips to licks and water might be made throughout the day and had the appearance of deviations from the day's route.

The summer activity pattern was rather different in several ways. Although the day was longer, most activities showed fewer peaks. This is most obvious in active feeding, in ruminating and in walking. This is probably an adaptation to the afternoon heat, since the main resting activity has its peak from 14h00 - 17h00. It is not the whole story, since the other two main "resting" activities, grooming and doing nothing, are not synchronised with this, although total resting activities still show the afternoon peak.



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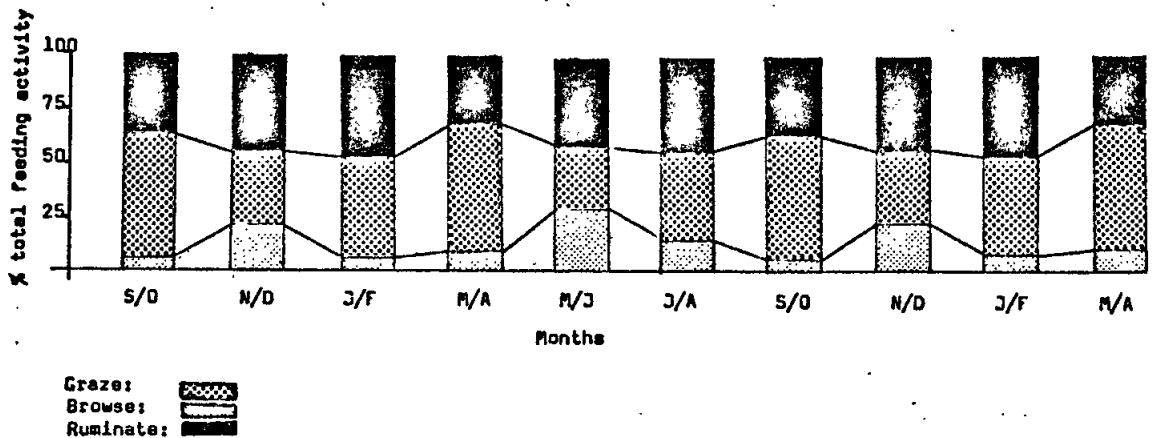


Figure 13. Annual cycle of activity in eland at Loskop-Dam Nature Reserve, June 1972 - May 1974. Both cycles partly repeated to show curve more fully.

- A. Relative proportion of time spent on all activities.
- B. Relative proportion of time spent on feeding activities.

The typical summer group was therefore usually sighted either resting or feeding in the open, fed intensively, then made a fairly long (0,5 - 1 km) move during the early morning, followed by a slower group movement as the animals grazed along. The group then slowed to a stop (or showed a short phase of walking, then stopped), after which the majority of animals ruminated and some members continued feeding. This afternoon resting bout finished abruptly when the whole group began moving and feeding again, normally upwind. This move was sometimes followed by a halt and a change of direction at sunset (see Chapter 4). Feeding began to increase in the late afternoon and presumably peaked again after dark (see Hofmeyr 1970). Once again, the areas and vegetation types used were highly variable and the "timetable" given is a description of tendencies rather than of distinct patterns regularly observed.

ANNUAL ACTIVITY CYCLE

The proportion of time spent by eland on various activities throughout the year is summarised in Fig 13. Ruminating is included as a feeding activity in Fig 13, since it is a form of food processing; active feeding alone (i.e. the process of obtaining "raw" food from the external environment) might have been misleading. Since the indications are that eland do more active feeding during the night in summer than in winter these records apply only to daytime activities. Much more time is spent on feeding activities during the dry season than in the rainy season. All non-feeding activities show an increase during the rainy season, the most prominent being "inactive" (Table 3). This presumably reflects either increased inactivity because of daytime heat, i.e. it may be an artefact of daylight-only observations, or else the lack of need for other activities: e.g. food is more nutritious, therefore there is less feeding. Since walking also increases at this time, and ruminating (the main resting activity) increases relative to other feeding activities, neither explanation is complete in itself. The increase in "walking" is a result of much clearer divisions of activity in summer; although animals probably move greater distances during winter, these movements are usually part of grazing



Table 3 : Proportion of time spent on activities by eland at Loskop Dam Nature Reserve in the dry and rainy seasons.

	<u>Dry season</u>	<u>Rainy season</u>
Doing nothing	0.10	0.19
Ruminating	0.24	0.22
Grooming	0.02	0.03
Walking	0.07	0.12
Grazing	0.39	0.34
"Normal" browsing	0.14	0.06
Browsing off branches broken down with the horns	0.02	0.01
Other activities	0.02	0.02

Table 4 : Correlation of protein and fibre content of grasses and weighted mean monthly group size with monthly feeding activities in eland at Loskop Dam Nature Reserve June 1972 - May 1974. (Spearman r)

	<u>Fibre content</u>	<u>Protein content</u>	<u>Group size</u>
% time spent on all feeding	+ 0.677 *	- 0.654 *	0.831 **
% time spent on active feeding	NS	NS	0.690 *

* : $p = 0.01 - 0.05$

** : $p = 0.001 - 0.01$

NS = not significant

or browsing bouts - summer feeding is much more stationary and is interspersed with bouts of "pure" walking. Grooming reaches its maximum somewhat later than the other season peaks, probably because insect pests continue to increase until cold kills most of them off.

The annual cycle of activities, particularly feeding activities, is highly correlated with cycles in rainfall, vegetation and other aspects of the ecology of the eland (see Chapter 4). In the short term, the temperature, rainfall and the various nutritional values of the plants taken, are so inter-related that it is not possible to distinguish the effects due to any particular factor (compare Figs 4, 5, 12 and 13). However, the nutritional content of the available food is probably the most important single factor directly affecting eland at Loskop; surface water is always available, the temperature rarely drops far below freezing, there is no winter snow, and summer temperatures are high but not unbearable. Figure 13 involving bi-monthly averages, obviously shows very similar curves to several of the main nutritional components. When the results are compared on a monthly basis, the correlation is less complete but is significant (Table 4) for all feeding although not for active feeding. Since the values refer to only a particular part of the food resources of the eland, it is not surprising that the correlations, although significant, are not near unity.

When the time spent on feeding is compared with group size, the correlation is higher (Table 4), suggesting that if the food values available to eland at all strata could be assessed, the effect of nutrition on eland activities would be seen to be much stronger.

FOOD SELECTION

The food selected by eland is highly variable, depending on availability, preference and, apparently, nutritional requirements (Skinner 1967, Kerr, Wilson & Roth 1970). Availability presents a particular problem at Loskop because of the mosaic of vegetation types, which vary in composition even in different stands of the same type. An eland's daily movement might take it through many such stands. In addition deciduous and pod-bearing trees, for instance, will have different biomasses available at various times of the year.



While such considerations are certainly important to the eland (see Chapter 4), they could not be quantitatively assessed. Even in the short term, it was rare to find consistent use of a single vegetation type or even regular use of several types.

In one sequence of observations, several cows were using one area and fed almost completely in the Acacia caffra - Combretum apiculatum - Themeda triandra tree savanna (Theron 1974) of the squares M5, N5 and O6 (Fig 3). These observations were made from June 25 - July 13 1973 and are summarised in Table 5, with the importance values of the species found in two surveys of that vegetation type in that area (taken from Theron 1974). For the sake of simplicity in recording, I considered a "selection" to have occurred whenever the animal stopped feeding on one individual plant and started to feed on another. This method was used because of the shyness of some individuals in the population. It may however, be criticised, since a variety of plant species with widely differing structures were eaten. The observations cover the "shrub" layer of the vegetation i.e. all dicotyledenous plants below two metres in height. All plants eaten above half a metre in height were identified, but below that level identification was less successful.

In a more general way, preferences were shown in the vegetation utilised. The records given in Table 5 refer to only one half of these elands intake at that time. The rest of the diet consisted of the centres of grass tussocks, forbs too small to be identified before being eaten, and litter. The proportions of this "grazing" to browsing varied considerably throughout the year (see Fig 13). Eland feeding on freshly burnt areas in summer necessarily ate only grass or else browse from over one and a half metres off the ground i.e. the regrowing or untouched sectors of the vegetation; some licking of ash and eating of litter and scorched browse was seen, but was rare. As the burns greened over, eland concentrated first on the regrowing grass tussocks, then switched to forbs and to young grasses. Similar changes occurred throughout the year and from one vegetation type to the next: even in midwinter the eland were not limited to one food

plant/.....

Table 5 : The utilisation of an Acacia caffra - Combretum apiculatum Themeda triandra community by eland at Loskop Dam Nature Reserve when feeding almost exclusively on it in mid-winter.

Species	Importance value (a)			Percent of selection
	Stand 104	Stand 102	Average	
<u>Combretum apiculatum</u>	31.8	8.5	20.15	4.3
<u>Acacia caffra</u>	36.3	22.6	29.45	38.8
<u>Lanea rugosa</u>	31.9	29.3	30.6	-
<u>Lanea discolor</u>	-	4.7	2.35	0.4
<u>Asparagus suaveolens</u>	2.2	4.7	3.45	*
<u>Dombeya rotundifolia</u>	41.6	62.9	52.25	0.8
<u>Lipia javanica</u>	1.1	80.6	40.85	1.2
<u>Dichrostachys cinerea</u>	1.1	15.1	8.1	20.1
<u>Argyrolobium transvalensis</u>	68.7	-	34.35	-
<u>Combretum zeyheri</u>	7.6	5.6	6.6	1.6
<u>Ozoroa paniculosa</u>	-	5.6	2.8	0.4
<u>Euclea crispa</u>	7.9	5.6	6.75	9.4
<u>Rynchosia nitens</u>	2.2	-	1.1	0.8
<u>Combretum heterotense</u>	9.3	-	4.65	*
<u>Acacia nilotica</u>	-	17.0	8.5	0.4
<u>Securinea virosa</u>	8.1	-	4.05	*
<u>Asparagus africanus</u>	4.2	5.6	4.9	*
<u>Combretum molle</u>	8.8	-	4.4	5.5
<u>Acacia karroo</u>	1.5	9.4	5.45	2.7
<u>Rhus leptodictya</u>	5.9	3.8	4.85	7.5
<u>Atrixia elata</u>	10.5	-	5.25	-
<u>Ximenia caffra</u>	-	1.9	0.95	*
<u>Maytenis heterophylla</u>	1.1	-	0.55	2.7
<u>Grewia monticola</u>	1.1	5.6	3.35	*
<u>Heteropyxis natalensis</u>	7.0	-	3.5	-
<u>Rhoicissus tridentata</u>	-	3.9	1.95	*
<u>Triumfetta sonderi</u>	2.4	-	1.2	-

Table 5 - continued

<u>Asdepias burchellii</u>	1.1	1.9	1.5	-
<u>Berchemia zeyheri</u>	1.1	-	0.55	-
<u>Grewia flava</u>	2.2	-	1.1	*
<u>Faurea saligna</u>	-	1.9	0.95	2.7
<u>Polygala hottentotta</u>	-	1.9	0.95	-
<u>Pterocarpus rotundifolius</u>	-	1.9	0.95	-
<u>Rhus zeyheri</u>	1.1	-	0.55	0.8
<u>Grewia occidentalis</u>	1.1	-	0.55	*
<u>Ochna pretoriae</u>	1.1	-	0.55	*

* = species known to be taken by eland at Loskop, but not observed being eaten during June 1973 in the Acacia caffra - Combretum apiculatum - Themeda triandra community.

(a) = From Theron 1974, using Louw and Grunow's (1969) importance value : $BW = (2 \times R\%D) + R\%F$.

$R\%D$ = relative percentage density

$R\%F$ = relative percentage frequency.

('Relatiewe persentasie digtheid', 'relatiewe persentasie frekwensie' respectively).

plant, or even one stratum of the vegetation. In one vegetation type e.g. the hygrophilic communities, the lowest level may bear the main winter food plants - still-green grasses, Olea africana seedlings (a favoured food), and forbs. Nearby in the Acacia communities, the main food source would be the higher vegetation levels - evergreen Euclea crispa, Acacia leaves, even, towards the end of the dry season, blossoms.

Eland are capable of considerable selectivity with regard to the plant parts eaten. Depending on the plant, they can use a very fast nibbling motion of the lips, stripping even very young



leaves off thorny plants but avoiding the thorns themselves. They may also nip quite small parts off with their lips or between their incisors and palate or they may draw plants through their mouths sideways, stripping off all soft tissues but leaving the woody stem. On the other hand, they may bite an old thorny twig off and eat it completely. The more delicate feeding seems to rely on the natural weak spots of the plant: the "nibbling" action moves the lips over about 6 - 8 cm (i.e. the width of the mouth) of stem at a time and is applied to the whole of that part of the plant. The more loosely attached leaves are dragged off, leaving the central stem (and the leaf ribs in Acacia species). When there is neither a distinct weak spot nor a strong base of attachment, e.g. in small forbs or old browse, feeding is on a much coarser level, twigs or whole plants being taken rather than leaves or stem tips. Other specialised feeding techniques include breaking down branches with the horns, and digging at the soil, again with the horns, to unearth roots and tubers (this was seen only once at Loskop, although it may be more common in other populations - Dorst and Dandelot 1970). Shortridge (1934) and Stevenson-Hamilton (1947) report eland going onto their hindlegs to reach leaves, resting their forelegs on the trunk of the tree. Stevenson-Hamilton records one animal dying as a result of a fall from this position. This feeding position was not seen at Loskop.

DISCUSSION

POPULATION STRUCTURE AND COMPOSITION

The structure of the population derived from sightings has several sources of error (see p39) but the relative proportions of each age class given are probably reasonably accurate. The high mortality of unweaned calves is surprising, considering that there are few predators at Loskop larger than black backed jackals (Canis mesomelas). There are, however, some leopard (Panthera pardus) and brown hyaena (Hyaena brunnea), both of which may take domestic stock of the same size as eland calves (Bearder, pers. comm.)- Roth et al.(1972) also attribute some losses of eland calves to jackal predation. There were, however, no definite signs

of predation on Loskop eland. All known mortalities were due either to accident, disease, or unknown causes - the latter deaths were usually attributed to snakebite.

In a semi-domesticated herd of eland in Rhodesia, mortality during the first months of life was 32% (Roth *et al.* 1972), which was mainly caused either by difficulties with the birth itself or else by poor mothering by the dams. In either case, such a calf would be unlikely to be sighted in the wild, which may account for the low maximum of calves sighted and would indicate that the population size is underestimated. When calves were kept in captivity at Loskop, the survival rate from birth to weaning was 80 - 100 per cent. Animals kept after this age almost invariably survived till their release and to adulthood. Mortality in the captive unweaned calf and young juvenile classes is therefore much lower than in the wild. While the actual cause of this difference is uncertain, the main advantages offered by the management regime used were veterinary care (rarely needed) and supplementary food, both in the late stages of pregnancy and for calf and dam while the calf was suckling: also there was almost complete protection of calves and dams from predators.

The change in sex ratio at birth from 1:1 (Dittrich 1970, Roth *et al.* 1972, this study), to approximately two adult cows to each adult bull in 1974, suggests that there is some differential mortality between the two sexes. This difference is, however, probably exaggerated by the fact that the original herd had only three bulls but thirteen females. Since the original animals still represent a quarter of the adult population, this initial difference in bulls is important. However, even taking this into account, the male/female adult sex ratio is still 2:3.

Records of the herd since introduction show more males than females dying (where sexes are given), usually through disease or suspected snakebite; both calves and adults show this mortality pattern. Emigration from the reserve cannot, however, be completely dismissed.

All other age/sex class records were affected by removals at some stage, but there seems to be little mortality after weaning.



The seriousness of preweaning mortality is shown in the importance of the original cows in the reproductive pool: relatively few of their offspring when raised unprotected have survived to breeding age, while their own mortality from the age of one month till eleven years is less than 30 per cent.

FEEDING STRATEGY

As Westorby (1974 : 291) remarks, modern ecology "has only one body of diet predicting theory that natural selection acts to maximise the capture rate of some nutrient." In the case of ungulates, this theory has been supported by studies of selection for specific nutrients (reviewed in Westorby 1974). Studies of selection in African ungulates have shown selection for vegetation type (e.g. Vesey-Fitzgerald 1960), individual species (e.g. van Zyl 1965, Lamprey 1963) and plant parts (Bell 1971, Sinclair and Gwynne 1972). Several of these studies have been directly correlated with nutrient content (e.g. Roth and Osterberg 1971).

Jarman (1974) proposed a general model of antelope feeding strategies in which the nature and dispersion of food items determines the feeding style. Large antelope are capable of surveying and moving over larger areas than small antelope, but cannot, for physical and physiological reasons, feed delicately enough to select the highly nutritious parts of plants from the parts of low value. They therefore tend to feed on large quantities of continuously distributed species while smaller animals are more selective. Jarman (1974) distinguishes five feeding styles based on these considerations.

Within the physical and physiological constraints given by Jarman's theory, selection for plant species and for seasonal variations in food value occur. Westorby (1974) proposes a model of "fallible nutritional wisdom" in which an generalised herbivore is capable of detecting its own needs and the value of its food intake in meeting those needs. There is a continuous intake of food which is characterised by a tendency to explore food plants (i.e. seek variety) and whose efficiency as an overall diet is assessed by long delay learning.



Eland are very flexible in their feeding behaviour. This is shown both in their choice of individual food species in response to their nutritive value (Kerr et al. 1970, Roth and Osterberg 1971) and in their change in feeding styles through the year.

The switch from grazing (for ease of recording, all feeding at ground level) to browsing (all feeding done off shrubs and trees) in the dry season at Loskop (Table 3) is probably a response to the drop in food values in the ground level forage as opposed to those at higher levels. Bonsma (1942) gives phosphorus levels in two Combretum species which were favoured winter browse at Loskop an 0.122 % in May; this is twice as high as in grasses at this time of the year (Du Toit, Louw and Malan 1940) but the level in the Combretum species drops to that found in grasses (about 0.05%) in June. This corresponds with a switch from graze to browse, then back again (see Fig 13). Other nutritional components follow the same curve, but less clearly. Roth and Osterberg (1971) show similar switches between individual browse species according to protein level in eland in Rhodesia. The Loskop "grazing" records obscure the very real changes in preference between monocotyledons and dicotyledons in the grass/herb layer, but such changes were observed, although not quantified.

In the short term, eland can be very selective, even in mid-winter (Table 5). Theron's "importance value" is closely related to the amount of food available, although it probably exaggerates the availability of deciduous shrub forage at the time of the study. There is therefore considerable selection of relatively rare species and avoidance of quite common plants taken at other times of the year. The basis of this selection is probably either directly or indirectly on the nutritive value of the plants available (see Westorby 1974).

Jarman (1974) classifies eland as having a type "E" feeding strategy, meaning that they are broad spectrum, non-selective feeders, who rely on taking in large quantities of low value forage for their food requirements. However, observations on the short term movements of eland (Chapter 4), and their response to local flushes and to seasonal changes in vegetation (Kerr et al. 1970, Roth and Osterberg 1971, this study chapters 3, 4) suggests that

although/.....



although they are capable of surviving on a type "E" diet, they may also employ a style "C" feeding strategy under the right conditions. Jarman (1974 : 223) describes style "C" animals as those who "feed on a range of grasses and browse, rather selectively, in a range of vegetation types within a fairly large home area. The diet changes seasonally, as does their preference for vegetation types".

This is perhaps to be expected, since Jarman's (1974) model is essentially a comparison of the responses of animals of different body size, mouth size, and food type (graze or browse) to the same dispersion of food plants with a given distribution of food values through the various plant parts.

The interpretation of the observed feeding strategy used by the more opportunistic feeders will depend greatly on the local conditions, especially on food distribution. If, for instance, the main food source of eland were forbs, its feeding strategy would be considerably different to that if it were feeding on tufts of grass. The possibility of eland depending on grasses in one area and forbs in another is confirmed by other studies (Lamprey 1963, van Zyl 1965, Wilson 1968a, Kerr et al. 1970). Van Zyl's (1965) study shows that several antelope classified by Jarman as style D or E feeders took predominantly grass species, while eland took more browse than any other species except impala, a style C feeder. The use of forbs rather than the more continuous grass species is characteristic of selective feeders, suggesting that eland are closer to the style C feeders than might be expected from their body and mouth size. (There is still, however, a considerable difference between the number of plant species taken by impala compared with eland and the other antelope recorded). Loskop eland are confined to a small home range (Sidney 1965, records one wild herd moving through 160 km as part of its range) in an area with a wide variety of vegetation types, which they are probably more familiar with than they would be if completely unrestricted. This would tend to emphasise any style "C" characteristics which eland possess.

Apart from the food level taken, eland have another feeding characteristic. Their nibbling and stripping techniques which

will affect the nature of the food available to them give them greater selectivity than a straightforward cropping technique.

One of Jarman's (1974) main arguments for differing feeding strategies is that larger antelope are not capable of being as selective as small ones. While eland may take almost all browse or graze species available to them at some time of the year (see Table 5, and Hofmeyr 1970) their style of eating is basically different to that found in Syncerus caffer, the only other member of Jarman's style "E" feeders which has been intensively studied. Instead of using the tongue to take in tussocks of grass or whole forbs, antelope are capable of being much more selective than buffalo (Field 1968, 1970). Size for size, this is true for eland, but they can only select for small plant parts by techniques whose effectiveness is greatly affected by the plant structure. Whether this makes eland more efficient feeders will depend on whether these methods will yield more concentrated food types than buffalo's feeding style and on the digestive efficiencies of the two species.

CHAPTER 4

SOCIAL ORGANISATION: GROUP
STRUCTURE AND MOVEMENTS

From such works as Estes (1974) Geist (1974) and Jarman (1974) it has become clear that the social organisation of antelope can only be understood in relation to the general ecology of the animal. To understand the adaptations seen in the various populations of eland it is therefore necessary to consider the distribution of the population in relation to the environment and to the annual cycle of activity.

GROUP SIZE AND COMPOSITION AND
THE ANNUAL CYCLE (Figures 14 and 15)

The annual cycle of behaviour in eland is closely related to group size and composition. At Loskop, the calving season (August - October) was marked by an increase in the group size, due mainly to aggregations of females and young (Fig 14). The females at first formed small nursery herds with only a few young of the year, although yearlings and subadults would also join these groups. The herds would amalgamate over the calving season itself, probably using the previous year's main nursery herd as a nucleus. At the same time, bulls would associate together and some mild aggression and sparring activities were seen.

After the peak of calving had passed, almost all females and young on the reserve were found in a single herd. Up until this time, males were rarely sighted with the nursery herd. From late October till January, the nursery herd always included at least two, and sometimes five or six adult bulls. Bull groups were also seen at this time, and in them the majority of the serious fights occurred. The nursery/breeding herd itself was relatively peaceful. In December and January, up to one fifth of the reserve was burned as part of a five-yearly schedule. The herds soon moved onto this area, and almost all the eland were to be found some-

where/.....

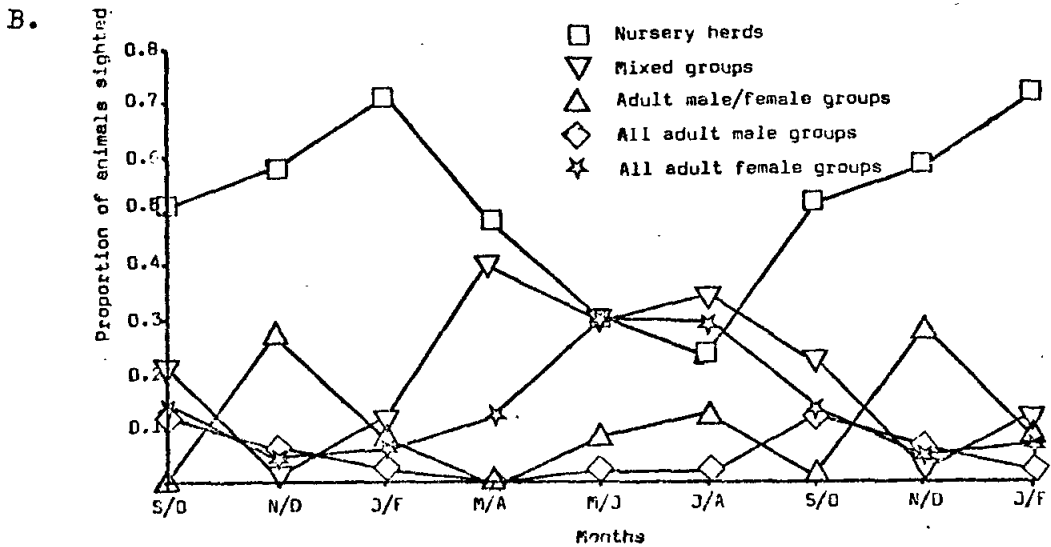
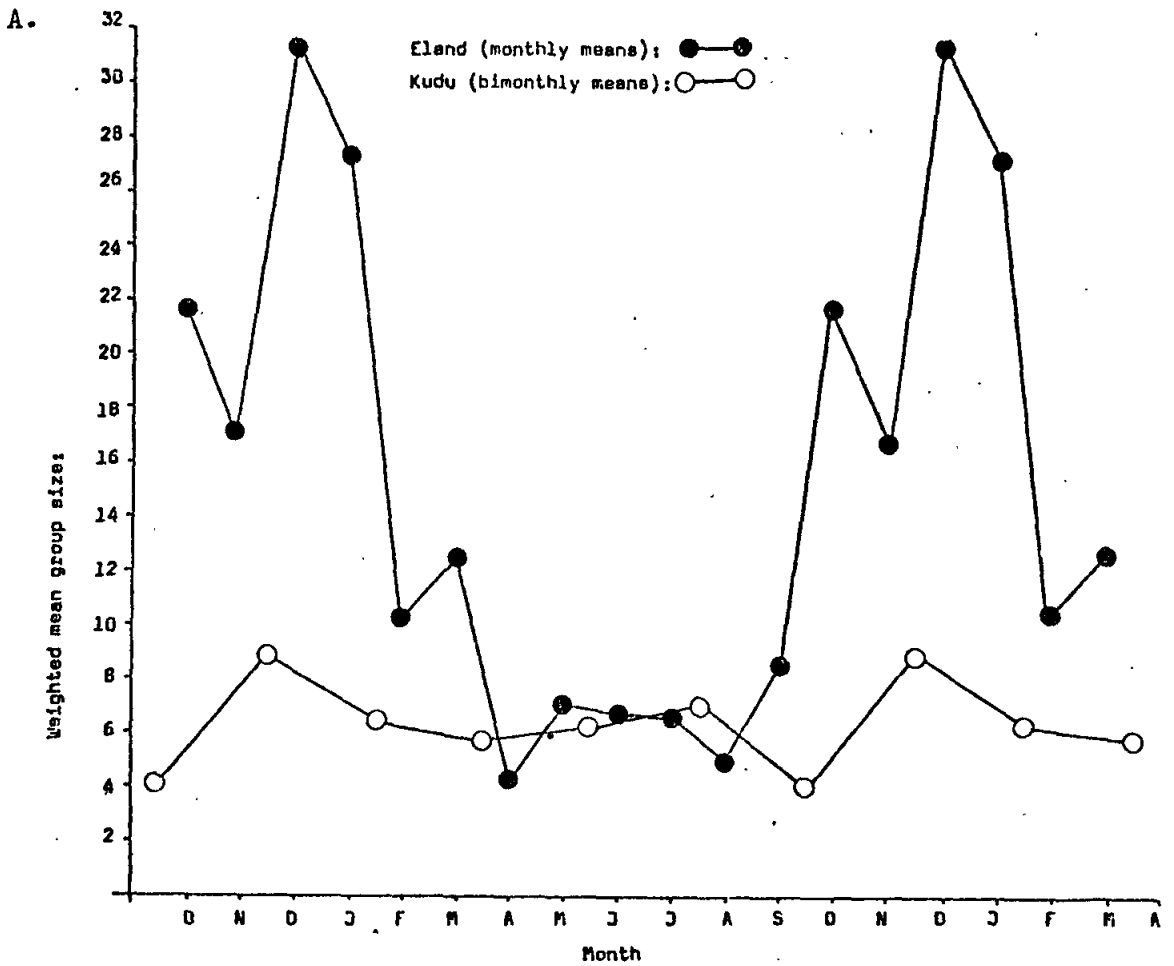


Figure 14. Seasonal variations in eland group size and composition at Loskop Dam Nature Reserve. Graphs partially repeated. June 1972 - May 1974.

- A. Weighted mean group size, with kudu group sizes for comparison.
- B. Proportion of eland in various group types.

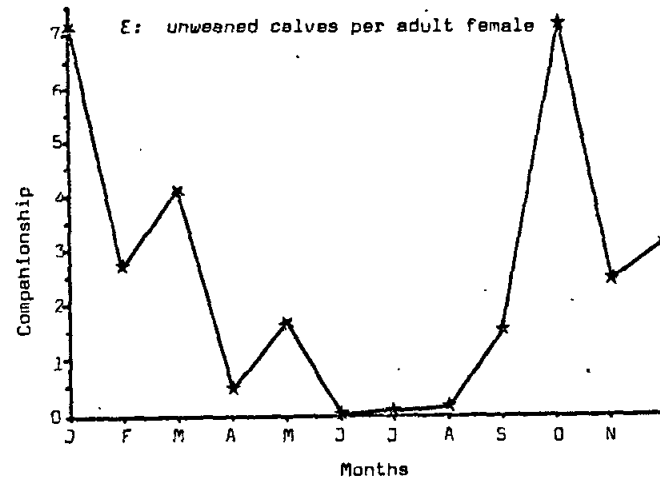
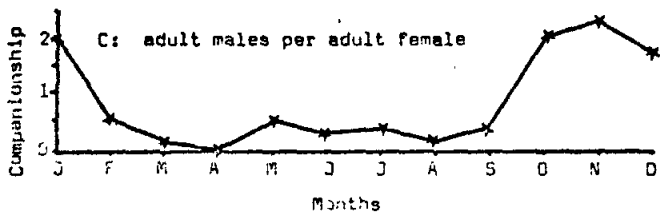
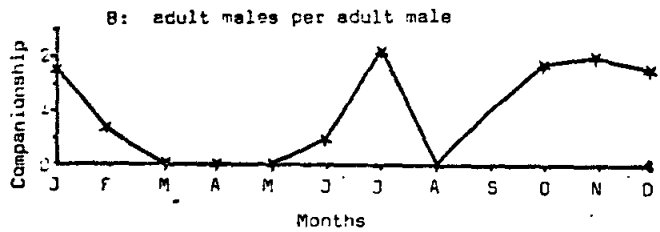
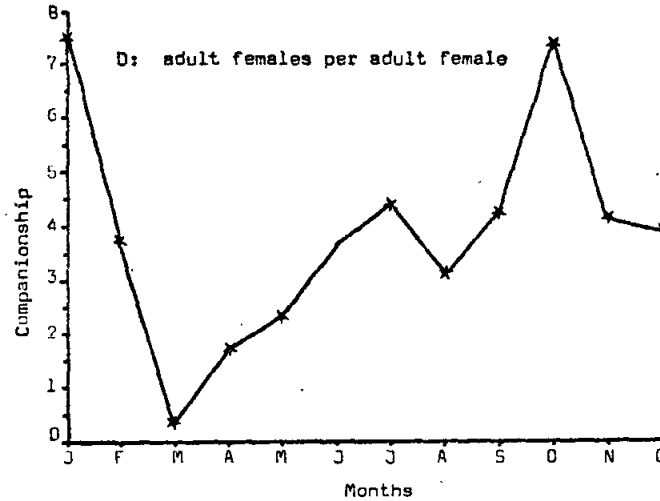
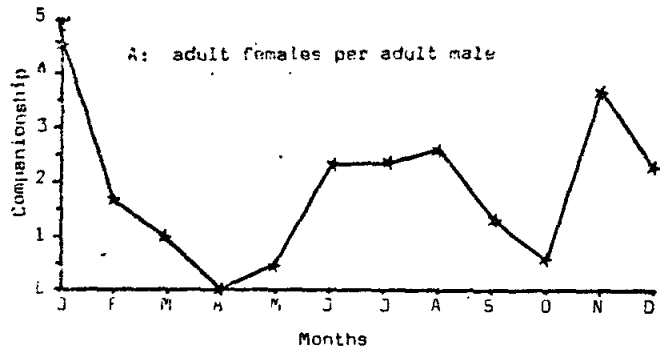


Figure 15. Association between age/sex classes in eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

A - E Companionship records.

F Proportion of bulls found with cows.

where on the burns. About this time, bulls and females began to move away from the main body of the nursery herd, leaving it sometime early in the day and rejoining it in the evening or the next day.

From February to April the majority of the calves were weaned. The dams were increasingly independent of their calves over this period and often moved in small 'mixed' groups for several days before rejoining the herd. By the end of April, the nursery herd consisted mainly of young animals, who generally remained together through the winter to form the basis for the next year's nursery herd. The splinter groups were at first very mixed as to age/sex class membership, but tended to become more homogeneous as winter proceeded. In Fig 14 the records for 'mixed' groups include pure calf, pure yearling and pure subadult groups, so this change is obscured, but the records for pure female groups show a definite increase during the winter months.

ASSOCIATION BETWEEN AGE/SEX CLASSES

The association between age/sex classes is summarised in Fig 15. The measure 'companionship' is the number of animals of a particular age class which the average individual has as fellow group members as suggested by Jarman (1974). Thus, 'female companionship to bulls' means that the average bull is sighted in the same group as x many females, i.e. has x female companions.

The overall association between age/sex classes is summarised in Table 6. This lists the Pearson correlation coefficients generated in the principal components analysis described in more detail in Appendix 2. The correlation coefficients were obtained from group sightings which had been fully classified as to age/sex class composition and counted. Each sighting was treated as a separate sample from the population and the number of animals in each of the age/sex classes was correlated with the numbers in the other classes.

Since the eland is a social animal, it is not surprising that the majority of correlations (all but one) are positive. The more similar the classes in sex, age and size, the more closely they are correlated. This is confirmed by the distribution of the points produced by plotting groups according to their values in the first

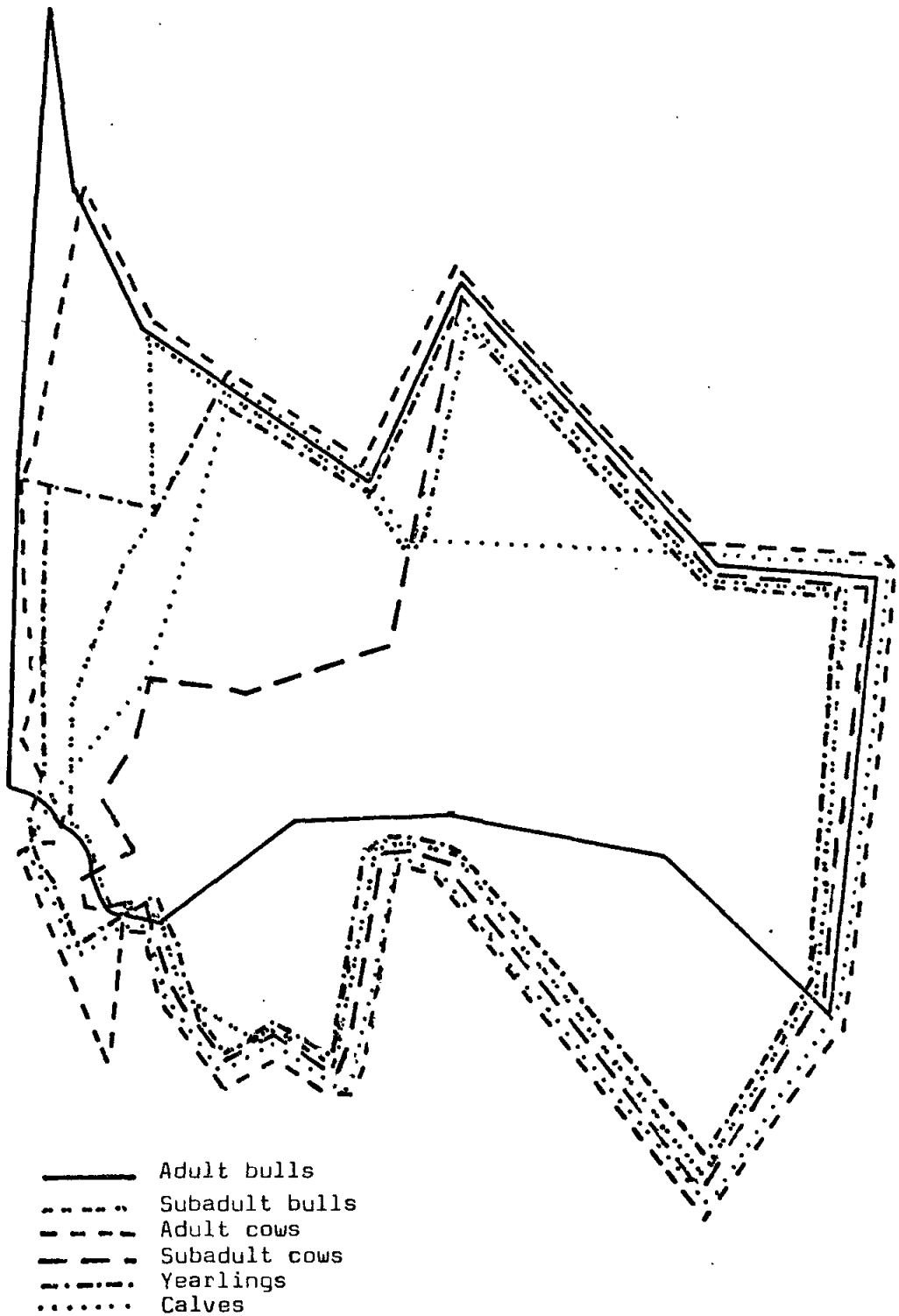


Figure 16. Principal components analysis (PCA) of eland group composition at Loskop Dam Nature Reserve. June 1972 - May 1974. The vertical axis is doubled to facilitate plotting. The actual distribution of points is given in Appendix 2. Cumulative component for first two components = 65.005.

Table 6 : Correlation coefficients of eland age/sex classes at Loskop Dam Nature Reserve, July 1972 - May 1974.

	Adult o	Adult ♀	Subadult o	Subadult ♀	Yearlings	Calves
Adult o	1.00	-0.04	0.13	0.15	0.09	0.18
Adult ♀		1.00	0.33	0.37	0.33	0.47
Subadult o			1.00	0.66	0.48	0.37
Subadult ♀				1.00	0.56	0.43
Yearlings					1.00	0.56
Calves						1.00

two principal components (Fig 16). Also, the older and larger the animals, the lower their correlation coefficients with other classes. This reflects a decreasing dependence on the nursery herd and increasingly independent movement generally with size and age. The highest association found, however, was between subadult males and females. This may represent a differential sexual strategy between subadults and adults, but the number of subadults is so small that the high coefficient may merely be due to both classes being seen only in large aggregations of animals. The sexual strategy possibility is, however, interesting in its own right and may be applicable to other species. It is therefore discussed in Appendix 3.

MALE/FEMALE ASSOCIATION

The annual changes in association between adult males and adult females are summarised by Fig 15A, D and F. These show an annual cycle of association, centred around the breeding season (November - February).

The curves illustrating the cow's companionship to bulls shows that the average male experiences wide fluctuations in the number

of females available to him (i.e. in the same group). On the other hand, the average female experiences a low level of male companionship at all periods except the rutting season (from this curve, October till January).

This disparity is partly due to the difference between male and female numbers, and partly to bias in the winter records. If the male numbers are low enough relative to the number of groups in the population, every male may have female companions but not all females can have male companions. This was the situation when males were recorded during the winter. They were usually sighted with a small group of females for several days running while in the meantime, several groups of females were sighted without males. Only when the nursery herd had reached its peak size did all females sighted have male companions. Male companionship values for females were therefore at least partly dependent on number of groups and the number of males available.

Winter values for female companionship to males were probably inflated by biased records. Only a few bulls were regularly sighted during the period April - August. These animals were sighted in the same area for several days, then disappeared. During that time they attached themselves to any group that they encountered (because of the age/sex class ratio, this usually included one or more females). No sexual activity was seen, but the animals involved were usually 'grey' bulls. Records from less restricted populations in southern Africa (Abbott 1968a, Keep et al. 1974) indicate that bulls are usually almost completely separated from cows during the winter, so the high level of winter female companionship for Loskop bulls is probably an artefact, although it may be a local variation which would have arisen regardless of confinement.

Adult female companionship for adult bulls drops in September and October. This corresponds with two other changes in the bull records. Companionship values for adult bulls to adult bulls increase rapidly at this time; also, the proportion of the animals sighted in pure bull groups is at a high level during September. There is therefore a positive move away from females and into male groups in September and October.

The curve "female companionship to bulls" then shows a sharp increase during the rut, except for December where the nursery herd proved unusually elusive: records are probably not as representative as for November or January. The very sharp drop in February was due to a decrease in the number of adult bulls sighted relative to other classes. They presumably began their autumn dispersion at this time.

MALE/MALE ASSOCIATION

Figure 15B summarises the annual cycle of association between bulls. Except for the peak in July, which was caused by an isolated observation of an aggregation on a flush of riverside grasses, there is a low level of companionship during the winter. This low level rapidly increases during the pre-rut period, when bulls begin to show an increase in aggressive activities and tend to be found in "pure" bull groups. This high level is maintained when the rut begins. This is partly a result of several bulls joining the nursery herd, and partly because bulls found away from the nursery herd usually had one or more male companions. Both this curve and the curve for male companionship to females follow the curve for the weighted mean group size very closely, suggesting that the factor governing group size is also "permitting" these associations to take place. Adult male sightings were relatively scarce at all times of the year and are therefore unlikely to have had a direct effect on the group size figures.

FEMALE/FEMALE ASSOCIATION

This association (Fig 15C) shows a rather different pattern to other age/sex class associations e.g. male/female. There is a slight drop in the number of companions in August/September, presumably because of parturient cows seeking isolation. As the cows come together to form a single nursery herd, the number of companions again increases. This increase was offset in November/December by many sightings of cows moving independently of the nursery herd. Some of these individuals had lost their calves, while others seemed to be temporarily separated from them for some reason. These cows

were/.....

were often accompanied by bulls, who frequently showed mild sexual interest (e.g. testing, keeping in a "tending" position).

The drop in the level of female/female companionship during February/March (the weaning period for most calves) was due to cows moving more and more independently of their calves and keeping away from the nursery herd for days at a time. Cows moving independently of the nursery herd in the summer were often found in smaller, more heterogeneous, groups than during the winter months, which tended to emphasise this decrease.

The average number of female companions per female during the winter months runs contrary to the trends for other associations and for the general records of group size. Adult cows aggregated more rapidly than other classes in response to artificial food sources (food supplements, licks). This mechanism may also have operated in the field, producing higher records for females than for other groups. The increase also reflects a tendency to form "pure" female groups during the winter (see Fig 14), so that female/female companionship increases partly at the expense of other female companionship records.

FEMALE/CALF ASSOCIATION

Trends in this association are summarised by Fig 15E. Only calves under six months (i.e. probably unweaned) were recorded here. The number of calves in the same group as the average female follows the general trend for association and group size, especially in the early months of spring (i.e. August - October). The calving peak is actually late August to September, and although a calf may be moving with the herd a week or so after birth, it is not usually found in a large aggregation of animals until it is about one month to six weeks old. The low record for August also reflects the wariness of dams with neonates.

During November and December, several cows known to have lost their calves were seen moving independently of the nursery herd, without any accompanying calves or yearlings. These sightings reduced the overall average for these months.

From February till April, calves were passing out of the six month age class, and during the winter months, unweaned calves were rarely seen. The association with females during February

till/.....

till April is slightly higher than that for other sectors of the population and decreases much less rapidly than that for adult female/adult female association. This indicates that the suckling bond tends to keep cows in the nursery herd when they would otherwise move singly or in smaller groups.

INDIVIDUAL COMPANION PREFERENCE

Cole's (1949) index of association was used to determine the degree of association between known individuals. Apart from indices from calf/calf sightings, the values were very low, rarely exceeding 0,40. This supports the impression, gained from field observations, that groups are "open" to newcomers. Individuals do, however, show preferences for other individuals as companions.

Calf/calf indices were highly variable, and depended on the age of the calf. With a group of unweaned calves (a small nursery herd), the indices were near unity (other calves in the same nursery) or else zero (calves in other nursery groups). Animals which were sighted both before and after weaning showed more intermediate values. This emphasises the cohesiveness of the calf nucleus of the nursery herd, which is a result of the highly conservative association between calves of six months or less.

When the associations within adult classes are compared, there is a difference in the distribution of indices (see Fig 17), particularly between adult females and old ("grey") bulls. This difference cannot be due to the lower number of (and therefore the decreased probability of encounter between) old bulls, since young and subadult bulls also have a low density but their indices still follow approximately the same distribution as adult females. This reflects the older bull's tendency to move independently of other animals. Young and subadult bulls have some companion preferences, although the groups are still very open.

The bases of the preferences, slight as they are, seem related to both the age and dominance of the animals involved. I had the impression that animals, particularly adult cows, of the same year class tended to occur together, but could not confirm this. However, when the differences in rank between animals were correlated

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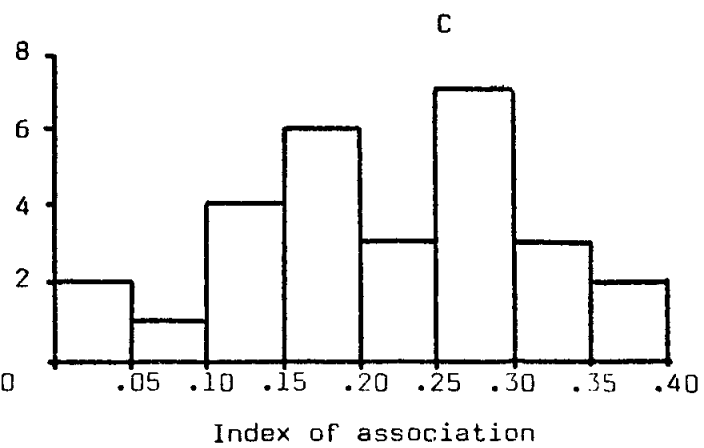
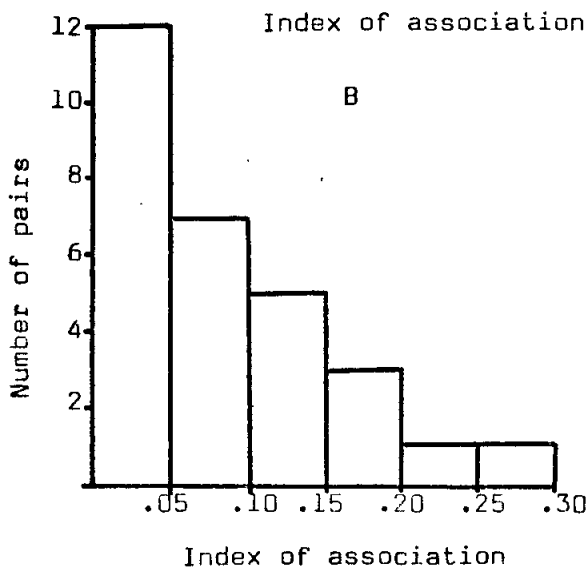
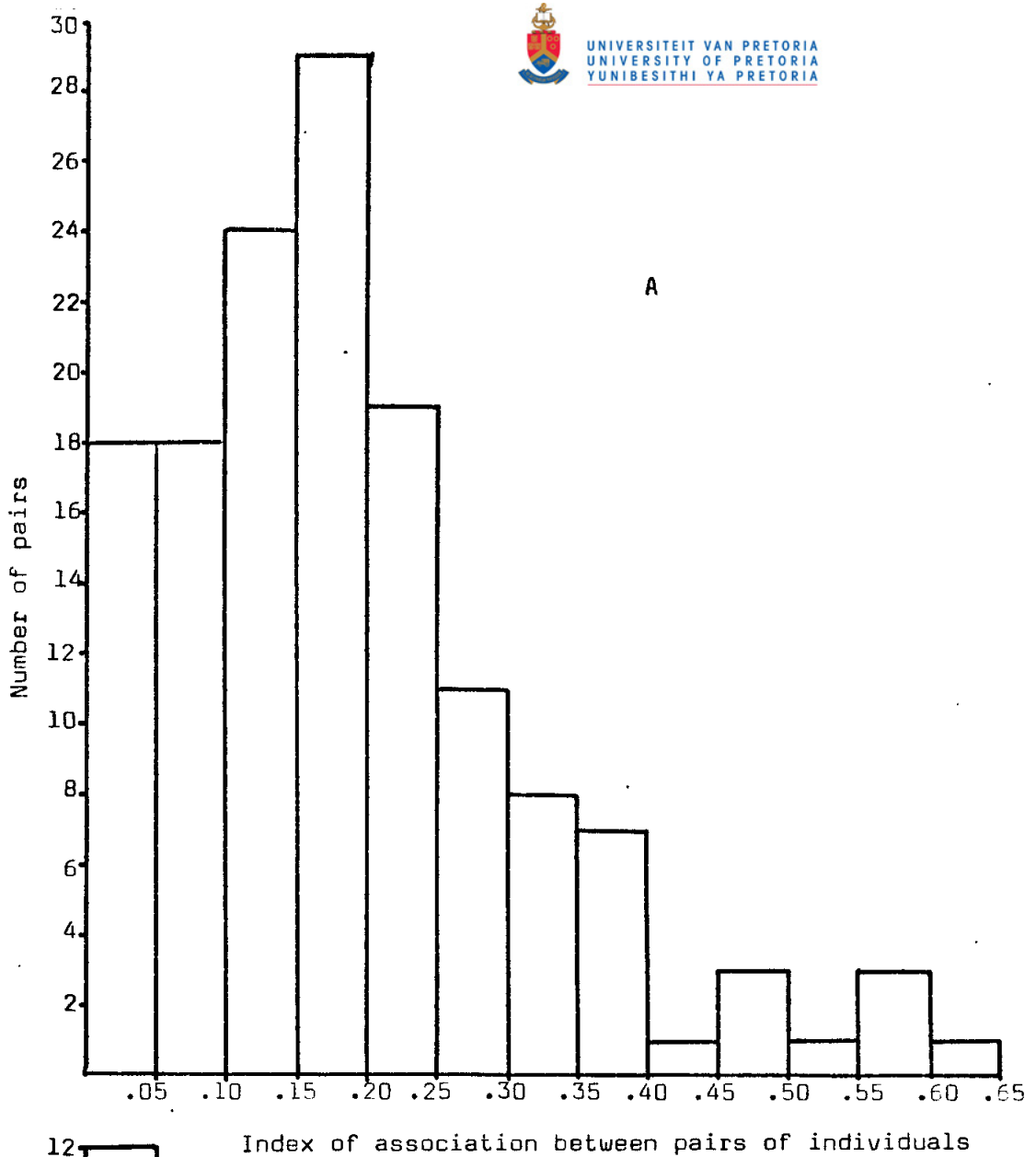


Figure 17. Individual companion preferences within age/sex classes of eland at Loskop Dam Nature Reserve, June 1972 - May 1974.

- A. Adult females
- B. Old (grey) bulls
- C. Young adult and subadult bulls.

with the average index for each rank difference, adult females showed a significant correlation (Spearman $r = -0,8091$, $p = 0,01$). With young bulls ("Brown" and subadult classes), the correlation was minus one, but with adult bulls, there was no significant correlation (Spearman $r = -0,5714$), again reflecting the independence of the old bulls. The tendency of animals to associate with others of a similar rank may, in fact, represent an association according to age, since the dominance of young bulls and (probably) of cows is dependent on age.

A principal components analysis was run on the records of individual association, as in Penzhorn (1975), for the whole population. This showed almost identical values for the first seven components, indicating either a random distribution or else several parameters affecting the population equally strongly. Since the analysis had already shown significant values for inter-class companion preference, it is likely that there are several factors involved, but too many for this form of analysis to reveal. This conclusion is supported by the information on preference vs. rank difference shown above.

GROUP AND INDIVIDUAL MOVEMENTS

Records of eland movements in the wild present a tantalizingly incomplete picture of the movement and behaviour of these animals in response to differing environments. For example, although Sidney (1965) records several migratory herds of the northern races (e.g. the Sudan; "local" migrations in Kenya, in the Serengeti National Park, Tanzania) he also records less extensive seasonal movements (e.g. up and down Mount Kenya; most groups in Zambia "roaming") as well as concentrations within a range at various seasons (e.g. on the Karamoja mountain range in Uganda; in the Gobabis district of South West Africa; in the Drakensberg, Natal). He records many local populations which are "well distributed" and, presumably, resident. Also, herds probably remain in the moorlands of Mount Kenya when the rest of the population moves down onto the lowland plains, while a herd on the higher reaches of Kilimanjaro may be sufficiently permanent to have adapted them-

selves/.....

selves to the cold by developing long, shaggy coats. Unfortunately records are usually limited to a few sightings, especially when the eland are at low densities; this is both because of their nomadic habits and because of their extreme timidity in the wild. Even so, this probably incomplete sample presents an impressive array of adaptations to local conditions.

Although there were few areas at Loskop where eland were not seen at some stage during the study, both individuals and particular group types tended to confine their activities to a particular part of the reserve (Figs 18, 19, 20, 21 and 22). It is not, however possible to call this area a home range after the definition of Jewell (1966), since the same animals might be seen pursuing "routine activities" at opposite ends of the reserve within 48 hours. In all probability the reserve is too small to allow a "real" home range to be shown. The tendency of individuals to be found in particular areas resembles a "core area" (Kaufmann 1962) rather than a home-range proper.

MOVEMENTS IN RESPONSE TO FOOD RESOURCES

The areas preferred by the different group types partly reflect seasonal changes in food availability in different parts of the reserve (for instance, the nursery herd was most frequently sighted in the summer, when most eland were on fresh burns). They also reflect a distinct ecological separation between some age/sex classes e.g. cows outside the nursery/breeding herd and bulls without females tended to be found at opposite ends on the reserve, in different veld types (see also Abbott 1968a).

Although it is possible to show differences in the general distribution of group types and individuals, and in rainy season/dry season distribution of the population, Figs 21, 22 the basis of these preferences can only be partially determined (Table 7.) This is because an eland group may, and usually does, move through several ecotypes during its daily movements feeding in each of them. The complex mixture of ecotypes found at Loskop (Acocks 1953, Wells 1960, Theron 1974), means that the eland experience a highly variegated habitat, both in regard to food resources and general morphology, even during a single day's feeding. The basis of group and

individual/.....

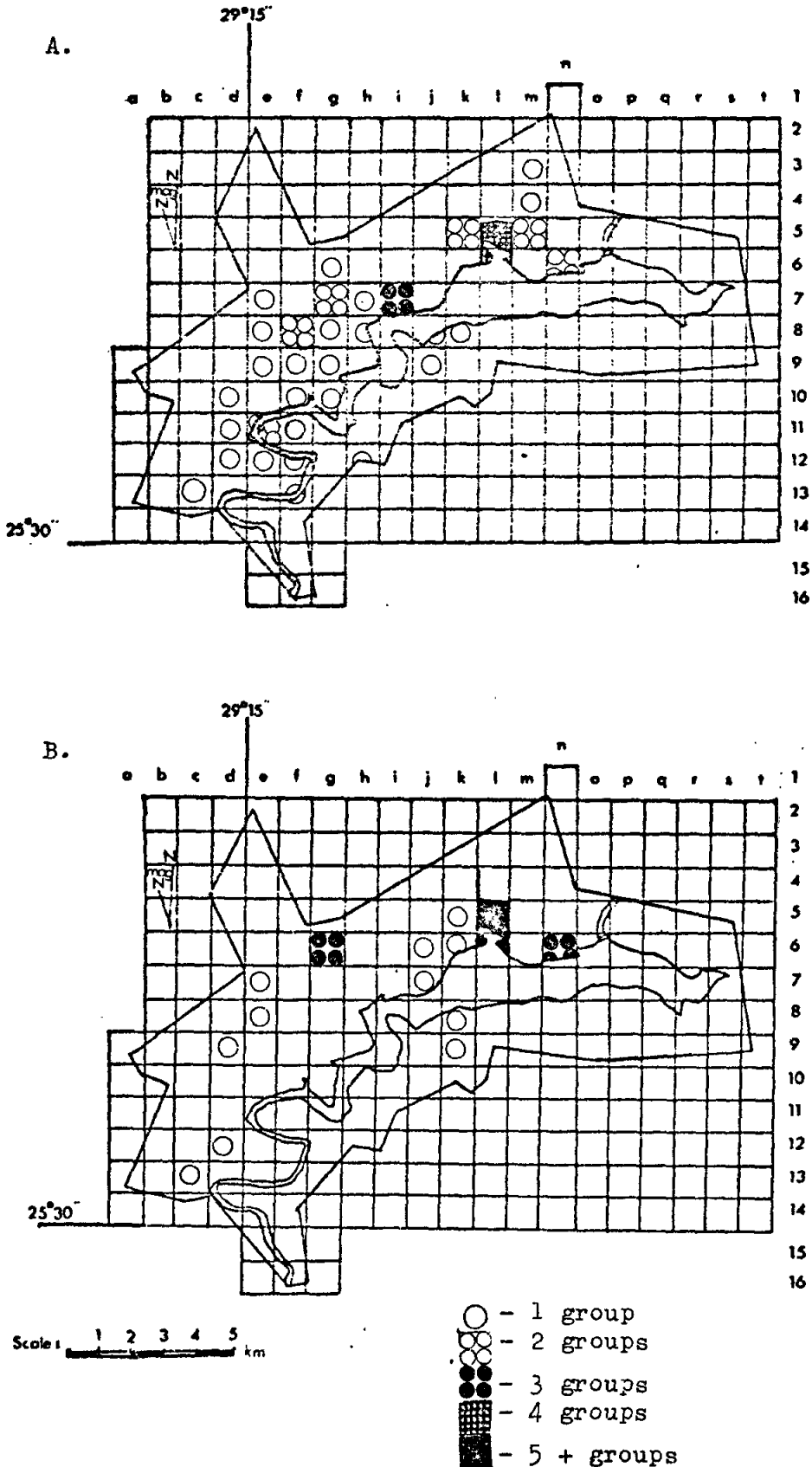


Figure 18. Distribution of eland group types at Loskop Dam Nature Reserve, June 1972 - May 1974.

Nursery and sightings. B. Adult male/female group sightings.

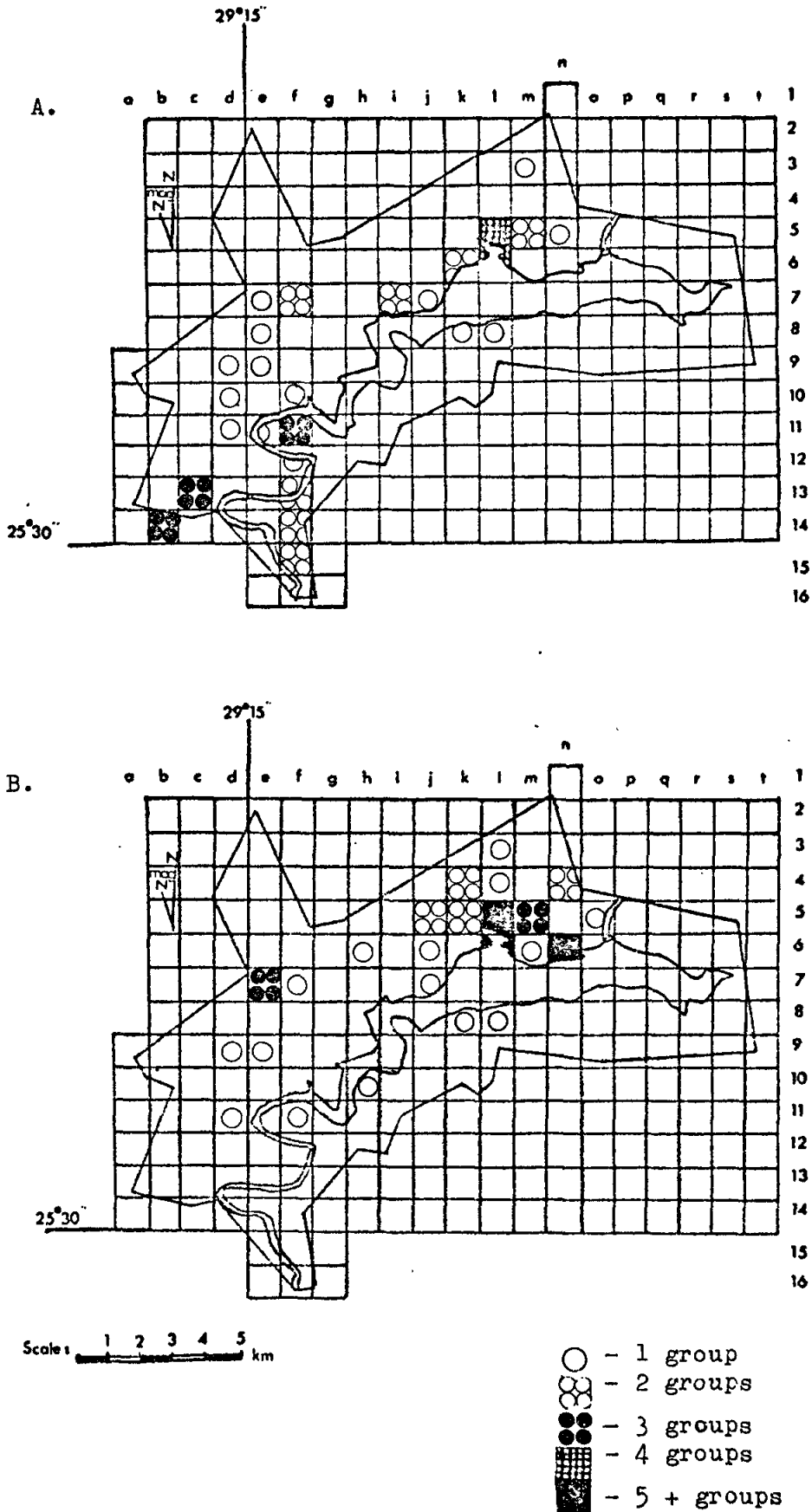
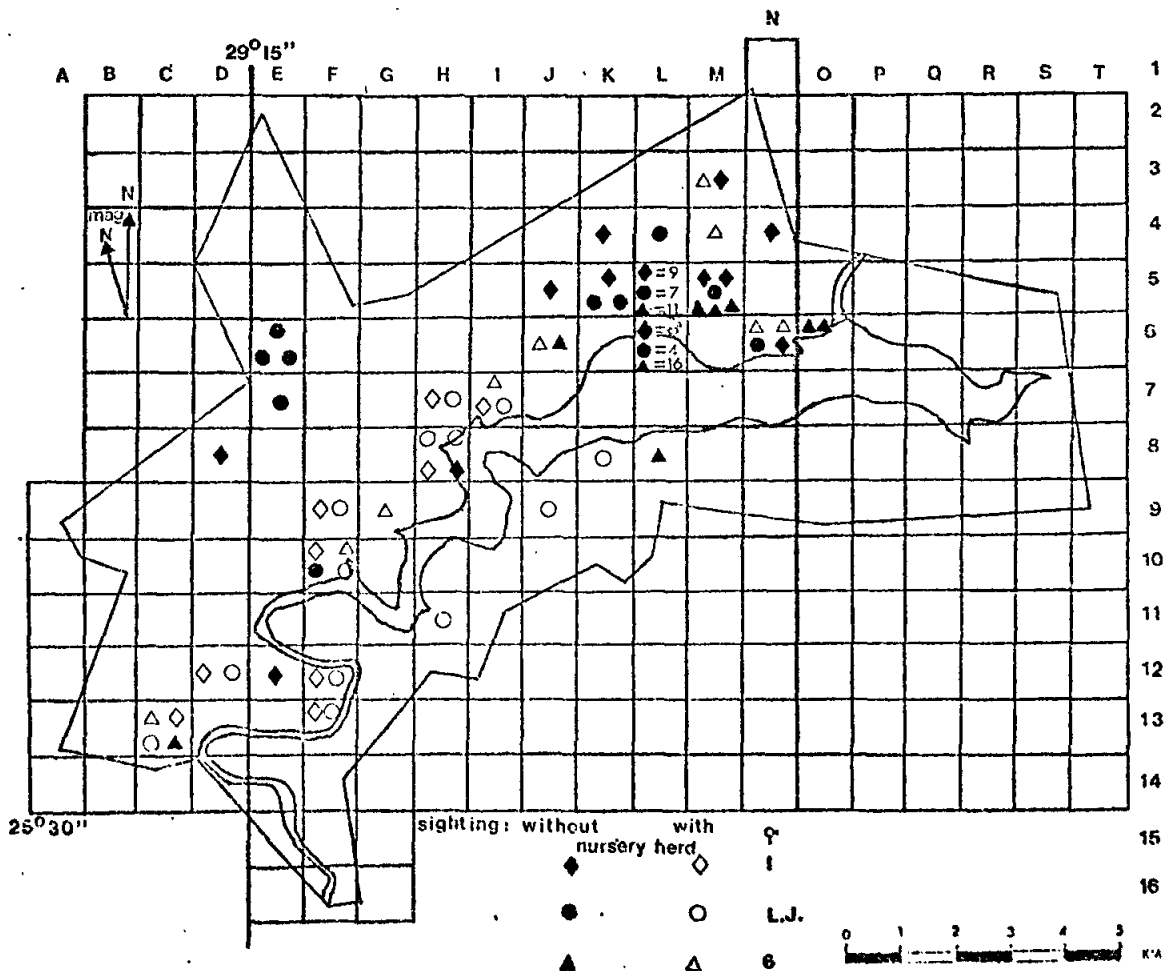
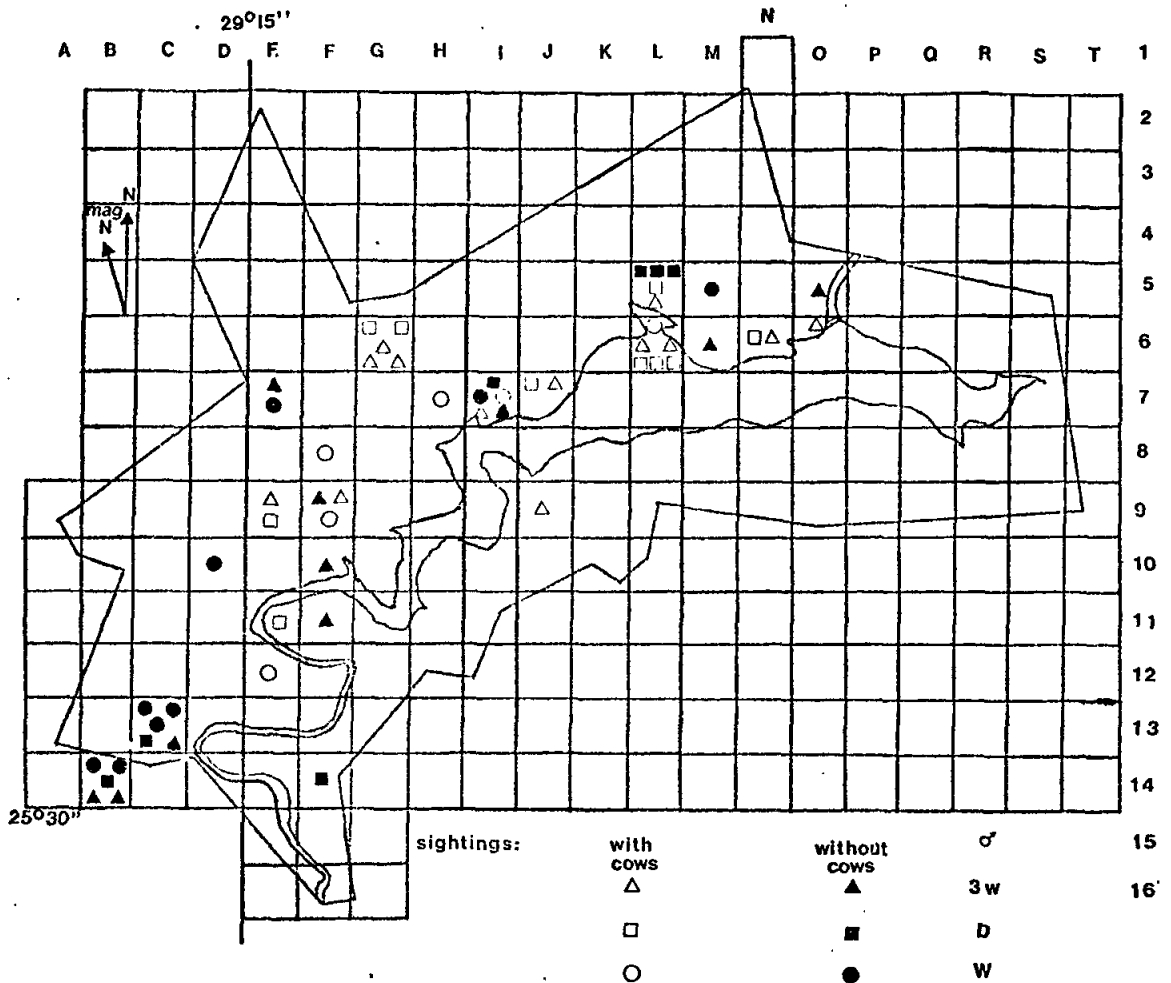


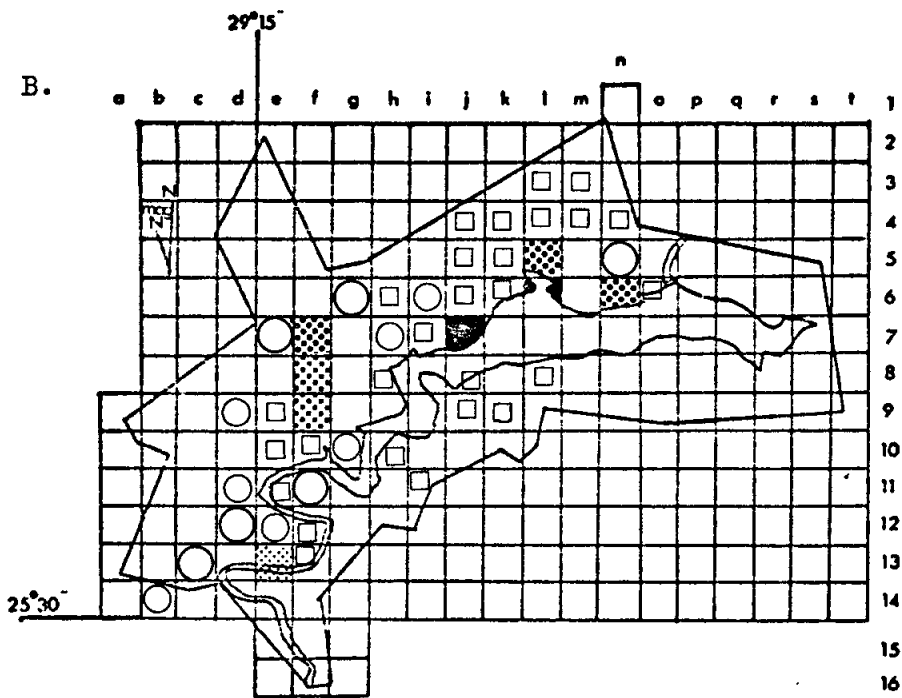
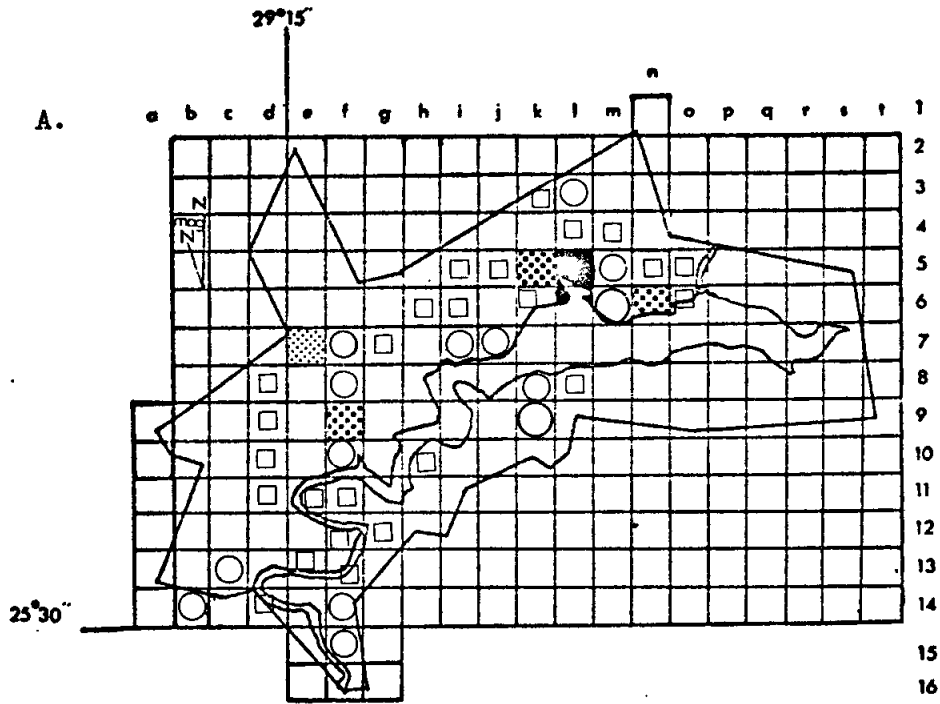
Figure 19. Distribution of eland group types at Loskop Dam Nature Reserve, June 1972 - May 1974.
 A. All-adult-male group sightings. B. All-adult-female group sightings.

Figure 20. Sightings of known individual eland at Loskop Dam Nature Reserve.

A. Three known bulls.

B. Three known cows.





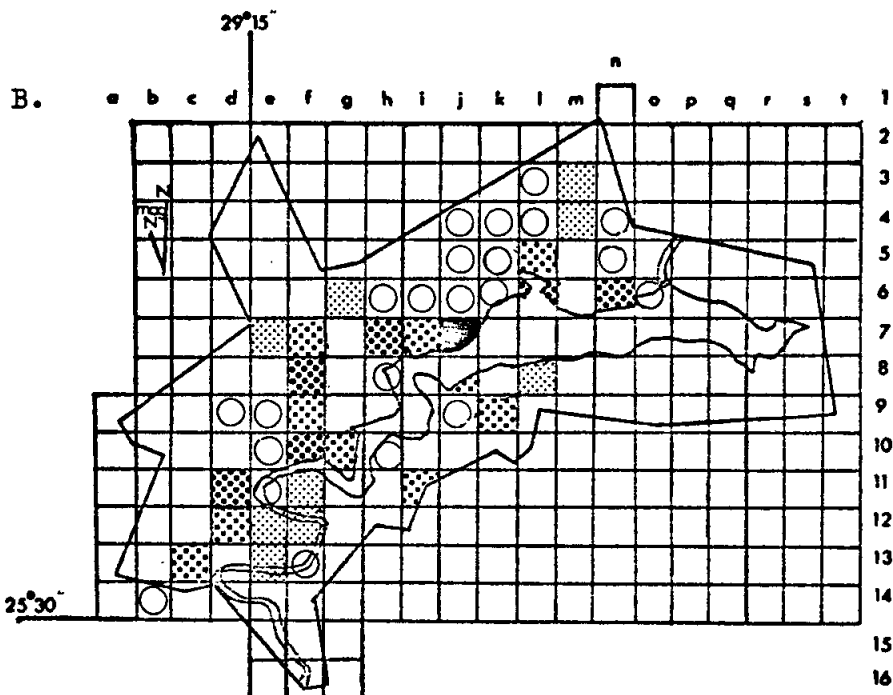
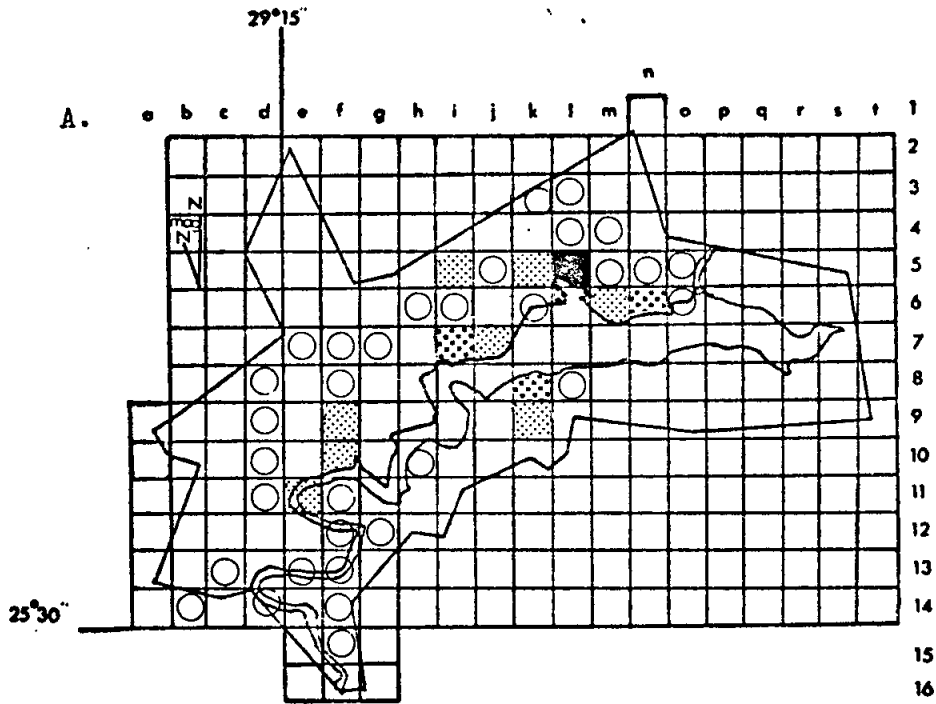
Scale: 1 2 3 4 5 km

- - 1 group
- - 2 groups
- - 3 groups
- - 4 groups
- ▨ - 5 groups
- ▨ - 6-10 groups
- - 10 + groups

Figure 21. Distribution of group sightings of eland at Loskop Dam Nature Reserve, June 1972 - May 1974.

A. Dry Season sightings

B. Rainy season sightings.



Scale 1 2 3 4 5 km

- 1 - 10 individuals
- ◐ 11 - 25 individuals
- ◑ 26 - 50 individuals
- ◒ 51 - 100 individuals
- ◓ 100+ individuals

Figure 22. Distribution of individual eland sightings at Loskop Dam Nature Reserve, June 1972 - May 1974.

- A. Dry season sightings
- B. Rainy season sightings.

Table 7 : Vegetation type preference of eland compared with that of kudu at Loskop Dam Nature Reserve
 June 1972 - February 1974.

	Number of animals sighted	
	<u>Kudu</u>	<u>Eland</u>
<u>Combretum apiculatum</u> tree savanna	61	17
<u>Diplorhynchus condylocarpon/Enneapogon pretoriensis/Loudetia simplex</u> tree savanna	29	235
<u>Acacia karroo/Setaria perennis/Loudetia simplex</u> tree savanna	55	72
<u>Combretum molle</u> tree/thicket savanna	4	27
<u>Combretum apiculatum/Acacia caffra/Themeda triandra</u> tree savanna	189	399
<u>Burkea africana/Loudetia simplex</u> tree savanna	48	439
<u>Acacia caffra/Setaria perennis</u> tree savanna	77	32
<u>Faurea saligna</u> tree and tree-thicket savanna	95	69
<u>Mundulea sericea/Tristachya biseriata/Rhynchelytrum setifolium</u> thicket savanna		
& <u>Protea caffra/Tristachya biseriata</u> tree savanna	23	89
<u>Tristachya biseriata</u> grassveld	12	8
Hygrophilic communities	41	27
Hydrophilic communities	-	12



individual movements is further obscured by the fact that the eland did not have a regular pattern of daily activity, although some activities were more likely to occur at some times of the day than at others (see Chapter 3). Some generalisations can be made, but for a proper understanding of the factors governing group size, composition and movement, it would be necessary to treat each group's daily activities on its own merits.

Jarman (1974) emphasises the opportunistic nature of large nomadic antelope. This was confirmed with respect to eland when the animals visiting a highly localised food source (e.g. a lick and some lucerne) were recorded over ten days, half of the known individuals (i.e. 30 animals) visited the lick for varying periods. These records included sightings of animals who had been seen up to 13 km away within two days of their sighting at the lick. This was in mid-winter, when the largest free-ranging group observed was 13 animals (the nursery herd, which did not visit the lick), and the (weighted) average group size was six. Most of the animals actually observed at the lick originally arrived in groups of two or three, but were seen to mix with animals who had the food for several days previously. A temporary aggregation of up to 13 animals was formed, but this dispersed when the animals were foraging during the day and when supplementary food was no longer present. The eland therefore responded quickly to an isolated source of food and adapted their movements accordingly. The maze of ecotypes at Loskop contains many small stands of vegetation, each with its own growing and fruiting seasons. While the movements of animals are almost certainly partly governed by these, as with the artificial food source, the actual details of the key foodplants and their importance at different times of the year must await a more detailed description. This would include: food taken in different habitats, the availability of the plants, (locally and over the whole reserve), their food value to the eland throughout the year, and the actual preference of eland given a choice between equally available species (as in Sinclair and Gwynne 1972). Such a study was outside the scope of the present work, but some records of preferred foodplants and feeding activities were made, and these are given in Chapter 3.

In spite of the various complications, several obvious cases of feeding governing movements were seen. On the level of individual, daily movements, several instances were seen of animals having special feeding preferences or techniques which separated them from other individuals and governed their movements, if only for a short time. In one of these cases, a cow was in the habit of visiting a pure stand of pod-bearing Dicrostachys cinerea saplings; she had learned the technique of pushing against the trees and shaking them with her horns to dislodge pods. Although other animals visited the little grove and took any pods they found on the ground, they soon moved on, while the cow fed out of sight of the rest of the group for several hours. On at least two occasions, she became separated completely from the group and was alone for the rest of the day. Trips to licks and to water sometimes caused similar temporary separations.

A more artificial situation on a larger scale was the case of the core areas of the oldest cows. These were tame animals who made extensive use of the licks, occasional food supplements and the piles of stable cleanings found beside the paddocks at Lombards Bay (L5,6 on the grid, Fig 20). All eland used these areas, but only the tame animals would stay for any length of time. Their dry season distribution was apparently centred around these resources. Figure 20B shows the distribution for: a tame, first generation cow, 6; a wilder, first generation cow, L.J.; and a half-tame second generation cow, 1. As for all females, sightings tended to be concentrated to the east end of the north side of the reserve, except when cows were with nursery/breeding herds, but LJ's sightings are much less localised than 1's or 6's. 1's sightings were well distributed when she was with nursery/breeding herds, but her other sightings (i.e. mainly dry season) were concentrated around the artificial food supplies. 6's sightings tended to be more localised at all times, although she did have an extensive range.

On the level of long-term preferences of particular age classes nursery herds, which were sighted both in the rainy and dry seasons, showed a tendency to concentrate on the more open flats beside the dam. This is particularly noticeable during the summer, as shown

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by the individual distributions of the cows described above (their nursery/breeding herd sightings were all in the summer months). Even in the winter, there was a tendency for the herds (almost all members being young animals) to remain on lower, more open ground than the rest of the population. There is a great difference between the food available to an unweaned calf or even a half grown animal and that available to an adult. The reactions of adult and calves show that browse from tall thickets and full-grown trees is very desirable, especially in winter. So too are fruits and blossoms when on the trees. A calf, however, cannot use its horns to break down branches, nor can it feed effectively above a metre from the ground (although bushes slightly taller may be broken or pulled down into reach). An adult, on the other hand, can break down branches which start at anything up to two metres, and which, when broken, will bring down foliage from the four metre level, although this is unusual. If this difference in resources is considered, the preference of the nursery herd for low, open areas is almost certainly due to the specialised feeding requirements of the herd.

On the level of the whole populations' preferences throughout the year, several key food resources are certainly involved. The area covered by squares G6 - 10, H6 - 9, I6 and 7 and parts of F6 - 10 and J7 were burned in January 1973. The distribution of the eland through the rest of 1973 was considerably affected by this, as can be seen from Figs 20 and 21.

Although I have far fewer sightings for the dry season than for the rainy season, the distribution of the sightings is about the same in both seasons, indicating that the eland are far more scattered during the winter. Part of the reason for the low sighting rate may be that the animals were using areas unknown to me - at least one cow left the reserve, although she was driven back. However, the sightings in the winter were concentrated in several distinct areas: the area around the camp (mainly old cows), the areas alongside the river where animals were seen to utilise the grasses growing on the mud as the dam level dropped, and in the higher levels of the reserve, leaving the intermediate zone more or less free. I also had the impression, from daily movement observations, that they were utilising the more closed plant

communities/.....

communities, such as the thickets and trees lining dongas. The latter case was very difficult to prove, since only the most thorough search on foot of each donga system would have revealed the presence of animals. It was not possible to cover the whole reserve in this way within a reasonable time. Each of these sectors represents either an underexploited food resource (the food around the camp) or else a more concentrated food resource (fruits, leaves, even flowers in the tree/thicket communities) than is found in the more seasonally variable summer range.

MOVEMENTS IN RESPONSE TO OTHER FACTORS

Movements are certainly not governed by food resources solely, at least in the short term. The factors involved can be divided into two distinct groups, social and physical. The identifiable social factors also refer to intra-group movement, which is, therefore, also considered here.

Social Factors Governing Movement

The movements of individual animals are governed partly by the behaviour of other members of the group. The cohesion of the group is maintained by "voting" (Walther 1972) determining the group activities. This mechanism may, however, also act to form temporary subgroups and is possibly the basis of the division and aggregation of groups throughout the year. When an animal starts to move away from the group, other individuals who are "ready" to move may follow suit, while animals which are in the midst of a bout of e.g. ruminating are less likely to follow. Whether the initial movement results in the whole group moving depends on how the first individuals are moving (in flight, at a walk to some definite objective, grazing), the state of the group, whether it is at ease or has recently been disturbed, its composition (calves are more ready to follow than other classes), the number of animals initiating the movements (single animals, whatever they are doing, will rarely ignore movements by the rest of a large group). Time of day, season, ecotype, terrain, are also probably involved. Adult, dominant animals are more likely to stimulate following than low

ranking/.....

ranking or immature individuals.

If, for instance, only a single adult animal starts to move away from a resting mixed group towards a water supply or a patch of browse, the adults remaining often ignore the movement completely, or follow it only with their gaze. In this case, the moving animal often stays within sight of the group and soon rejoins it. If, however, the same animal stimulates several calves or yearlings to follow suit while the mature members of the group remain ruminating, the new subgroup will move further from the main group and will act more independently of it, sometimes becoming completely autonomous. Such subdivision was often seen during the daily movements of groups, and the splinter group formed might not be seen with any members of the original group for several days, if at all.

Adult dominant animals are particularly effective in initiating movements of individuals or of the whole group. Leyhausen (1971) describes such behaviour as part of the normal intra-group movements of cattle, with dominant animals "pushing" the group along while "attractive" animals "pull" other individuals after them. Although this sort of interaction probably occurred continually within the eland groups, it was only noticeable in certain instances. Within a stationary or slowly moving feeding group, the only signs of leadership/followership were the instance described above of individuals leaving the group and the tendency of calves to group around larger animals. There was no sign of particular individuals governing the direction or organisation of the intra group movements, except in the marginal case of dyadic interactions over browse plants (see Chapter 5). When large groups were moving quickly, either in flight or in the evening moves, there was a more obvious organisation and the effect of dominance was pronounced. The dominant individuals, especially the old bulls, would be found towards the rear, while the younger classes formed outriders and the front rank of the group. That the dominant animals would often begin to move by walking into the rear of the group, and that moving animals were often more concerned with what was going on behind them (shown by head and ear position) than what was in front, support this interpretation. In

more/.....

more artificial situations, dominants were seen to drive groups of subordinates in front of them when disturbed, especially when approaching strange objects (e.g. with semi-tame individuals when moving towards people; with a newly captured group being driven into a runway in a boma). The situation was, however, reversed when there were several calves with one or two females, at least in "normal" walking; in this case, the calves would fall into single file behind the nearest cow.

The older and larger animals were more effective than others in both initiating and preventing flight. When the tame cows were with a group, other group members were unlikely to flee from me even if they were apparently very disturbed. On the other hand the tame calves would follow the flight of a larger, less tame animal. In the wild, I would often see calves or subadults give little dashes to and fro when the group first became aware of me, but group flight rarely followed unless one of the adult members began walking or trotting away. Sometimes, however, numbers of calves fled together, and then the rest of the herd followed.

Within the group, grazing movements and orientation are as in cattle (Hafez and Schein 1962), although the number of animals showing parallel orientation was highly variable, as was the separation between them. These apparently depended on whether the nature of the terrain and the homogeneity of the grass/herb layer would permit such orientation without seriously affecting the animal's foraging. The orientation with respect to neighbours was less noticeable when groups were browsing off well dispersed shrubs and thickets, and it broke up completely in the denser habitats when animals were browsing off trees, the movement and orientation of animals being governed by the position of food trees rather than their companions (except during approach/avoidance interactions).

Physical Factors Affecting Movement

Wind direction is normally assumed to be important in the daily activities, especially movements, of game animals. It has been described as particularly important in eland who are supposed

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to flee into the wind - if an attempt is made to turn them, they are reputed to turn at bay (Maberley 1963). The valleys and hills of Loskop were filled with continually changing eddies of wind, so that the orientation of the group with respect to wind was problematical. However, when groups could be followed closely, especially nursery herds movements in the late afternoon seemed very closely linked with wind direction. The group would move into the wind during its later feeding periods, or else would stand ruminating until about an hour or half an hour before sunset, when all members would then form a compact bunch and walk or trot uninterruptedly downwind for up to one kilometre. By the time the whole group had made the journey, the sun was usually behind the hills; the period of dusk which followed was marked by a distinct change in behaviour. They were then much less timid and the group would sometimes approach me sniffing inquisitively - much more closely than they would during the day. This is presumably a predator defence strategy, since any nocturnal hunter following their scent trail must approach them from upwind; it is however, ineffective against animals following their wind-borne scent (this may account for their increased curiosity - to check out any possible predators).

This same evening move usually involves a change of ecotype. Sclater (1900) records that eland remain in closed habitats during midday and only move out into the open during the cooler parts of the day and night. This however, was only partly true at Loskop; usually the move involved such a change, but even during mid-summer the same group might, on successive nights, move into the hills, into a donga, and into open grassland. While shade is undoubtedly sought out at times, and may govern daily movements to some extent, it is also often ignored, with moves of up to half a kilometre taking place in the open sun at 40°C.

As with gazelles (Walther 1972) rain can cause flight behaviour. This was seen several times when nursery herd calves were suddenly caught by a heavy downpour. In these cases, flight was rarely in any particular direction. In milder rain, animals would sometimes move into sheltered valleys, although on other occasions they would remain in the open or in light shade. The effect of

rain/.....

rain on movements is also seen where it restricted animals - they tended to remain ruminating or browsing in closed habitats rather than moving into the open, although they did move out into the rain eventually.

The terrain at Loskop presents several obstacles to the free movement of eland, although these can be negotiated at need. When the river was in flood, there was little movement between the two sides of the reserve, although I have seen a cow swim out of her depth, when panicked, into the water of Lombards Bay. Her swim was, however, less than thirty metres. During the winter the river level might drop to a matter of centimetres at the western end of the reserve, and animals passed freely through this. The steeper rocky outcrops were also avoided except when they would have necessitated an extensive detour or when the animal was in flight. The geography of the reserve forced the animals to pass over areas of extensively exposed rock if they were to cover any distance, but they rarely lingered in these areas and utilised only the less exposed slopes in their normal feeding movements. Despite their jumping prowess, they seem unwilling to jump any obstacles unless in flight, and although the reserve perimeter was at some places fenced to only 1,5 metres, and at one point was a gate 1 metre high, there is only one known instance of eland escaping. More natural obstacles which were avoided rather than jumped were narrow dongas, fallen trees and small, sheer drops.

From the variety of movements listed by Sidney (1965), it seems that eland group size, composition and movements are very dependent on local conditions. In particular, eland are highly adaptable in adjusting their dispersion and utilisation of resources from season to season. This would seem to be borne out by the records of group size, composition and movement at Loskop (see e.g. Table 8). The pattern of movement and group formation seems to be well adapted to utilising the complex of ecotypes found within the reserve. This adaptation seems to be effected by the process of group formation and division.

Table 8 : Correlation of monthly weighted mean group size of eland at Loskop Dam Nature Reserve with nutritional content of grasses (Spearman).

	<u>Group size</u>
Crude protein content	+ 0.691 *
Crude fibre content	- 0.573 *
Soluble ash content	+ 0.639 *
Potassium content	+ 0.729 * *
Calcium content	NS
Magnesium content	+ 0.568 *
Sodium content	+ 0.576 *
Phosphorus content	+ 0.644 *
Chlorine content	+ 0.563 *

DISCUSSION

While the relationship of group structures to social behaviour will be considered elsewhere (Chapter 9), there are several points related to the mechanism of group formation which are best treated separately. The subdivision effect described under "Social factors governing movement" almost certainly governs small scale independent movements in most aggregations of animals. Its importance in eland movements is, however, shown by the fact that only groups of three or two members were seen with exactly the same individual composition two days running, also by the very low association indices between individuals (see "INDIVIDUAL COMPANION PREFERENCE").

When such a split takes place, the distance covered, the number of animals involved and the time will reunion (if the two groups are still recognizable) is highly variable. Probably seasonal factors acting directly on this subgroup formation process are the main causes of variations in group size, rather than there being a distinct social mechanism for division and aggregation. For example, in winter a browsing or drinking subgroup moves much

further/.....



further from its ruminating companions than in summer, reducing contact between the two groups and favouring independent movement. This almost certainly applies to the process of group formation and division within the confines of the reserve (see Table 4). Less restricted populations must, however, be governed by additional mechanisms, e.g. ecological separation of age/sex classes in winter.

Even at Loskop, there are probably ecological pressures on bulls, forcing them apart from females except during the summer, when the animals restrict their movements to particularly good grazing areas. This period corresponds with the rut. There is external evidence of ecological separation between males and females outside the breeding season (Abbott 1968a, Roth *et al.* 1972, Keep *et al.* 1974), and even within the confines of Loskop there is a distinct difference in the distribution of all-male and all-female groups (Fig 19). This is reflected by individual records (Fig 20). Females tended to be found in the north eastern sector, while males were found in the south west. While there is no direct evidence of any particular factor being involved, the rather extreme dimorphism between males and females would suggest that, following Jarman's (1974) arguments re body mass and feeding strategy, the two sexes would have divergent feeding strategies. This would tend to keep the two sexes apart, especially in periods of restricted food supply (i.e. winter). Calves are probably similarly ecologically separated from other members of the population (see "Female/Calf Association").

There are therefore three main factors which affect eland group formation and movements in the Loskop population: the tendency of individuals or groups to feed opportunistically and to range widely unless utilising a concentrated food resource; the loose-knit nature of the group and the ease of subgroup formation; the ecological separation between age/sex classes, and even some individuals. These factors could conceivably explain the distribution and movement of almost all eland populations, except possibly the migratory ones, but would require detailed information on the annual cycle of behaviour in each population for substantiation.



CHAPTER 5

SOCIAL BEHAVIOUR

Although the eland is a social animal, occurring in herds of possibly up to 1,000 individuals (Smithers 1971), it has a very limited repertoire of social behaviours. Apart from the mother/infant relationship, all interactions seem very casual, with the exception of some rutting season fights. In fact, the major part (over two thirds of field observations) of overt interactions seen were aggressive ones. Apart from aggressive behaviours, the main social interactions observed took the form of non-aggressive contact between individuals or else social investigation i.e. sniffing.

Eland overt dominance interactions fell into two distinct types, both of which had characteristic complexes of behaviour patterns. The most frequent were those involved in everyday expressions of stable dominance relationships between two individuals, which were simple exchanges involving the approach of one individual (with or without threats) to another, followed by an avoidance response by the second individual (compare e.g. Rowell 1966). Less frequent, but more spectacular, were exchanges where there was direct conflict between two individuals and which apparently involved rank determination (see Table 9).

The basic difference between the two forms of dominance is apparently that the animal "assume" that there will be no retaliation from its subordinates following an aggressive approach, except under certain circumstances. This is typified by Shank's (1972) division of aggression in feral goats into two forms - the "rush" association and the "clash" association. The "rush" is an all-out attack which invariably results in the opponent fleeing, while the clash is a forcible head to head conflict: the goat's day to day reinforcement of the dominance hierarchy is in the form of "rush" attacks and the derived threats. It is possible to make a similar division in the overt aggression of the eland, where the threats seen in stable dominance interactions are derived from the

all-out/.....



all-out charge (comparable to Shank's rush, 1972) rather than from challenge and fighting activities.

Table 9 : The expression of dominance and aggression in eland at Loskop Dam Nature Reserve

<u>Behaviour</u>	<u>Relative Frequency in wild</u>	<u>Relative Frequency in captivity</u>
Fights	0.08	-
charge	0.06	0.02
contact	0.08	0.19
approach/ avoidance	0.18	0.18
threat	0.18	0.18
no contact, no threat	0.60	0.61
	Total interactions in wild = 610	Total interactions in captivity = 2048

NB. Calf/calf "play" fights are not included

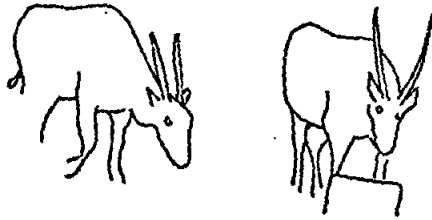
BEHAVIOUR CHARACTERISTIC OF
STABLE DOMINANCE SITUATIONS

NO CONTACT, NO THREAT APPROACH/AVOIDANCE

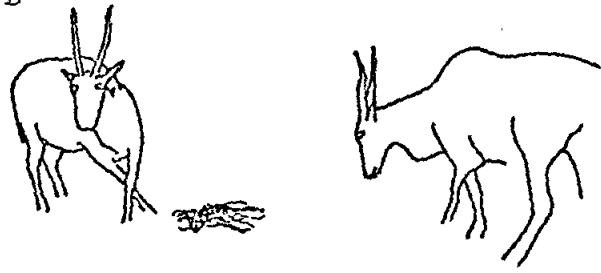
The animal "confidently" approaches another, walking directly towards it. If the displacement is centred around a trough or food plant, the dominant animal usually walks and moves its head as if it were about to feed at the same spot (Fig 23). The "intention" to feed head movement involves extension of the neck and head towards the feeding point with ears forward. It may occur slightly earlier in approach/avoidance than it would in feeding with no subordinate present. The impression given by this approach is that the dominant animal almost completely ignores the subordinate unless

the/.....

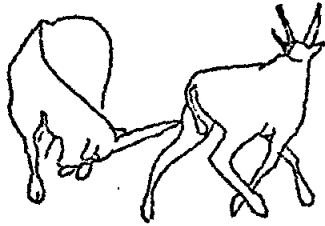
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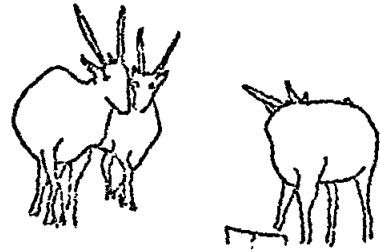
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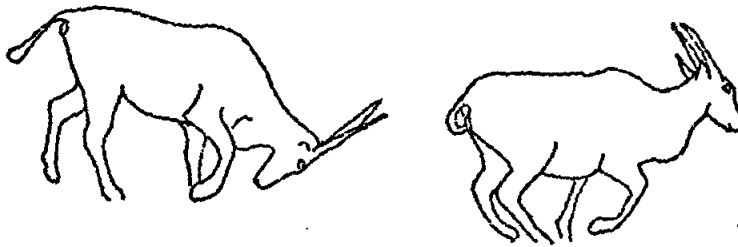
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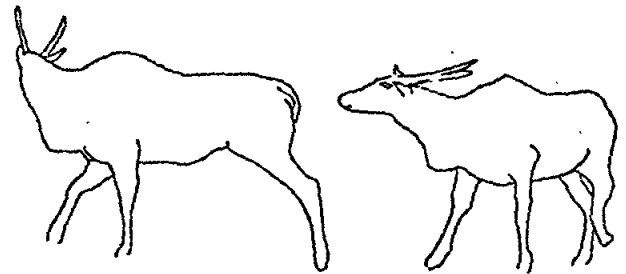
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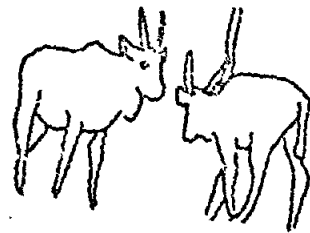
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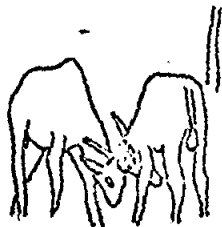
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L



M



Figure 23. Stable dominance interactions and general aggressive activities in eland at Loskop Dam Nature Reserve and the National Zoological Gardens, Pretoria. June 1972 - May 1974.

- A. A dominant cow approaches a lick showing feeding intention movements. The subordinate at the lick is about to turn aside.
- B. A dominant cow approaches a subordinate with a horn threat.
- C. A dominant cow horns a yearling, making light contact.
- D. Two low ranking cows beside a lick flinch away as a nearby dominant cow makes rapid head movements while grooming.
- E. The full charge.
- F, G. and H. are drawn from photographs taken with the same lens and are at the same magnification. F: the cow is 20 m from and approaching the observer, who is near her lying out calf. G: she is 10 m away and has her ears back in preparation for a charge. H: after the charge, she is 15 - 20 m away and watching the observer's retreat.
- I. A dominant cow drives a subordinate for 15 m with nose out-stretched.

J-M. Play fight between giant eland.

J. The bull approaches the cow, who stands watching him.

K. Both lower horns and fold ears back.

L. Horn engagement.

M. The bull turns away from the cow, lifting his head, the cow keeps her head low and ears back.



the latter fails to get out of the way.

Apart from this "pure" form of the "confident" approach, several other forms were included for the sake of convenience. These were behaviours where the horns were not threateningly dipped towards the opponent, but other activities which might be construed as aggressive were seen e.g. some forms of grooming, and head tossing. The simplest case of this was when the ears were flicked back during the approach, usually when the dominant animal was two to three metres away from the subordinate. Grooming was characteristic of all aggressive situations and is treated separately. There was a slightly ritualised version of the confident approach, which involved a slower movement and a higher head position in the initial stages, similar to that seen in (Fig 24).

In addition, on one occasion a cow used the "head-and-neck-stretched-forward" (Walther 1974) posture to drive another female some fifteen metres (Fig 23). This is not normally a threat display in eland, but rather a sexual display, according to Walther (1974). Persistent driving, resembling courtship "tending" (McHugh 1958), occurred on some occasions, but the driving animal was up to ten metres behind rather than at the recipient's hindquarters and the former's body was noticeably "erect" (Walther 1974).

THREAT APPROACH/AVOIDANCE

Threat approaches were at first indistinguishable from non-threat approaches, since the dominant animal might cover up to thirty metres to another one but only show threats in the last three or four metres. With a long distance approach, however, the recipient was usually aware of the approach and moved away long before the first animal arrived. The use of threats was therefore partially determined by the response of the recipient. If an approached animal moved on quickly, no threats were seen, but if the recipient of an approach were slow to react the aggressor would first threaten, then horn. There were, however, times when a dominant animal threatened or attacked regardless of the response of its subordinate.

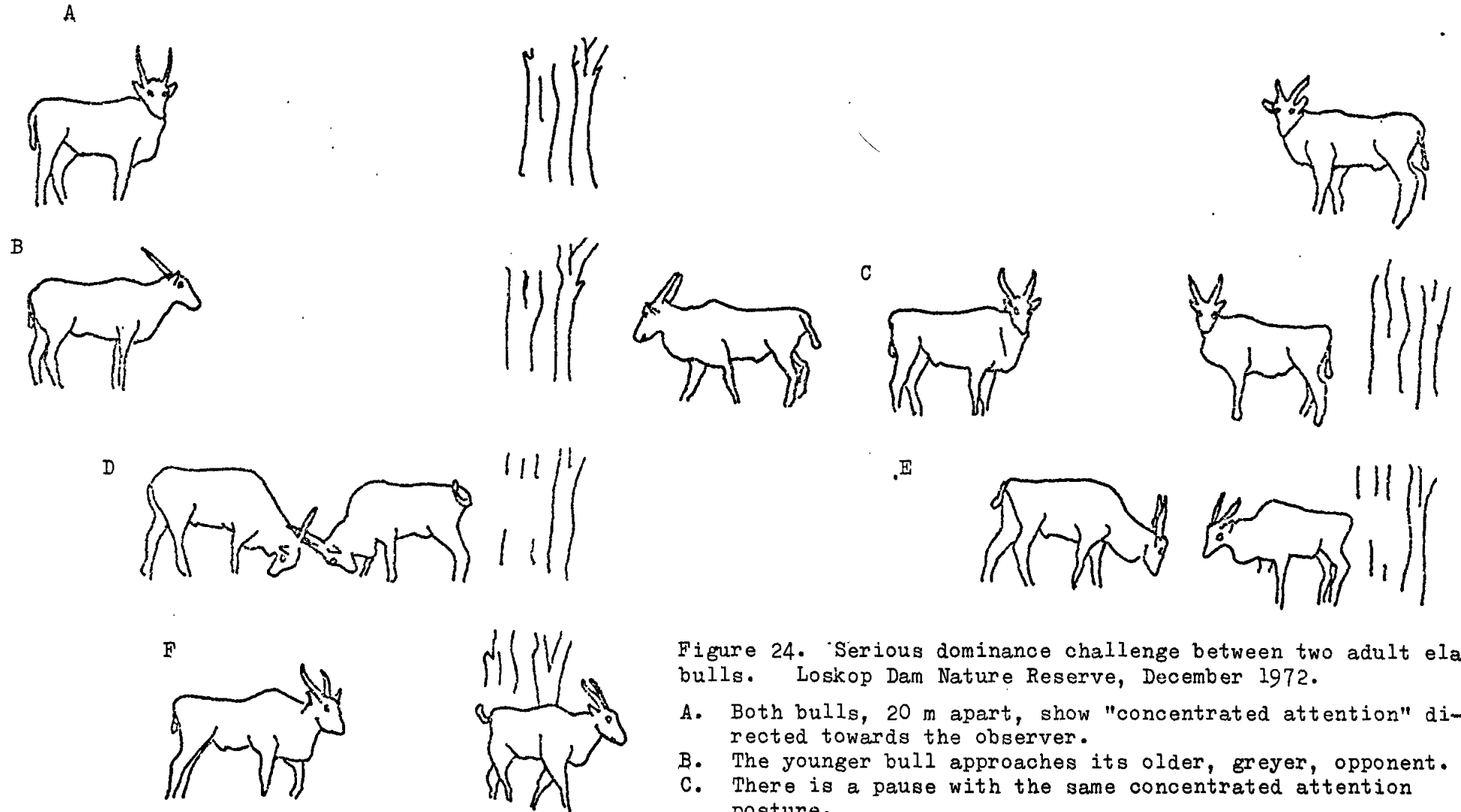


Figure 24. Serious dominance challenge between two adult eland bulls. Loskop Dam Nature Reserve, December 1972.

- A. Both bulls, 20 m apart, show "concentrated attention" directed towards the observer.
- B. The younger bull approaches its older, greyer, opponent.
- C. There is a pause with the same concentrated attention posture.
- D. Horn engagement follows immediately.
- E. The challenger backs away from the older bull, who advances - changing his position for the first time.
- F. The subordinate turns and walks quickly away, ears back.



The range of distinct motor patterns comprising threat is quite large. Those directly derived from the "charge" are hooking or twisting movements of the horns directed upwards and towards the body of the opponent from a variety of positions intermediate between the "normal" head position and the "low presentation-of-horns" posture (Walther 1974). There were however, three "typical forms" of these threats - those delivered from the extremes ("normal" and "low") and a position about half-way between the two ("horning", "horn sweep" and "hooking" respectively).

When displacing another individual, the approach was usually from the side or the rear, but displacement did occur from the front, and once again the threat action used, although directed towards the head of the opponent, was not a challenging action but a confident one; compare Figs 23 and 24. The action is the same as that shown by the victor after the fight.

Eland frequently shook their heads as they came alongside an animal they were displacing. The headshake occurs in a variety of contexts and its general interpretation is uncertain. In this case, however, the recipient seemed to regard it as a curtailed "horning" or "hooking" action and moved away.

On one occasion, a cow was seen to displace another by means of the "high presentation-of-horns" (Walther 1974) and a very stilted walk, which probably does not occur in any of the other tragelaphines (see Walther 1974).

The head-nod, which Walther (1974) considers exceptional in eland, occurred quite frequently when the displacement approach was made from almost directly behind the recipient.

Walther (1974) states that the downward sweep of the horns into the low presentation position was seen as a threat in eland. However, I never saw the head low position without some hooking or horning action as well.

CONTACT APPROACH/AVOIDANCE

Contact in the displacement situation was usually an extension of the threat actions. Although many of these are derived from the "charge", the contact involved was usually fairly light - on

some/.....



some occasions, animals were seen to stand still following an approach and then very gently touch their horns to the side of the recipient. In actions such as the head-shake and the nod, the side or front of the horn, rather than the tip, usually touched the subordinate.

Some of these actions, however, appeared to involve considerable force. Cows pestered by strange calves trying to suckle were often particularly savage in repelling the calves, but the really powerful attacks in this situation were often "spanking" actions (i.e. with the sides of the horns). When an animal apparently attempted to horn at another with all of its strength, the recipient usually fled so quickly that contact was never made. The "charge" itself was rarely seen, and when it was, the charging animal seemed to be slower than its victim. I never saw a charging animal make good contact, partly because it did not run as quickly as the one fleeing, and partly because the "charge" position with horns down (Fig 23E) was rarely maintained for more than a few seconds before the aggressor finished its attack.

An uncommon contact aggressive action was for the dominant animal to approach the subordinate from the rear, place its nose between the subordinates hindlegs and lift and push, causing the recipient to stagger forward, off balance. This action was used several times by bulls on cows, once between cows, but never between bulls.

Apart from these actions involving the head and horns of the aggressor, animals were seen to brush others aside with their flanks. This often occurred where there was a great difference in rank e.g. bulls to cows, cows to calves: calves sometimes had to be very nimble to avoid being trampled. The action was usually seen when one animal approached another from the rear, and involved contact of the aggressor's shoulder with the recipient's side. Sometimes this action was a very distinct nudge.

RESPONSE OF THE RECIPIENT IN APPROACH/AVOIDANCE SITUATIONS

I attempted to measure the distance at which an animal normally avoided the approach of another. Although this distance

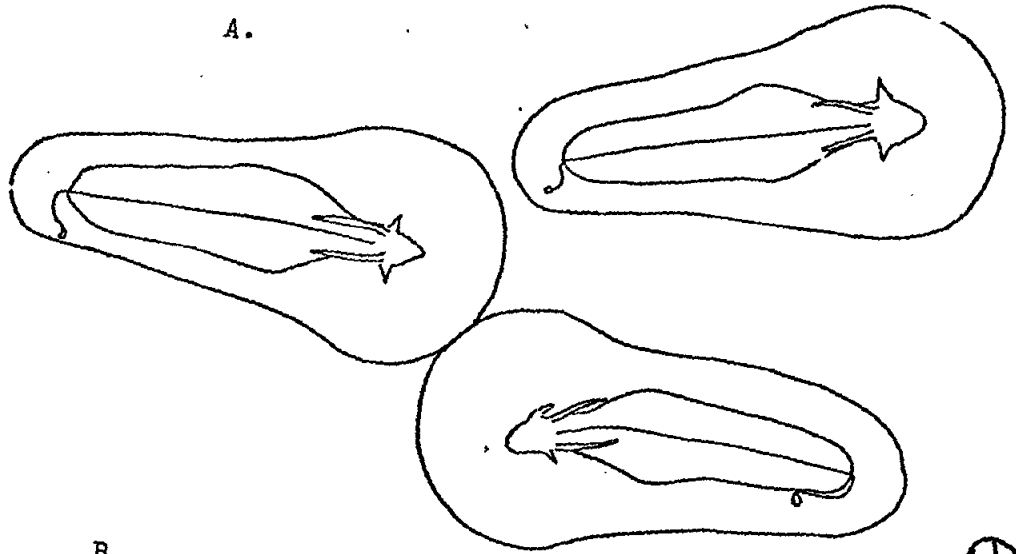
was usually between two and five metres (cattle avoid at about two metres - Hafez and Schein 1962) it varied, depending on the immediate history of the groups and the individuals involved. I have already mentioned dominant animals "parasitising" food location by subordinates: on many occasions cows were seen to keep this up for a complete feeding period (up to five hours), by which time their victim would be very nervous, and would flinch away from any movement by a dominant animal within ten metres of her. Prior to this final state, a low ranking cow sometimes attempted to keep by her food when a superior approached, and fed for a short while side by side with the high ranker before being chased off. Members of groups which have been through a period of intense aggression (bulls fighting, the captive group at feeding) may also show exaggerated avoidance distances. In addition to this, animals avoided a head-on approach much sooner than a head-to-tail approach. I found that the best way to consider the avoidance distance was as a pear-shaped field around the animal's body, the actual size of the field varying according to the situation (Fig 25).

The posture during active avoidance was also variable, and depended again on the animal's history as well as the form of aggression shown. Some individuals would sometimes race away from a look in their direction, while others would just step aside from a charge. The most characteristic position was to walk away with the head and neck slightly lowered. With a more rapid avoidance, the animal walked briskly or trotted away with its head held up and its ears back, as in alert flight from a non-social stimulus. The extreme - all out flight - involved a canter or gallop, with the posture typical of those gaits.

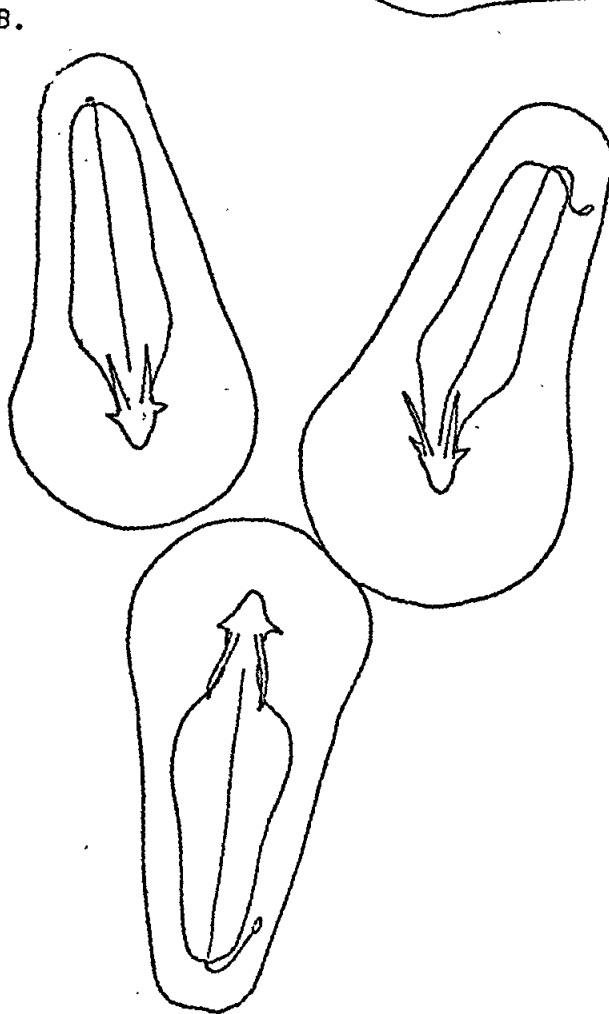
The actual direction of avoidance is usually straight forwards and slightly to the side when an approach is made from the rear. Approaches from the side are best interpreted by considering that the pear-shaped "personal field" of the superior is pushing the inferior's field aside.

Apart from an overt dominance interaction, occasionally an animal moving from one place to another will make a semi-circular detour in order to keep at a distance from a dominant animal. Such active avoidance of a "passively" dominant animal was similar

A.



B.



C.

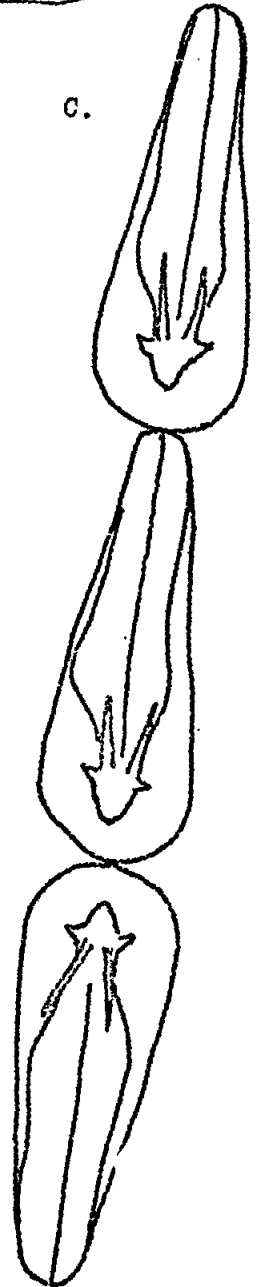


Figure 25. Personal fields in adult eland interactions. Loskop Dam Nature Reserve, June 1972 - May 1974. The fields are drawn with two main centres of curvature - at the base of the tail and between the horns. In fact, the size and shape of the head field probably depends on the head position and on a pivot point somewhere in the neck. A more elaborate description would also give each animal a "passive" field and a larger field which operates when it is the active initiator of an exchange.

- A. Two animals are equidistant from the head of a third, dominant animal but the one facing the dominant animal is forced to look away because of the size of the head fields, while the one facing away is unaffected.
- B. Two animals face a third, dominant, individual. One, with a greater personal field, looks away, while the other is undisturbed. The two "inferiors" might be two individuals with different histories or the same animal at different stages in its relationship with the dominant animal.
- C. At licks and with other voluntary crowding, the fields around most of the body is greatly reduced, but it remains fairly large around the head. The central, dominant animal is at the lick and has one subordinate queueing behind it, while another attempts to approach the lick from the front.



to the milder forms of approach/avoidance as far as the behaviour of the lower ranking animal was concerned. Lowering the head as if to sniff the ground was often seen here. Walther (1958a) interprets this action in other tragelaphines as a ritualised feeding behaviour.

BEHAVIOUR CHARACTERISTIC OF DOMINANCE CONFLICTS

Dominance fights were variable in length and in the component behaviours involved. They were also variable in "seriousness". Many fights had a playful appearance but ended with the dominant animal winning, which made it difficult to determine the difference between "play fights" (if these do, in fact, occur) and those involved with dominance. If, however, a distinction is made between adult and juvenile types of fights, then there are several characteristic features. Juvenile fighting is dealt with elsewhere (Chapter 8). There were three phases to the adult fights: the challenge; the approach and the fight proper; the defeat and the assertion of dominance by the winner.

CHALLENGE

The main form of challenge was some sort of approach combined with fixation of attention on the opponent. This would usually be the "concentrated alert" posture directed to the opponent (Fig 24). If the recipient turns away, the interaction may end there or the challenger may go on to the assertion of dominance phase. If the animal challenged does not turn away, the challenger will approach him at a walk, which may be slow and stilted. When an animal is joining a group, it may horn savagely at the ground ("Bodenforkeln" - Walther 1964a) during the challenge.

Other challenges include grazing towards the head of the opponent and mounting the opponent. Both of these actions are used more frequently after the fight by the victor, and there is therefore some dominance involved as well. Mounting and chinning are used in other situations to ask the question "are you going to move?" (e.g. at licks; by male on female in sexual preliminaries;



when mildly disturbed), and in fights it also seems to say this, rather than "I want to fight you".

APPROACH AND FIGHT

Once the challenge has been accepted i.e. when the recipient either stands or moves towards his opponent, there may still be some distance separating the two individuals. During the approach, both participants sometimes look aside in the "alert" posture, usually with their attention fixed on something external to the fight (in the field, usually myself). This is similar to the "displaced alarm display" seen in wildebeeste (Estes in litt.) and many other species (e.g. blesbok, Novellie pers. comm.; bon-tebok, David 1973). During the initial stages of the approach, the walk and stance are approximately "normal", but towards the end, the contestants start to lower their horns into the "horn presentation position". This begins several metres before the two actually meet. As Walther (1958a) notes, the presentation position may be very extreme.

They close in this position so that the horns interlock. There is often considerable jockeying for position before the two engage properly, with one animal parrying the approach of another until he can bring his own horns forward into a suitable position. This jockeying may sometimes constitute most of the fight, and I have seen one bull terminate a fight by turning away when he could neither engage his own horns nor deflect his opponent's from their threatening, flat position.

Once the horns are engaged properly, the combatants push and heave forwards, twisting their heads and necks. The object of this stage of the fight seems to be to twist the opponent's head to one side so that he can no longer push with his full strength. Animals are often pushed to one side as they attempt to keep their head and body in a straight line; this in turn usually causes the opponent to twist his head in order to maintain a good horn engagement. The actual point of contact between the two animals depends on their horn shape, and it often seems that the animals are pushing head to head rather than horn to horn.



Once an animal breaks off, having been forced aside by its opponent, it may present its horns again immediately and reengage. This often happens with both combatants in any single fight. This sequence of engagement/reengagement continues until one animal breaks off and turns his head and body away from his opponent.

THE DEFEAT AND THE ASSERTION OF DOMINANCE

In turning away from his opponent, the defeated animal may lift his head quickly and turn, supported mainly on his hind-legs. This usually occurs if neither animal has been exerting his full strength and the fight has had a "ritualised" appearance. Turning away in the midst of a vigorous tussle, however, has some danger, and the defeated animal instead retreats slowly. His opponent follows with horns still lowered until the other has disengaged and stepped away. The dominant animal continues to step forward with head and horns vertical while the other tucks his ears and horns back and turns away. The dominant animal may then just stand, looking "alert" at his opponent, or he may enforce his dominance in some way. This may be "driving" for a short distance, mounting, or it may be a series of grazing movements in the direction of the opponent. After a vigorous fight, the victor may charge his opponent as the latter turns away. These charges are normally avoided but it seems from such instances as Steinhardt's (1921) that the animal will complete the attack if he can catch up with or corner his opponent. Assertion of dominance was not always seen, and in these cases it was often difficult to say whether there had actually been a defeat.

Following the drive or chase, both participants may show intensive grooming or "displaced alarm" (Estes 1969).

COW FIGHTING

The above describes most interactions (dominance and aggressive) between bulls older than one year. The fights between cows are usually similar but of a much lower intensity. In only one instance was there a fight comparable to the really savage, almost completely unritualised ones sometimes seen in bulls. In this



case, the course of the fight was rather different to the above descriptions in the preliminary phase. A dominant cow approached the other and stood two metres in front of her in the dominant's "grooming demand" posture. The other cow repeatedly groomed her own side (the one away from her opponent) before stepping to her superior with ears low and head to one side, groomed the other's forehead and quickly stepped back, turning her head aside again. The higher ranker maintained her "erect" position for a few seconds, then stepped forward, lowering her horns. The subordinate retreated rapidly, horns laid back, but the dominant continued to advance until the subordinate lowered her horns and allowed engagement. The fight which followed was about three minutes long (about the same as bouts between bulls) and was unritualised, finishing when the subordinate animal broke away and raced off from a charge by the dominant.

OTHER ACTIVITIES ASSOCIATED WITH FIGHTING

A pair of bulls fighting within a group may be ignored, watched or emulated by other group members. Rarely was there any attempt to disturb a pair of fighting animals. In one instance, though, a pair of bulls were fighting about fifteen metres from an old bull who was dominant to both of them. After they had had horns engaged for about one minute, the dominant bull walked over to them and stood by their heads, looking past them in the "alert" posture. The two immediately disengaged and began nibbling grass, nose to nose, without moving their bodies. The old bull stepped forward and the other two turned away from him and began grazing away, side by side.

The presence or approach of a newcomer was often enough to stimulate fighting within bull groups - resulting in both "newcomer/resident" and "resident"/"resident" fights - during the rutting season. Adult cows rarely reacted to newcomers in this way, although subadults and yearlings of both sexes did, especially when excited.

There were also "fighting storms" where almost every individual would suddenly decide to fight his neighbour. These occur-



red at any period during the day in bull rutting groups, but were rarely seen at any other time. They were sometimes, but not always stimulated by something in particular (e.g. the appearance of an female in oestrus).

When bulls were very excited and were charging, they were sometimes heard to give a deep, full-voiced belching bellow which I find impossible to render phonetically. This sound also occurred when cows were enraged by another e.g. when one took fright and tried to force her way past a dominant cow, the recipient turned and charged her, bellowing.

NON-AGGRESSIVE SOCIAL INTERACTIONS

These include sexual activities (but see Walther 1964a, 1974), social grooming, and social investigation. The expression of most of these is linked with the rank of the individuals involved (see Table 10). I have few records for sexual interactions per se, but it should be noted that young adult bulls interact with adult cows at a considerably lower level than do old bulls, suggesting that their relative youth prevents them from obtaining access to females.

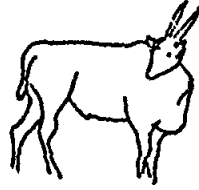
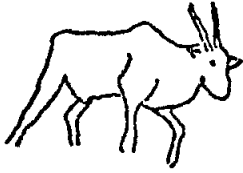
SEXUAL BEHAVIOUR

Although courtship and mating behaviour does not seem to be as elaborate as in other tragelaphines, there are several behaviour patterns which can be recognised and which are similar to sexual behaviour in other bovids.

Tending (McRugh 1958)

This behaviour basically involved the bull keeping close to the cow. His normal position was to her side and rear (Fig 26), and he would sometimes "drive" her considerable distances at a walk. Driving is widespread in ungulates, sometimes in the form of chases e.g. chamois (Hediger 1955), mountain sheep (Geist 1971) and roe deer (Fraser 1968), but chasing never occurred in eland and prolonged driving of any sort was rarely seen - cows often urinated

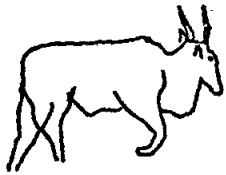
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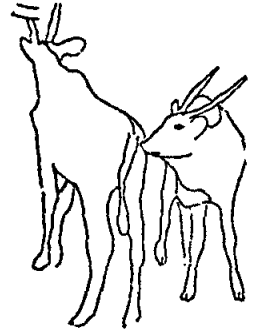
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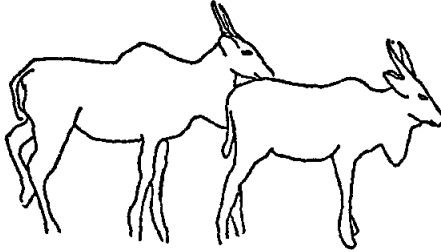
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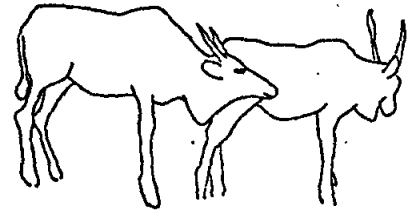
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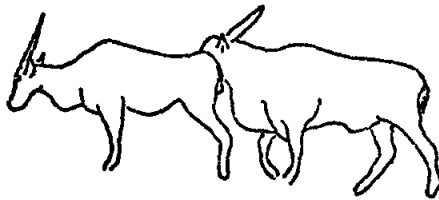
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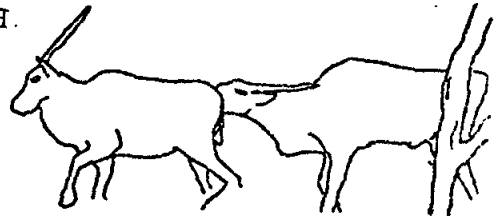
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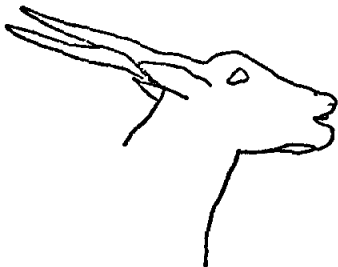
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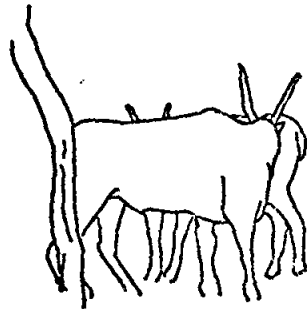


Table 10 : Interactions between captive eland. Loskop Dam Nature Reserve. June 1972 - May 1974.

Type of interaction and age classes involved	Direction index	Correlation of frequency with dominance rank		Correlation of frequency with density		
		Receiving	Doing	Receiving	Doing	
<u>All aggression</u>						
Adult/adult	0.940	-0.511 *	0.467 *	-0.360	-0.090	All interactions observed were divided into:
Calf/calf	0.819	-0.127	0.200	-0.091	0.127	
Adult/calf	0.732	-	-	-	-	
<u>Non-contact,</u>						
<u>Non threat approach</u>						
Adult/adult	0.939	-0.494 *	0.467 *	-0.341	-0.090	Aggression
Calf/calf	0.829	0.092	0.222	-0.092	0.037	Non-aggressive contact
Adult/calf	0.732	-	-	-	-	Sniffing
<u>Threat approach</u>						
Adult/adult	0.950	-0.449 *,	0.244	-0.431 *	0.067	Since each showed significance, they were then further subdivided into the age classes and interaction classes shown here.
Calf/calf	0.929	-0.301	0.639 * *	0.200	-0.341	
Adult/calf	1.000	-	-	-	-	
<u>Contact approach</u>						
Adult/adult	0.957	-0.550	0.378	-0.483*	-0.315	* : p = 0.01 - 0.05
Calf/calf	0.755	0.073	0.309	0.091	-0.2182	* * : p = 0.001 - 0.01
Adult/calf	0.938	-	-	-	-	

Type of interaction and age classes involved	Direction index	Correlation of frequency with dominance rank		Correlation of frequency with density	
		Receiving	Doing	Receiving	Doing
<u>All sniffing</u>					
Adult/adult	-	-0.045	0.089	0.387	0.545 *
Calf/calf	0.583	-0.273	-0.163	-0.091	0.026
Adult/calf	0.513	-	-	-	-
<u>Nose sniffing</u>					
Adult/adult	-	0.106	0.178	0.107	0.536 *
Calf/calf	0.643	-0.382	-0.309	-0.346	0.273
Adult/calf	0.665	-	-	-	-
<u>Anus sniffing</u>					
Adult/adult	-	-0.049	0.089	0.273	0.159
Calf/calf	-	-0.076	-0.273	-0.076	-0.273
Adult/calf	0.773	-	-	-	-
<u>Non-aggressive contact</u>					
Adult/adult	-	-0.636 ***	-0.410	-0.477 *	-0.434
Calf/calf	-0.556	0.055	0.309	-0.018	0.309
Adult/calf	0.658	-	-	-	-
<u>Grooming socially</u>					
Adult/adult	-	-0.407	-0.654 * *	-0.386	-0.018
Calf/calf	0.581	-0.182	0.455 *	0.127	0.418 *
Adult/calf	0.786	-	-	-	-
<u>"Chinning"</u>					
Adult/adult	-	-0.461 *	-0.2163	-0.444	-0.3865
Calf/calf	-0.637	0.220	0.436 *	-0.147	-0.400 *
Adult/calf	-	-	-	-	-



when bulls began to drive them, which resulted in the bull "testing" the urine (see below) and usually ended his interest temporarily. The tending bond itself, however, was more durable: where tending was particularly intense, the bull would go through his normal activity cycle of feeding, ruminating etc, always keeping within two or three metres of the cow. This behaviour lasted at least one day in several cases, and probably longer. This period is probably analagous to the "acquaintance" phase (Walther 1964a) of other tragelaphines, although it may serve other functions (Parker 1974a). Mutual grooming, sniffing etc, as described by Walther (1964a) for greater kudu, did occur but only very rarely. This is possibly because the population was restricted in range and all animals were familiar with the rest of the herd, so that the "acquaintance" phase was much reduced and mingled with the tending phase proper.

"Testing"

All animals tested other's urine from time to time by sniffing, licking or drinking it, then giving flehmen. While cows were not seen to respond to bulls nudging or licking by urinating, contrary to most horned ungulates (Ewer 1968), they frequently urinated when driven hard by a bull (i.e. at a fast walk). However, calves sometimes caused cows to urinate by persistently rubbing and chinning on the females' sides. Urination in response to pressure on the hindquarters is therefore a functioning reflex in the eland, even if it was not seen in the context of courtship.

The actual flehmen was very characteristic of animals with inflexible facial musculature (Estes 1972). The nose was thrown up and the lips were curled away from the incisors. Bulls might hold the position for half a minute or even longer before walking off, usually leaving the urinating animal. While most age/sex classes gave flehmen casually, just lifting the head in whatever position they happened to be, bulls seemed to stand slightly more erect and often turned their heads at right angles to their bodies. Estes (1972) discounts the possibility of flehmen as a

visual signal, attributing it to an olfactory mechanism, but it may have a secondary function as a display in the eland, judging by this slight ritualization in the bulls.

~~Other Courtship Activities~~

Apart from testing and the tending bond, eland courtship was mainly limited to the bull rubbing his head along his partner's flanks as he walked alongside her, and to licking and nuzzling her anal region. Walther (1958a : 371) states that the bull rubs his forehead between her hindlegs" in der gleichen Weise, wie er sonst sein Revier markiert," but this was not seen at Loskop. A form of "Auflegen" (Walther 1958a) was frequent, but it involved the chin rather than the throat as in some tragelaphines, and I prefer the term "chinning" or "chin resting" (Fraser 1968) because of its similarity to this behaviour in Bovini. Mounting itself followed chinning if the cow stood, and the bull laid his neck along her back in the typical tragelaphine posture (Walther 1964a), with the cow standing in the head low posture.

Both chinning and mounting occurred in non-sexual contexts and were apparently as complete as the reactions of their partners allowed them to be - bulls mounted as a challenge to fighting or when inciting flight, and often showed erections, while their partners usually showed the head-low position when receiving the mount, regardless of what happened after.

I never saw signs of any phylogenetically-old fighting activities, such as neck-wrestling ("Halskampf" Walther 1964a), in courtship. Walther (1974) reports that eland cows show a symbolic form of biting ("snapping") which they direct towards bulls which come too close. There was rarely a bull in the captive group, and bulls were always avoided at licks, while in the wild they kept their distance unless tending or displacing a cow, so the relevant situation rarely arose. I did sometimes see violent "ducking grooming" when a cow was being driven closely, but this activity was common to many other situations which involved mild aggression, as well as to non-social grooming.

Posselt (1963) and Skinner and van Zyl (1969) both report



horning and pawing the ground as courtship activities. Pawing was not seen in the Loskop eland nor is it reported by Walther (1974), but a discomfort action similar to pawing does occur in "tense" situations, which may account for this anomaly (Chapter 2). Ground horning was common to many encounters during the rut, often when females were not present, and does not seem to be specially linked with courtship. It occurred on a few occasions as a fight preliminary as well as when bulls were joining groups of females, and I prefer to think of it as a display of virility to both sexes (Posselt 1963 : 85 states that the bull "..... presents a picture of great strength and an impression that he would welcome applause").

Mounting and chinning also occurred in a variety of non-sexual contexts. They were particularly frequent in calves, but were also used by adults in mild disturbance situations e.g. if a group suddenly became aware of me watching them, one animal might chin or mount another, this usually caused the recipient to move and then the whole group would stampede. In some cases, especially with young calves, the recipient did not move and both would stand looking at me (or else just the chinning animal would look) for some while before going about their previous business calmly. The action was also used to drive an uncertain or wary subordinate towards a point of interest: this was seen in both adults and calves. Walther (1958a) states that chinning in antelope seems to be a "last question" before mounting. In the eland, the question ("will you move?") seems to have become generalised into a variety of contexts (Fig 27).

SOCIAL INVESTIGATION ("Kontrollieren")

According to Walther (1964a) investigation of others by sniffing is an important part of the social behaviour of all Tragelaphus species. In eland, it was found mainly in connection with sexual activity or in mother/infant interactions. In addition to this, calves showed sniffing directed to most other individuals, especially peers. In the captive group, it was noticeable that

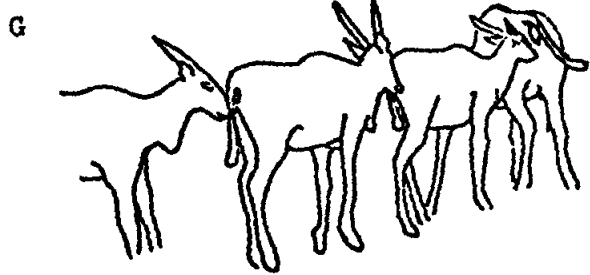
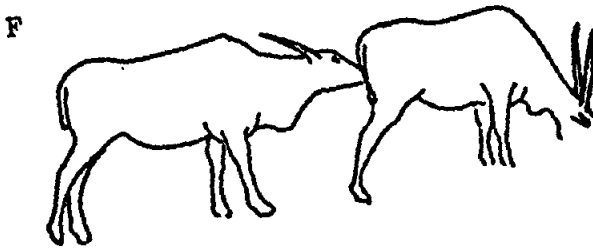
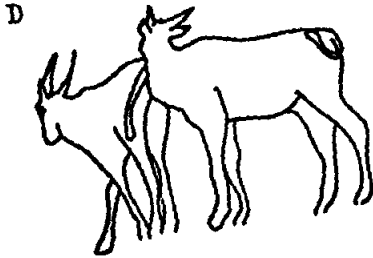
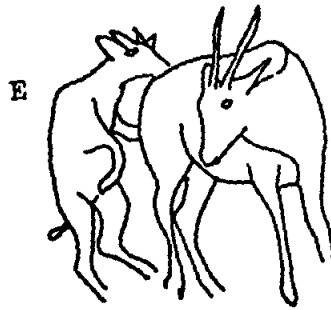
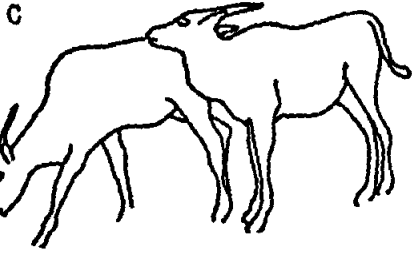
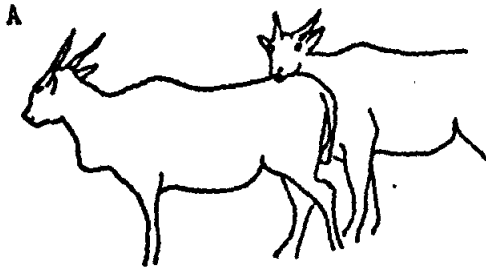


Figure 27. "Displaced" sexual behaviour patterns in eland at
Loskop Dam Nature Reserve and the National Zoological
Gardens, Pretoria. June 1972 - May 1974.

- A. A wild cow chins her tamer neighbour on becoming aware of the observer.
- B. The T. derbianus cow drives the younger bull towards the observer by chinning and nuzzling his hindquarters.
- C. A 6 - 8 month old calf chins another spontaneously, possibly as an assertion of dominance.
- D. A subordinate calf chins an older, dominant one, which then leaves its food trough.
- E. A young heifer attempts to mount a newly introduced, strange cow.
- F. A subordinate adult cow nuzzles and licks a dominant animal's vulva while queueing behind it at a lick. The dominant animal eventually turned on the other and drove it away.
- G. Captive calves queue to sniff the vulva and urine of a newly introduced cow.



new animals were frequently inspected, both nose/nose and nose/anus, which Walther (1964a) records in detail for kudu.

The normal posture associated with social investigation is the same as that shown in investigation of any object at about shoulder level (see Chapter 2, "alarm and investigation") where the nose and neck are extended forward and the ears are held outwards and pointed to the front. The posture may be assumed some two to ten metres away from the animal being investigated, depending on the circumstances. With strange animals, with dominant ones or with sexual partners, the posture tends to be assumed earlier than, for instance, amongst familiar peers.

Social investigation was not linked with the rank of the individuals involved, and was probably concerned with circumstances unconnected with aggression or dominance e.g. the relative familiarity of the individuals involved.

SOCIAL GROOMING (Allogrooming)

Within each of the adult and subadult age/sex classes, the relative dominance of the animals involved is of prime importance, at least in determining the solicitation of grooming. With younger animals and with inter-class exchanges, dominance/subordination effects are less noticeable, on the part of the more dominant animal at least. Figure 28 shows a dominant cow soliciting grooming from a subordinate. As with cattle (Sambraus 1969), eland seem to need both to groom and to be groomed. In the case of a high ranking animal wishing to groom an inferior, the nose is held out and the head lowered in the same manner as that of the inferior (grooming) animal in Fig 28 and the approach is slow.

Social grooming in adults may involve licking by one or by both partners, but usually by one only, the inferior. It is not possible to make many generalisations about older animals, since they very rarely groomed socially (but see Table 11). Most of the observations in the field or in captivity involved three individuals. The subordinate animal in these exchanges seemed very timid and easily scared off by movements of the partner or by external noises. Only one pair seemed to be fully at ease when

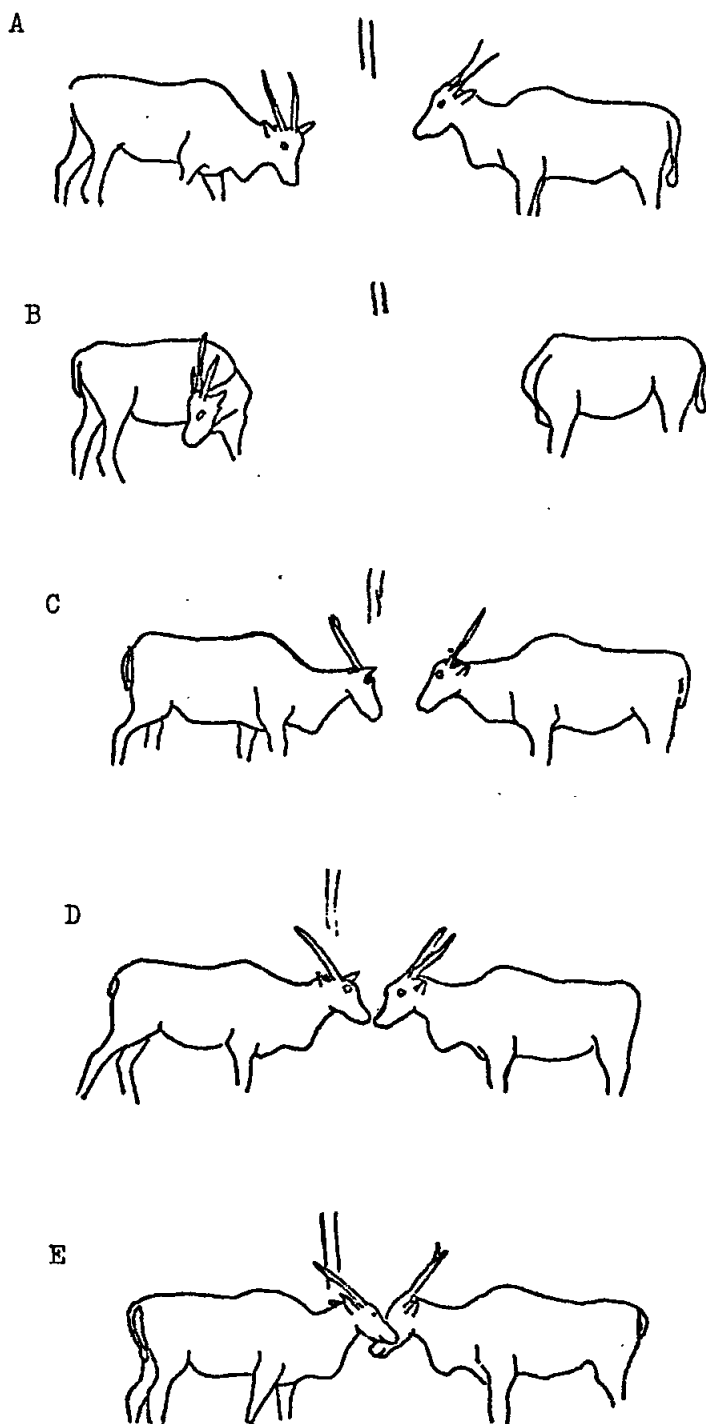


Figure 28. Social grooming between adult eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. A dominant animal (right) approaches and stands head-on to a subordinate who flinches away.
- B. Both individuals groom the side furthest away from the other.
- C. The subordinate animal looks at the other and begins to approach, ears forward head low.
- D. There is a pause as the subordinate cow reaches the others face and she shows signs of uncertainty, switching her ears in various directions.
- E. Eventually she licks the others face, ears back. At no time did the dominant cow change her original position, nor did she prick her ears forward.



grooming each other. In addition, on the few occasions when mutual grooming between adult cows was seen, it was often interrupted by the seemingly deliberate direct approach of another animal. Once a bout was broken off for any of these reasons, it was never resumed.

Grooming of or by calves and yearlings, on the other hand, was much more frequent, and was readily reciprocated. The development of calf allogrooming is dealt with elsewhere, but it is interesting to note here that while adults normally only groomed shoulder to shoulder in opposite parallel (except in sexual situations), the orientation of calves was much more variable and the areas groomed were rather different. In general, the only areas groomed in adult mutual grooming were the face, neck and shoulders. Vulvae were very rarely groomed by other cows in the "queuing" situation; this often seemed to disturb the recipient, usually the individual feeding, and sometimes lead to horning towards the groomer, a subordinate. Calves, however, concentrated on all points which might be said to have a quality of "looseness" - ears, dewlap, the hairs on the back of the neck, the dorsal ridge, the tail (Fig 29). This is discussed more fully elsewhere (Chapter 7).

In at least one small male/female group during the breeding season, licking various parts of the body, especially the external genitalia, was seen between sexes.

When two animals are mutually grooming, shoulder to shoulder, they nearly always lick at similar frequencies. It is possible that being licked stimulates licking and the effect of this is to synchronise the movements of the two animals. Experimentally, whenever I groomed a young calf by scratching her, she respond by licking for long periods anything which happened to be near (my leg, a piece of stone, my rucksack) usually in time with my scratching.

SOCIAL ASPECTS OF SELF-GROOMING

Social interactions of all sorts were often accompanied by self-grooming actions by participants. It would be difficult to prove this association statistically without a continuous recording of all activities, which was not possible under field conditions.

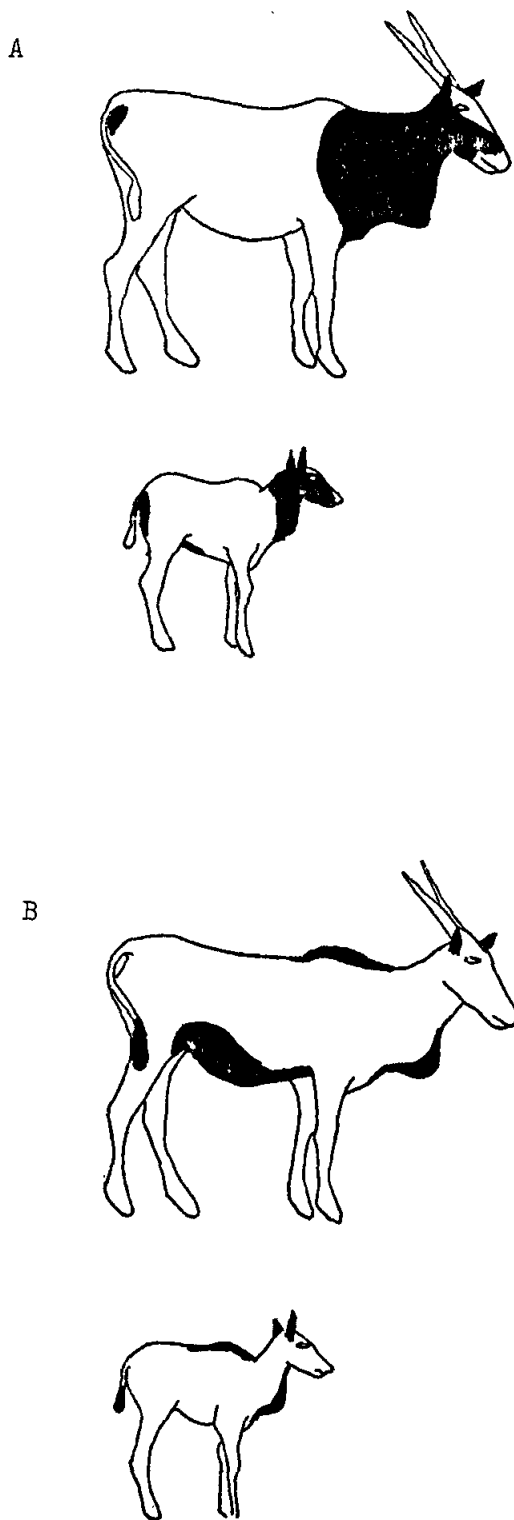


Figure 29. Areas groomed socially in eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. By adults.
- B. By calves.

The calf-groomed areas represent points of concentration rather than exclusive areas. Areas groomed by adults were much more sharply delineated.



Table 11 : Areas groomed socially vs. areas groomed by self in eland (Captive group) at Loskop Dam Nature Reserve June 1972 - May 1974.

	<u>Alone</u>	<u>Socially</u>
Forehead and face	34	47
Neck and dewlap	49	91
Chest	69	91
Ears	10	24
Tail	6	16
Anus	4	60

All alone/all social: $\chi^2 = 85.14, P < 0.001$

However, not only the frequency but also the nature of the grooming activities varies according to the social situation, particularly when grooming in aggressive interactions are compared with grooming in non-social situations. The profiles of these grooming activities are compared for both field and captive situations (Tables 12-15). The profile of "non-social" grooming itself varied according to whether the animals were at licks, in captivity or free-ranging, probably partly because of differences in the visibility of the various actions and partly because of the presence of flies etc at the heavily utilised licks and paddocks. For the purposes of this comparison, grooming in aggressive situations was defined as that which immediately preceded, was concurrent with, or immediately followed any aggressive or dominance activity. The records from both participants were pooled, since the orientation of the grooming with reference to the opponent is probably of importance in any difference between the two; I was unable to record accurately the relative positions of the participants and therefore have no basis for a comparison between dominant and subordinate animals.



Table 12 : Self grooming, not associated with social interactions in different situations, by eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

	<u>Captivity</u>	<u>At licks</u>	<u>In the field</u>
grooming shoulders	28	6	45
grooming forelegs	30	6	4
grooming hindquarters	21	1	3
scratching backs	15	7	17
grooming side and ducking grooming	54	8	8
grooming udder or penis	5	8	6
Head shake	76	6	21
Other head movements	162	10	8
scratching face on trees	30	5	35
scratching the rest of the body on trees	17	18	36

All captivity/all licks/all field :

$$\chi^2 = 232.25, \quad P < 0.001$$

THE ORGANIZATION OF SOCIAL BEHAVIOUR WITHIN THE GROUP

There were two main factors which governed the frequency and type of interaction between individuals. These were the dominance hierarchy and the age/sex class of the individuals involved. The interaction matrix shown in Fig 30 summarises the partner preferences for social behaviour recorded during field observations. The matrix was derived using a method similar to Altman's (1968a) matrices for rhesus monkeys, but with some variations, described



Table 13 : Self grooming in aggressive encounters and in non-social situations in the captive group of eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

	<u>Non-social</u>	<u>Aggressive</u>
grooming shoulder	28	2
grooming foreleg	30	8
grooming hindleg	12	1
vulva scratching	6	1
vulva grooming	3	1
scratching back	15	5
grooming side	40	7
ducking grooming	14	7
rub forehead on trees	10	3
rub rest of head on trees	20	1
rub rest of body on trees	17	1
Head shake	76	27
Head nod	58	48
Head loop	25	7
Head low	16	10
Head toss	61	69
grooming udder	5	11

All non-social/all aggressive :

$\chi^2 = 85.43 \quad P < 0.001$



Table 14 : Self grooming in aggressive encounters and without social interactions in the field by eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

	<u>Non-social</u>	<u>Agonistic</u>
Grooming shoulder	45	8
Grooming the rest of the forequarters	29	13
Grooming the hindquarters	10	3
Scratching on trees	71	2
Head shake	21	9
Head toss	8	7

All non-social/aggressive :

$$\chi^2 = 27.53 \quad P < 0.001$$

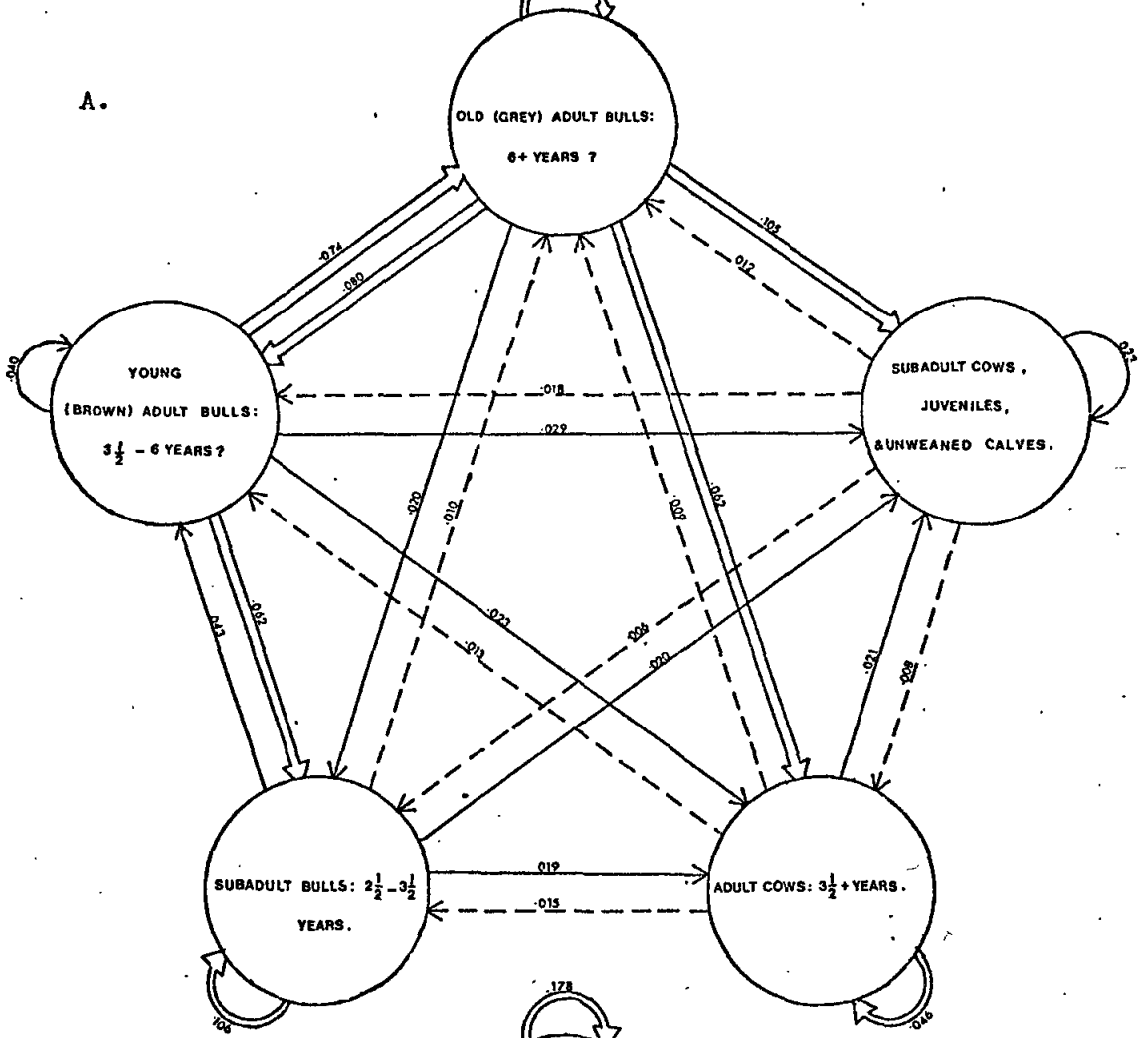
Table 15 : Head movements associated with grooming by eland at Loskop Dam Nature Reserve, June 1972 - May 1974. Non-social situations vs. non-aggressive social situations (Captive group).

	<u>Non-social</u>	<u>General social</u>
Head shake	76	18
Head nod	58	12
Head loop	25	7
Head low	16	5
Head toss	63	16

All non-social/all general social :

$$\chi^2 = 1.22 \quad P = 0.80 \quad \text{N.S.}$$

A.



B.

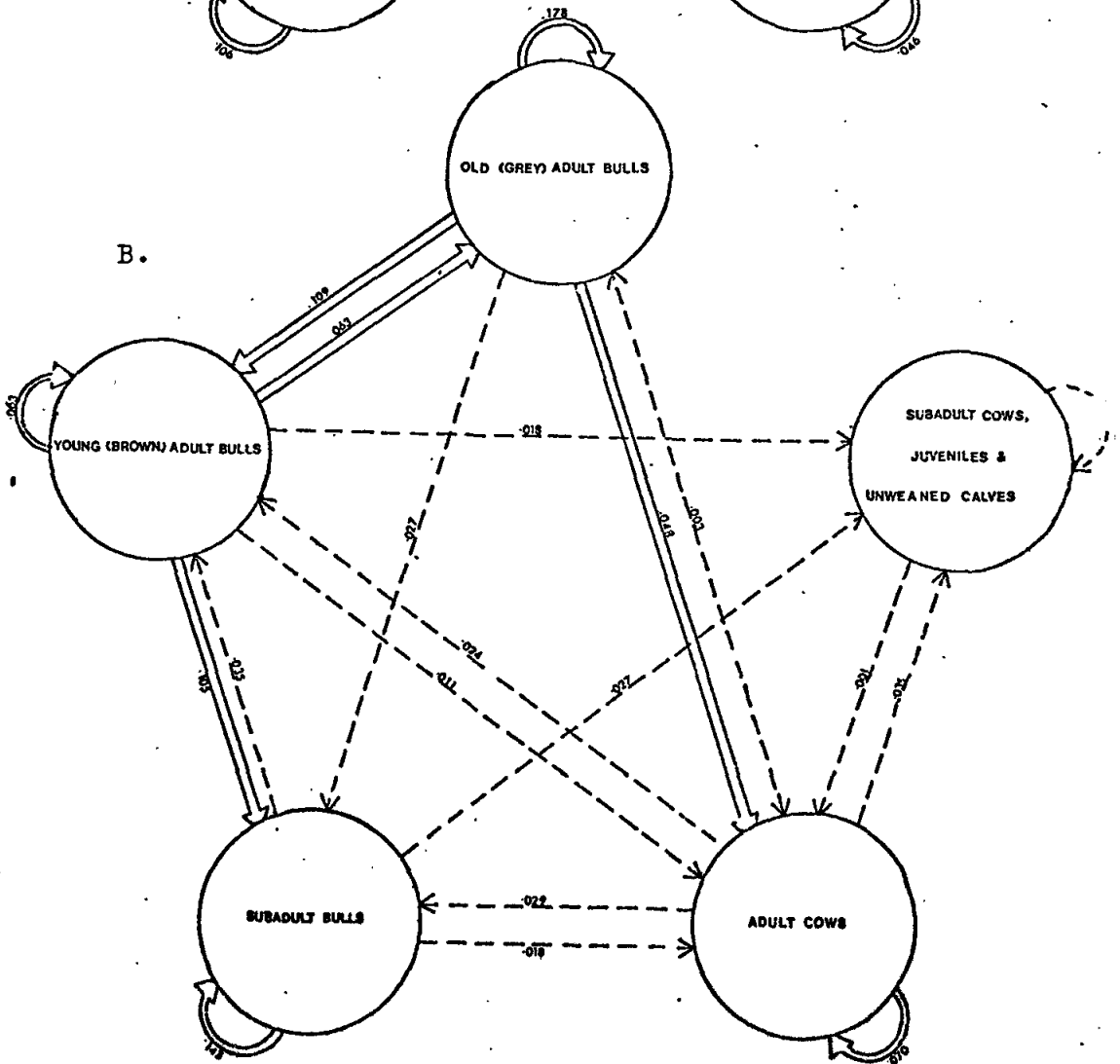


Figure 30. Social interactions within eland groups at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. All interaction types. Double lines represent interactions which occurred more frequently than expected, single lines those as expected, and broken lines those less frequent than expected. Numbers along lines represent the proportion of all interactions to be expected occurring between the classes indicated in an "ideal" population where each age class is equally represented and is equally available to all others. Predicted from the frequency of interactions observed at Loskop Dam.
- B. Aggressive and dominance interactions only. Double lines represent frequencies higher than average, broken lines those lower than average. No lines connecting particular classes indicates that no aggressive or dominance interactions were seen between those classes.

in Appendix 4. There were four distinct types of activity which were common to all age/sex classes and which contributed to the matrix. These were: aggressive or dominance interactions; social investigation (Kontrolieren: Walther 1964a); social grooming; and behaviour based on sexual motor patterns (chinning, mounting etc). The partner preferences were significantly different to a random distribution ($\chi^2 = 391.8$, 16 degrees of freedom, $P < 0.001$), the values which were significantly higher than expected being those relating to bull/bull interactions, while those lower than expected were mainly those involving the heifers, yearlings and calves.

More than two thirds of the interactions seen in the field were aggressive or were dominance based. A matrix is therefore also given for dominance and aggressive activity only, but it cannot be tested statistically as it stands because several expected frequencies were too low. At least two more age/sex classes would have to be pooled to produce suitable values, and this could not be done while retaining meaningful divisions of the population. (The reduced matrix would, however, certainly be significantly different to a random distribution).

Rowell (1966), in describing dominance in captive baboons, uses only those interactions involving the pattern "A approaches, B retreats" to define dominance relationships. An unusual form of this, which has not yet been described in the literature to my knowledge, was seen in eland. This involved interactions at licks and at other limited resources, where the dominant animal would use the lick and the subordinate would stand behind, waiting until it had finished. I called this behaviour "queueing"; it is basically similar to the situation seen in primates (cf. Goodall 1968) and other species (e.g. reindeer, Espmark 1964), where a dominant animal retains access to a resource with others waiting until he is finished with it, its peculiarity is in the positioning of the subordinate animal with respect to the dominant one (i.e. to the rear and very close: Figs 25 and 27). In deriving the dominance relationships, both the active "approach/avoidance" interactions and queueing were used.



In adult animals, the dominance relationships were found to be highly conservative and linear. I was able to determine relationships between 14 cows over a matter of three weeks in 1972 and again in 1973. The animals were then ranked according to the number of individuals each dominated. The rankings for 1972 were very significantly correlated with those for 1973, giving a Kendal correlation coefficient of 0.9101. It was not possible to compare rankings amongst bulls in the same manner, since they were never all sighted within any reasonably short period, nor were all the possible combinations of individuals seen to interact. From an examination of the results of interactions over the whole study period, however, a linear hierarchy also appears to exist in the bulls.

As with most such hierarchies, there were anomalies. Within the known cow hierarchy, these were limited to animals of the oldest age class - the 9 - 11 year old cows who had founded the herd. It was also within this age class that the changes in the hierarchy from 1972 to 1973 were observed. These circular dominance relationships were sometimes seen acted out e.g. where three cows were trying to use a lick, each dominant to one of the others, they circled the lick, each one avoiding the animal behind and driving the animal in front. Although these triangles occurred, they were very unusual. Of the 91 possible inter-individual relationships in the known cow hierarchy, in 1972 there were only three which went against the hierarchy and in 1973 there were four. So far I could tell, anomalies did not exist in the bull groups; certainly in the results of fights in any particular group of bulls seen, the relationships were linear.

The basis of dominance was very obviously a combination of age and size in the bulls. The one bull remaining from the herd founders was in very poor condition, but was still avoided by all other bulls; I never saw him fighting, however, and it may be that if he had fought he would have lost to a younger challenger, as found by Roth et al. (1972). Apart from this one bull precise ages for the others were not known and the animals were classified according to whether they had achieved the grey coat of the older bulls or whether they were still brown. All grey bulls

were/.....



were dominant to all brown bulls. Within these classes, the animals were ranked roughly according to size, but it is again not possible to compare sizes properly, since bulls were rarely seen "shoulder to shoulder". It was, however, possible to do this for a group of nine cows, all from the same age class (10 - 11 years), whose shoulder heights were compared as they stood together at licks etc over a period of two days in March 1974. Their ranks were positively correlated with their shoulder height (Kendal correlations = 0.5278, $p = 0.03$). Although significant, the correlation is not perfect and other factors play a part; the smallest cow in this sample ranked highly, probably because she was very aggressive, while a large but low ranking cow gave the impression that she could not be bothered to get involved with the others, either aggressively or socially.

In order to determine the effect of rank on the social behaviour of the individual, the records for the captive group were analysed by calculating the average number of times that each animal gave or received a particular form of social interaction in every hour of observation. This frequency was then correlated with the animal's rank. Because the composition of the group varied considerably, a measure was also taken of the average number of companions each animal had during its captivity and the frequency of the interactions was also correlated with this. The Kendal partial rank correlation coefficient was then used to determine if density had seriously affected the interaction rates. Although the density did affect the rate of interaction, the correction applied by the partial rank coefficient made very little difference to the values of any of the correlations. Since the corrected coefficient cannot be tested for significance, the uncorrected correlations are given here (see Table 10).

In addition to the correlations, a "direction consistency index" (Rowell 1966) was calculated for each interaction type and is included in Table 10.



DISCUSSION

DOMINANCE AND SEXUAL BEHAVIOUR

Estes (1974) has suggested that the eland is the only antelope which has a dominance hierarchy similar to that found in Bovini. He considers this a necessary adaptation in large, nomadic, open habitat species, since sociality is necessary as a form of predator defence as well as being a result of food utilisation strategies (considered in more detail in Jarman 1974). Sociality itself implies a low inter-individual distance and considerable exploitation of the same resources; rank hierarchies result almost necessarily. (Even solitary animals, such as cats, will show the same adaptation following enforced proximity and sharing of resources in captivity). The key point of similarity between Bovini and Taurotragus is dominance determining access to females; other gregarious antelope species have dominance hierarchies within nursery herds or batchelor herds (Estes 1974) but rely on territoriality or a harem system for reproduction.

It is not possible from my results to say for certain that a dominance hierarchy determines access to females, since matings and advanced sexual foreplay were rarely seen. However, when they were seen, the male was almost always a grey bull; in addition, old bulls were seen driving younger ones from females, although mating did not follow. In small herds, this apparently results in a harem system rather than a dominance system. According to Roth et al. (1972) a group of up to eight females was certainly controlled by one bull (probably in competition with a limited number of familiar individuals) and a later herd bull apparently controlled 23 females in competition with up to eight bulls aged four years or older. In contrast to this, Skinner (pers. comm.) reports seeing several different bulls copulating within one wild herd on the same afternoon and apparently paying very little attention to one another. This placidity has also been noted by Astley-Maberly (1937) and Shortridge (1934). The situation may be similar to that found in Newfoundland caribou (Beregrund 1974 : 403), where single males sometimes control small herds by preventing subordinates contacting females, but where the herd gets too large for one male to control, several males may share it.

The Rhodesian semi-domesticated herd may, however, be atypical in that all of the males in the herd must encounter each other fairly frequently and are in competition for their supplementary food rations (compare Lott's 1974 comments for bison), which will reinforce the hierarchy and strengthen the position of the top male. Also, the breeding season of the Rhodesian herd is spread over a much longer period than is normally found in the wild (Roth et al. 1972; Skinner 1967, Skinner and van Zyl 1969, Spinage 1973), so that the number of simultaneous oestruses will be reduced and competition for any particular female will be correspondingly increased. This would presumably result in the most dominant male increasing his proportion of successful fertilisations.

Most of the more detailed information on the dominance hierarchy was obtained from the captive group, i.e. from calves and females. Bulls were less social animals, seemed either to avoid or ignore one another when feeding, and were rarely seen together at licks, so that the relative dominance of the males was determined mainly from the results of the rutting season fights. The captive group results are therefore more or less irrelevant to the bull hierarchy.

The matrix (Fig 30) on the other hand, indicates that old bulls interact with females far more frequently than either young or subadult bulls. This seems to be an active process on the old bull's part, since cows initiate interactions relatively infrequently with any bull class, while both young and subadult bulls interactions with females are not significantly different to the "random" pattern. If bull/bull interactions are viewed strictly in terms of aggression (Fig 30B), the majority of interactions are seen to be initiated either by bulls of the same age class as the recipient, or else the class above. Young bull/bull interactions are slightly anomalous here, but at first glance it would seem that most aggression is initiated by superiors, while challenges to existing relationships (at least between classes) are comparatively rare. Aggression initiated by superiors was mainly in the form of dominance assertion while that from one class to a higher was always in the form of chal-

lenges/.....



lenges, so that there was approximately one challenge for every two assertions of authority. While the younger animals never won these fights, it would seem from this that dominance is actually very strongly contested even between mismatched animals (but note the very low level of interactions in either direction between old and subadult bulls - the mismatch is probably too great).

Although the old bulls showed the highest level of intra-class fighting, I had the impression that it was the younger grey bulls which were involved (judging by general conformation, the development of the dewlap and the degree of grey colouring). The oldest bull on the reserve was always very thin but was able to command respectful avoidance without a fight even at the height of the 1972 rut, despite the many challenges given and received in the old bull age class. He never followed a cow in the wild when another bull was present, and other bulls tended cows in his presence without him showing any interest, so it may be that he was tolerated rather than respected by the other bulls. The combination of my impression of the younger grey bulls fighting more and the apparent supremacy of the oldest bull does, however, suggest that age may be partly involved in determining dominance, perhaps through colouration. Nyala (Anderson pers. comm.) and other Tragelaphus species showing strong sexual dimorphism (Walther 1964a, 1974, Estes 1974) certainly do have elaborate dominance displays and signals (including body size) which apparently help to reduce fighting, so it would be surprising if the eland did not have at least some vestiges of such a signal.

The position of a male in the hierarchy, if it determines his access to females, can be very important to his reproductive success. Altmann (1962, In: Goss-Custard, Dunbar and Aldrich-Blake 1972) suggests that the males in a linear rank hierarchy, such as is found in many primates, will successfully fertilise several females or none at all, depending on their rank. Roth et al. (1972) report males keeping absolute control over all available females for several years, so the situation can be even more extreme than in the comparatively easy-going primate groups. This would in turn imply that the challenges to the dominant



animals would be potentially extremely strong, which is what appears to have happened. Fights in the rut were often savage, but there were many ritualised fights which seemed to consist of nothing more than light fencing with the horns and perhaps leaning forward onto the opponents forehead; the eland, therefore, may either fight to the death (Steinhardt 1921, In: Walther 1958, Roth et al. 1972) or else assess the partners' strength by sight or by a token fight. Geist (1971) records both ritualised and unritualised fighting in mountain sheep, but there the animals are unable to do any real harm to each other very quickly; with the eland, however, the horns are very potent weapons. Geist (1966) does record deaths by horning in a variety of species, and the only remarkable thing about fighting in eland appears to be their readiness to switch from one extreme, (such as is found in Skinner's report to me of males copulating almost side by side without antagonism) to another (as in Roth et al.'s 1972 records, where access to females seems limited to one bull until he dies or is removed). It seems that this readiness is probably connected directly with the number and sexual availability of females in the herd - inaccessibility of females increasing the tendency to fight savagely. See Parker (1974b) for a discussion of the probability of such escalation under various conditions.

DOMINANCE AND FEEDING

Both bulls and cows exerted dominance to obtain access to food resources. If one animal approached another as if to feed on the same tree at the same place, then the second animal interpreted this as an expression of dominance and would either avoid the first animal or drive it away, depending on their relative ranks. A similar interaction occurred at licks (Fig 23).

Breaking branches sometimes involved much time and energy, and dominant animals were sometimes seen to follow subordinates around in midwinter, waiting for them to break branches and then driving them away. Again, the displacement action was often an approach with intention to feed. This utilisation of other's work was seen where animals pushed against trees to dislodge seed pods, and the intention to feed approach was sufficient to dis-

lodge/.....

lodge inferiors.

Another example of the social importance of browsing includes an instance of literal commensalism, where one cow fed on Strychnos cuccoloides fruits by breaking them between her hind teeth; her companion listened to the noise of the fruits being crushed, walked across to her, and fed off small pieces of fruit which had dropped from her mouth. This continued for two hours.

Animals in browsing groups are therefore very aware of what others are doing and are continually prepared to initiate or to receive a dominance approach. This is, in fact, the framework within which most of the mild forms of aggression were recorded. Adult animals were intolerant of others feeding off the same plant unless it was a particularly large and wide-spread tree, but this intolerance did not appear until the age of about six months. Prior to this, calves often fed mouth to mouth for long periods, and it was not uncommon to see four or more of them feeding off one plant less than 25 cm high.

Espmark (1964, 1974) reports a similar situation in reindeer, where the dominant animals drive the others from patches cleared of snow and suggests that this sort of relationship may be important in the survival of animals living in marginal habitats, such as roe deer in Scandinavia. Eland at Loskop were not subjected to the extreme environmental stresses seen in Espmark's (1974) study (50 - 70 % of mortality in roe deer was due to starvation), but there was a noticeable drop in the condition of all animals. In the more marginal eland habitats, such as the Kalahari, dominance could quite possibly be important for individual survival in poor years. Even in the relatively stable bushveld, the exertion of dominance to obtain choice foods was a normal part of the animals behaviour (above) and became much more prominent in winter or when the available high level browse was limited by overbrowsing.

DOMINANCE AND NON-AGGRESSIVE INTERACTIONS

From the captive group records, it would seem that the reception of general non-aggressive contact is strongest in the lower ranking animals. On breaking the "non-aggressive" results down

into/.....

into smaller classes, however, it seems that the two major contributing patterns have quite distinct relationships to dominance rank. The performance of social grooming is mostly by low-ranking adult animals, while its reception is apparently unconnected with rank. The reverse holds true for chinning amongst adults. Both of these interaction types were infrequent in captivity, and there is insufficient data for a direction index.

Grooming was seen in three situations: in response to a grooming "demand" from a superior; in response to a soliciting approach from an inferior; and apparently spontaneously when one animal was standing close to another (e.g. when queueing at licks). Since there is no association of rank with reception of grooming it seems that low ranking animals are more responsive than higher rankers to all of these cues. This may have been because the animals under study consisted of a group of the bottle-reared herd founders (who were all high-ranking) and some of their first and second calves, who experienced a more normal upbringing. It was, however, my impression that the negative correlation of performing social grooming with rank extended to the animals in the wild population as well.

The reverse argument may apply to chinning in adults. Since there is no correlation of the performance of chinning with rank, low rankers must elicit chinning more frequently than other members of the adult population, regardless of the rank of the chinning animal. This would seem to be partly because chinning asks the question "will you move?" and can be either a mild assertion of dominance or else a "request" from a subordinate. Highly dominant animals sometimes react very aggressively to being chinned, while low rankers are generally more docile, so it is probable that the "question" is only put to dominant animals who are not likely to retaliate strongly i.e. to low rankers who are nevertheless dominant to the chinner. Sniffing seems unconnected with rank, which is probably to be expected, since it is presumably necessary for an animal to be equally aware of both its superiors and its inferiors.



AGE/SEX CLASS AND SOCIAL BEHAVIOUR

Apart from the dominance interactions classes mentioned earlier, the most striking result in the matrix diagram is the interaction of old bulls with subadult females, yearlings and calves. This is partly an artefact, since the known calves only represented a small proportion of the total, and their interactions may not have been representative - the interest shown by the bulls was in the form of sexual investigation and driving and was, perhaps coincidentally, seen only on the few occasions that the known subadult females and calves were with known bulls. Bull/subadult female interest was rarely seen except on these occasions.

Also surprising is the fact that calf/adult female and calf/calf interactions were not higher, since calves were apparently much more socially active than adults when in captivity. This is probably the result of two factors. Firstly, calves, although sporadically very active, spend much time lying either sleeping or resting. Also, their peak of activity is usually after the dusk move, which was a period under-represented in my samples because of the difficulty of keeping up with the animals and making observations on them as they moved a kilometre or more in semi darkness.



CHAPTER 6

COMMUNICATION

In the ethological literature, communication may be defined so as to include all possible interactions between two animals, or it may cover only a very limited range of exchanges between individuals (McKay 1972). However, even definitions as different as Tavolga's (1970) and McKay's (1972) recognise a system containing three elements: an emitter (an individual producing an energy change in the environment); an energy output; a recipient (an individual capable of detecting the energy change). In field behavioural studies, "communication" may take place without these elements being obvious. A working, field definition of communication must therefore allow for a series of subjective judgements by the observer. This section therefore includes aspects of eland behaviour which I know or suspect to be important in altering or reinforcing the behaviour of other eland. (See Sebeok 1968, Sebeok and Ramsey 1969, and Hinde 1972, for other definitions and discussions). The above is a definition for convenience only. As Lennenberg (1969) remarks: "Communication can only be defined in somewhat arbitrary terms and no matter how it is defined, it never represents a unified or even clearly related behavioural unity".

VISUAL COMMUNICATION

The main forms of visual communication seen in the Loskop eland are listed in Table 16. The actions involved are described in detail in the relevant chapters. In addition to these, there are several other probable visual signalling mechanisms in the eland. The reasons for considering them as signals are given below.

In addition to recognisable signals, there is also the effect of social facilitation. The point at which social facilitation shades over into signalling is uncertain. Performance of almost



all general behaviour patterns (Chapter 2) may cause another nearby animal to follow suit, which would be social communication but not signalling. Table 16 and the descriptions given below show that some of these activities are also modified to serve as signals (i.e. ritualised - Huxley 1923, In: Tembrock 1968).

Table 16 : Visual signalling in eland at Loskop Dam Nature Reserve
June 1972 - May 1974.

- Key:
- (1) Supported by quantified data.
 - (2) Supported by general field observations.
 - (3) Supported by other authors on eland.
 - (4) By analogy with other species.
 - (5) Described by Walther 1958, 1974, but not observed in this study.
 - (6) Described in "general behaviour" section.
 - (7) Described in "social behaviour" section.
 - (8) Described in "maternal and ontogeny" section.

"Broadcast" indicates that the action is apparently performed without reference to a particular individual.

"Directed" indicates that the action is directed towards particular animals.

Where alternative interpretations of similar actions are suggested in the literature, they are given in decreasing order of probability as they appear to apply to eland.

Actions without apparent social value or which appear to operate via facilitation are included where they appear to be related to social signals.

<u>Posture or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
Normal walk (2, 4, 6, 7)	Directly towards another animal	Dominant animal, all classes	Subordinate (directed)	Expression of dominance	Avoidance
		Subordinate bull	Dominant bull (di- rected)	Challenge	Await fight
		Calf	Adult female (directed)	Intention to suckle	Rejection with threats Sniff nose and groom but not allow to suckle. Sniff nose and allow to suckle.
Slow, slightly stilted walk, erect posture. ("Driving") (2, 3, 4, 7)	Behind and to- wards another animal.	Dominant animal. All classes.	Subordinates. Usually same class as sen- der. (directed)	Expression of dominance. Desire for re- cipient(s) to move in a par- ticular direc- tion.	Recipient moves away from sender usually in the same di- rection as the sender is moving.
		Subordinate bull.	Dominant bull (directed)	Challenge (rare)	Recipient turns to- wards and awaits the approach of the sender.

Table 16 continues

<u>Posture or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
		Adult and sub-adult bulls.	Females older than one year (directed)	Sexual interest.	Recipient urinates and/or moves away.
Flight jumps (2, 4, 6)	As animal begins flight within an otherwise undisturbed group.	Usually young animals.	All classes? (broadcast)	Flight intention? Excitement?	Others follow?
	When the herd is moving quickly at a trot when fleeing or when two groups are joining.	All classes, usually younger animals.	All classes (broadcast)	Excitement? (c.f. Walther 1969) showing position of herd members? Epidiatic display, (Wynne-Edwards 1962).	Others often follow suit.
Intensive grazing (2, 4, 6)	Within normal group movements and feeding bouts One animal moves towards another grazing.	Dominants of all classes.	Subordinate of same class (directed)	Intention to feed at the same spot. Mild dominance.	Subordinate moves away, usually still grazing.
	Between fighting bouts, one animal moves towards another.	Winner of previous bout. All classes.	Loser of bout. Same class as sender (directed)	Intention to feed on same spot. Testing dominance.	Recipient moves away. Recipient treats as a challenge and presents horns.
	As an interruption to a bout.	Both combatants.	Both combatants. (directed)	Neutral activity? (Estes 1969)	Resume fighting?

Table 16 continued

<u>Posture or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
Complete or incomplete grooming movements of the head. (1, 2, 4, 6, 7)	As part of normal grooming bouts.	All classes.	All classes (broadcast)	Cutaneous irritation, bites etc.	None apparent, except for possibly following suit.
	Following disturbance, from non-social source.	All classes.	All classes (broadcast)	Cutaneous irritation, bites etc, possibly stimulated by ruffling of coat in flight. Transition activity by reason of disinhibition? (van Iersen and Bol 1958).	Some facilitation to follow suit.
	Accompanying dominance and aggressive interactions.	All classes.	All classes usually the same as the sender (directed)	Cutaneous irritation. Disinhibited transition activity. Aggression? Frustration?	Facilitation. Avoidance of dominant animal showing sudden grooming movements.
Scanning alertly (2, 3, 4, 6)	Apparently spontaneously in crowding.	Dominant animals of all classes.	All nearby subordinates (broadcast)	Skin irritation. Aggression?	Avoidance by subordinate.
	In "queues".	Subordinate animal behind dominant.	Dominant, usually of same class as sender (directed)	Frustration? Skin irritation?	Dominant animal may show unease and turn on subordinate.
Scanning alertly (2, 3, 4, 6)	Non-localised disturbance outside group.	All classes.	All classes (broadcast)	Possibility of danger?	Recipient becomes more alert.
	Sudden disturbance usually fighting or violent aggression within group.	Timid or low ranking animals especially calves.	All classes (broadcast)	Social unease?	Other animals nearby may also become alert.

Table 16 continued

<u>Posture or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
Concentrated attention (2, 3, 4, 6)	Located disturbance outside the group.	All classes.	All classes (broadcast)	Possibility of danger. Strange eland approaching.	Recipient follows direction of attention.
	On sender joining a group. From 20 - 100 m.	All classes.	All classes within the group (directed)	Social interest in recipients and intention to join the group.	Recipients return attention and may show aggression (bulls) or investigatory approach (calves and yearlings).
	Within the group as a preliminary to most social exchanges (c.f. Marler 1968).	All classes.	All classes (directed)	Social interest in the recipient. Intention to interact.	Recipient returns attention precipitating the exchange. Recipient looks away, usually discontinuing or preventing the exchange.
	Prior to dominance conflicts, directed away from the recipient.	Mainly adult bulls. Occasionally sub-adults and females.	Usually the same class as the sender (directed)	Avoidance of aggressive eye contact. Challenge with some escape tendencies (Estes 1969). Emphasised ignoring of opponent (Geist 1971). "Lurking watch and/or ritualised swing out movement" Walther 1965 quoted in Walther 1974.	Recipient follows direction of interest or keeps eyes fixed on the sender.
	During courtship after "testing" and towards one side.	Mainly adult bulls.	Cow? (directed)	Neck display? Displacement activity by disinhibition or transition? (Lind 1959, Ierson & van Bol 1958).	None apparent.

Table 16 continued

<u>Posture or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
Erect posture, ears folded back, looking to one side of recipient (2, 7)	Following the approach of one animal to within five metres.	All classes. Usually dominant to recipient.	All classes. Usually the same as the sender (directed)	Grooming invitation or demand.	Recipient approaches hesitantly and grooms sender. Recipient turns aside hurriedly after sniffing towards sender.
Nose, head, neck stretched forward horizontally (2, 4, 6, 7, 8)	Investigating a strange object.	All classes.	All classes (broadcast)	Interest in the object.	Nearby animals may also show interest.
	Prior to suckling attempts apparently to identify female.	Calves.	Adult females (directed)	Attempting to identify female wishing to suckle.	No change in posture, implying rejection. Turns and sniffs towards calf.
	Initiating non-aggressive contact or play fights.	All classes.	All classes Usually lower ranking than recipient.	Non-aggressive interest. Negation of dominance or else active submission (several authors). Latest review in Shank 1972). Dominance intention to neck fight (Walther 1974).	Await approach in "normal" posture (6) Reject approach with threats (7).
Head and neck lowered towards ground, ears variable in all situations, usually directed towards ground (1, 2, 6, 7)	During casual grazing.	All classes.	All classes (broadcast)	Animal is feeding or interested in the ground.	None apparent.
	As one animal passes close to another.	Subordinates in adults and sub-adult classes.	Dominant animals of the same class as the sender (directed)	Animal interested in the ground rather than the dominant individual? Defensive threat?	None apparent.
	As one animal breaks off a vigorous fight and retreats. (ears usually back).	Usually subordinate bulls.	Dominant bulls.	Defensive threat. Surrender.	Dominant animal usually advances on the subordinate with horns tilted slightly forward until the latter turns w y.

Table 16 continued

<u>Position or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
	A dominant animal approaches another when the latter is using a lick or other food source at ground level.	Dominant animals of all classes.	Subordinates, usually same classes as sender.	Intention to feed at the same spot. Dominance.	Subordinate usually avoids dominant.
Adult female urination posture (2, 4, 6, 7)	Normal urination or urination following chinning, tending etc.	Female.	All classes (broadcast)		Approach. Sniff urine drink it. Flehmen. Rub forehead in it.
Mounting intention posture (2, 3, 4, 7)	Adult courtship.	Adult bull.	Adult female (directed)	Bull wishes to mount	Move away. Stand and receive mount.
	Close proximity in calves.	Calf.	Calf (directed)	Intention to mount - will recipient move?	Move away, from intention posture or from the mount itself.
	One calf preventing another from feeding or access to some other resource.	Calf.	Calf (directed)	Intention to mount will recipient move away from the resource?	Move away from the intention posture or from the mount itself.
	Sender wishes to approach some object with company?	Calf.	Calf (directed)	Intention to mount will recipient move towards the object?	Move away from the intention movement, turning to one side or else walking straight towards object with sender following.
Chinning (1, 2, 3, 4, 7, 8) with or without contact.	As for mounting intention - all situations.	All classes especially calves.	Usually same class as sender (directed)	As for all mounting intention situations.	As for all mounting intention situations.

Table 16 continued

<u>Position or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
	Mild disturbance.	Same.	Same.	Will recipient flee?	Same.
"Horn threats" (1, 2, 4, 7)	As one animal approaches another. Also following fights.	All classes, dominant animals.	Usually same class as sender.	Intention to attack usually to charge. Dominance. (directed)	Recipient avoids sender.
Head nodding (1, 2, 4, 7)	Following mild disturbance or frustration.	Calf.	All classes (directed)	Threat?	None observed.
Horn presentation (low level) (2, 3, 4, 7, 8)	As one animal approaches another head on.	Calf.	Calf (usually) (directed)	Play fight invitation.	None observed. Move away. Place horns into "horn lock" position and fight.
		Adult bull. May also be sub-adult or female.	Usually the same class as sender and dominant (directed)	Challenge.	Lock horns.
Neck stretch (1, 2, 4, 8)	Calves isolated from another or having been rejected from suckling frustration. Often between bouts of contact calling.	Calf.	Dams? (broadcast)	Frustration, expressed as the otherwise obsolete defensive threat "Senkrechtiges Naseheben" (Walther 1964a)? Highly movement as a milk demand display?	Very rarely female may approach and investigate the calf.

Table 16 continued

<u>Position or action</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
Head loop. Goose-step. (together or separately) (1, 2, 8)	Apparently spontaneously and following rejection in calves.	Calf.	? (broadcast)	Frustration expressed by phylogenetically relict aggressive activities?	None observed.
Head toss.	During intensive grooming bouts.	All classes.	All classes (broadcast)	Skin irritation?	None.
	During "displacement" grooming.	All classes.	All classes animal causing disturbance? (directed)	Skin irritation?	None.
				Frustration?	None. Avoidance. Aggression.
	As an isolated activity following disturbance.	All classes.	All classes? (broadcast)	Frustration? Conflict?	None apparent.
	During social (usually aggressive) interactions.	All classes (subordinate animal).	All classes (usually the same as the sender, dominant) (directed)	Indicates frustration, combined with negation of weapons i.e. minimising threat.	Recipient may also head toss.
All classes (dominant animal).				All classes (usually the same as the sender. Subordinate. (directed)	Specifies that the aggressive approach is a mild one?

EARS AS SIGNALLING ORGANS

Ear position often serves a communicatory function in mammals (e.g. Leyhausen 1956 and Trumler 1959 - In: Ewer 1968, Andrew 1963, 1972). In the eland, it is important in several signals but there is no single causation underlying all such situations.

In general, if the ears are pricked upright and point to the front, the animal has its attention fixed on something. ("Concentrated attention" Andrew 1972). In a social situation, this usually means a readiness to interact with the animal being watched, either aggressively (i.e. as a threat or challenge) or more peacefully (as in a calf approaching its dam to suckle).

The ears are pricked upright and to the rear under two main sets of circumstances. Firstly, when an animal is very interested in something to the rear: e.g. the animal avoids threats from another. Secondly, it is seen in threats. In the latter case, it was often seen at the end of a threatening approach - a dominant animal would approach a subordinate with ears pricked forward, then about two to five metres from the subordinate would flick its ears back briefly. This flick often coincided with the movement of the subordinate and it was impossible to tell which came first. In intra- and interspecific threat, this position preceded the charge. The position is not simply ear protection, since subordinate animals often assumed the more functional-looking ears-folded-back-and-down position, while during the actual charge or flight, all animals held their ears out horizontally, to the front (see Figs 23 & 24). The ears-pricked-to-the-rear position in aggression seems to combine both the ears-back protective posture and the high tonus of a dominant animal.

As indicated, the folded-back-and-down position is seen in submissive animals (Figs 23, 24, 27, 28). It is often shown by calves amongst themselves or when interacting with elders (Fig 27) and probably indicates readiness to defend but minimises any possible offensive connotations. It is also characteristic of resting or ruminating animals (i.e. low postural tonus).

The ears-held-out (facing forward, back or down) position is characteristic of fighting, although its exact function is not

clear. If the ears were held folded close to the neck they might become pinched between an opponent's horn and the neck itself in adult fighting, but this seems a remote possibility. A similar position is seen in grazing.

I had the impression that the more horizontal the ear positions assumed, the more submissive or friendly the animal involved was. This may explain the "grooming demand" posture where the dominant animal stands erect but folds its ears back in a typical submissive position. Such a demand position must necessarily be a compromise between assertion of rank and an indication that no harm is intended.

It is not possible to detail the basis of the ear positions found in all postures, since each seems to have a slightly different functional basis. The main principles have, however, been indicated. As Hinde (1972 : 205) remarks, such analysis in detail would be interesting but cumbersome when applied to the complete display behaviour of a species.

GROOMING AS A VISUAL SIGNAL

The pattern of grooming in eland varies according to the social situation (Chapter 5). Eland seem to employ self and social grooming as aggressive or appeasement signals, or at least to interpret them so, e.g. Fig 23 shows two subordinate cows flinching away from a sudden ducking-grooming movement. Dominant animals would sometimes become very aggressive when nearby subordinates repeatedly made violent head movements during grooming. Subordinate cows in queues often alternated anal licking of the dominant with chinning, and the dominants would sometimes violently attack (in Fig 27, a subordinate shows clear signs of expecting this).

The grooming actions shown in cases of aggression or frustration are usually those which involve not only simple movements but also those which are very rapid and sudden: this rapidity seems to be the basis of their effect on the recipients. In most animals (e.g. primates, Sparks 1967) placatory actions performed close to another animal in social contexts are usually slow, predictable, involve smooth transitions from one phase to another

and are therefore "reassuring". The use of grooming movements has the opposite effect in many cases, which suggests that there is in eland some signalling function involved.

The grooming movements "head toss" and "head shake" were often seen without any other grooming actions during mild intra group disturbances, especially approach/avoidance situations. They were not particularly associated with dominance or subordination (head tossing in 80 encounters had a direction index of +0.60, $\chi^2 = 3.2$, N.S.) and were often performed by both participants simultaneously. Head tossing, the more ritualized of the two, was interpreted by subordinates as a mild threat, but was ignored by dominants. Since the horns are concealed briefly from the recipient, the action seems by antithesis (Darwin 1873) to be a denial of strong aggressive intent, its meaning depending partly on context (Table 16).

BODY CONFORMATION AS A VISUAL SIGNAL

The most obvious visual characteristics in adult eland i.e. the extreme sexual dimorphism and the prolonged growth phase of young bulls is relatively unexploited in terms of displays. In the present study, I rarely saw anything which could be described as a distinct broadside display of the type seen in e.g. nilgai or kudu (Walther 1958a, 1964a, 1966, 1974). Although bulls were sometimes seen to graze parallel to each other for some distance, there was no apparent result, nor was there any sign of possible ritualisation (except perhaps for the relative positions of the bulls). The only distinct broadside display was seen as part of a grazing-across-the-bows action, which prevented the forward movement of the recipient, but this was also uncommon. Massive dewlaps, pronounced dorsal ridges and a general emphasis on the forequarters are often seen in animals which apparently rely upon displays of strength for dominance e.g. gaur (Schaller 1967), bison (McHugh 1958, Lott 1974), and nilgai (Walther 1958). While eland possess these characteristics, indicating that size is an important factor in dominance, they do not usually emphasise them by displays in the wild. Schaller (1967) notes that the gaur, which apparently



has a very similar society to the eland, also seems to rely on a simple visual assessment of size, usually without displays. The lack of behavioural emphasis of size is probably due to the eland's open habitat preference: tragelaphines which live in herds in denser habitats appear to have a much more elaborate repertoire, and to use it more (e.g. Walther 1964a; see also appendix 5).

T. derbianus, inhabiting denser woodland and probably moving in smaller herds, has a much more impressive appearance and has the dewlap emphasised by normal tragelaphine throat markings. Not only is the broadside ritual reduced in T. oryx, but also the ritualised structures involved in the display are (relatively) de-emphasised, since the Cape common eland's markings are considerably reduced compared to other tragelaphines. Moynihan (1970) remarks that displays may be lost through excessive use. If an animal were to move from a dense habitat to a less dense one, its normal frequency of displays will probably increase with the increase in the probability of encounter. If in addition the animal were forced for ecological reasons to form dense herds (Estes 1974, Jarman 1974), then the habit of displaying (say) every time one bull meets another would not only be exhausting, it would also tend to debase the value of the display even further. Walther (1974) records displays that I have not observed in the field; these are probably the result of bulls being forced into proximity with other animals for long periods and being forced to increase the frequency of their low value displays in order to get the same effect as a "wild" display.

This phenomenon of an increase in individual performance of a display combined with a decrease in its importance in evolutionary terms is more closely examined in Moynihan (1970).

The value of size in courtship is uncertain, since I have no information on successful courtships (i.e. culminating in fertilisation) in the wild. From the mating activities that were observed, the cow appears to have little choice: access to her is decided amongst the males by dominance, although a cow could probably outrun a bull if she really objected to him. It seems therefore that size is probably mainly important to the male's reproductive success in that he must be large enough to dominate all other bulls competing with him.

Even as it is, the body size and colouring of a dominant bull is impressive and represents a considerable investment of energy and (probably) life expectancy in the ritualisation of the body into a visual signal (c.f. Beregrund 1974). Bulls probably rely on a simple visual assesment of each other's sizes for daily interactions and learn their own value relative to the size of others by the results of rutting season fights (c.f. Geist 1971).

OTHER PHYSICAL CHARACTERISTICS

In the routine expressions of dominance, animals almost never attempted to displace individuals of higher rank. On the few occasions this happened, the dominant animal made as if to avoid the approach, then seemed to realise what was happening and savagly turned on the usurper. Individual recognition from a distance would therefore seem to be essential to the smooth running of the dominance hierarchy.

Several others (Astley-Maberly 1937, Posselt 1963, Abbott 1968a, b) have remarked on the variability of horn shape and body conformation in eland cows. This may be important in identifying animals to one another - visual identification certainly occurs even between quite young calves.

While it is not possible to say what characteristics contribute to recognition, born shape may be a key factor. I could identify most of the female animals at Loskop (without field glasses) over fifty metres, purely on the basis of horn-shape - bulls' horns were more regular in shape, presumably because of selection for efficient intrasexual binding organs and weapons. It is unlikely that the cow's horns are variable because they are being lost through evolution since they are rarely so deformed as to reduce their effectiveness as offensive weapons rather than "binding" organs (Geist 1966); also, they are used (sometimes) in rank determination conflicts. They are certainly not reduced to the same extent as in female Thomsons gazelles (Estes 1967). It is however, unlikely that this variability has specifically evolved as a source of individual recognition.

Several physical characteristics of the mother are important

in/.....

in the orientation of the neonate's suckling attempts, but the ritualisation (in the sense used by Tembrock 1968) here is in the calf's perceptual and motor organisation rather than the dam's body. The factors involved are considered in more detail in chapter 7.

AUDITORY COMMUNICATION

The eland does not seem to rely greatly on auditory communication. Early writers (e.g. Sclater, Drummond, Lydekker) rarely report any vocalizations. Astley-Maberly (1937) records hearing "belch-like grunts" in a grazing group, a description echoed by Abbott's (1968a) "belching grunts". Stevenson-Hamilton (1947) records "low rolling grunts" from both sexes as being the only vocalisation apart from calf bleating. Tembrock (1963) gives two sets of frequency ranges for eland calls ("long call" and "call") but does not describe the calls themselves.

Steinhardt (1921, In: Walther 1958) records that one bull, after goring another, went to the remainder of the herd "dumpf grunzend" ("dull grunting"). Posselt (1963) records a "deep throated" alarm bark, a "reedy lowing note" as a mother-infant contact call, and remarks on the silent nature of the animal.

Field observations and those on captive animals supported the contention that there are only a limited number of calls, and that these are rarely used. Three apparently distinct continua of sounds were noted: contact calls; alarm barks; aggressive vocalisations: see Table 17. Only the first of these was recorded on tape, since the other calls were heard on only a very few occasions and never when recording was possible.

CONTACT CALLS

These calls occur between dam and calf; such a series is illustrated in Figs 31 & 32. The majority of contact calls could be phonetically rendered by the traditional "moo" used to describe cattle lowing. This rendition was conveniently short and was retained, while calf calls were given the general name of "bleats". Comparison of these calls with the "menh" of Bos (Kiley 1972),

Table 17 : Vocal Communication Between Eland at Loskop Dam Nature Reserve. June 1972 - May 1974.

<u>Signal</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
"Whimper"	In a neonate calf, spontaneously at first, then connected with rising and suckling attempts.	Calf.	Dam?	That the calf lacks certain stimuli e.g. physical contact?	Dam eventually approaches and licks the calf or stands nearby to facilitate suckling. Dam may also give grunts or similar low volume calls.
	As the neonate calf is separated from other eland, especially its dam.	Calf.	All classes especially the dam.	Same, except that the stimuli are probably those associated with proximity rather than contact.	Often none apparent. A lactating cow, particularly the dam, may approach or call.
	As a calf approaches the dam after a bout of contact calling.	Calf.	Dam.	That it is the calf which has been calling which is approaching? Anticipation? Decreasingly unpleasant stimulus contrast?	Dam sniffs at and usually stands to allow suckling.
	As a calf approaches strange calves.	Calf.	Calves.	That the calf wishes to approach and make social and/or physical contact?	The strange calves may whimper. They will usually investigate the approaching calf.

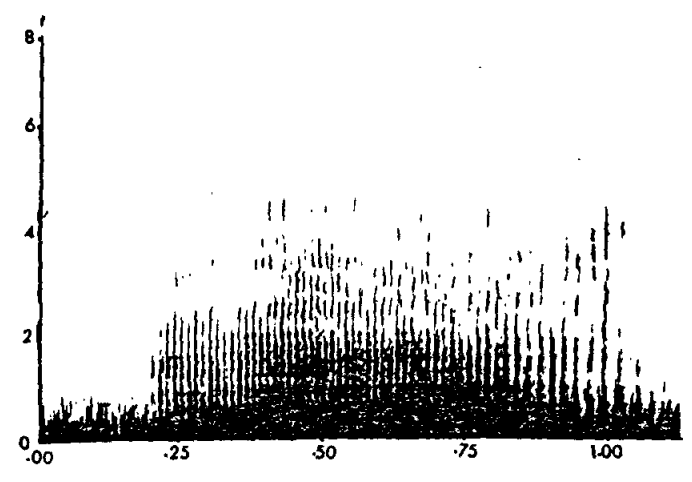
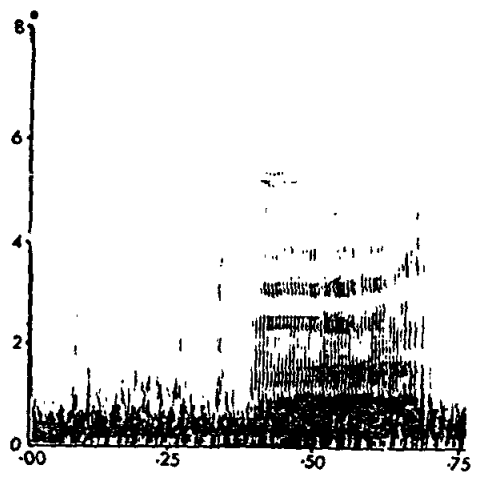
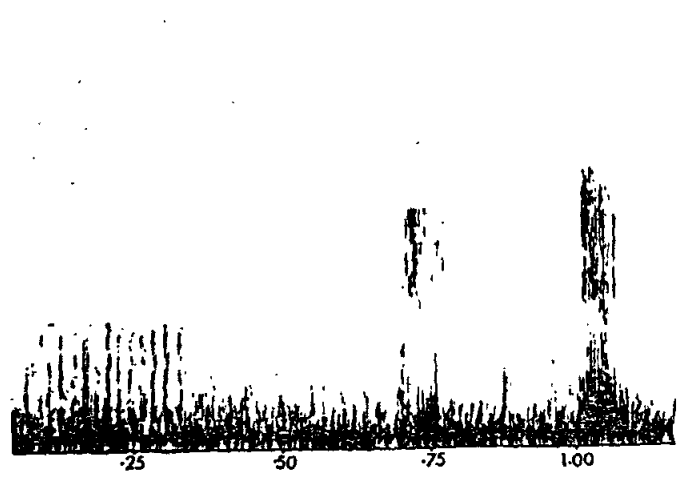
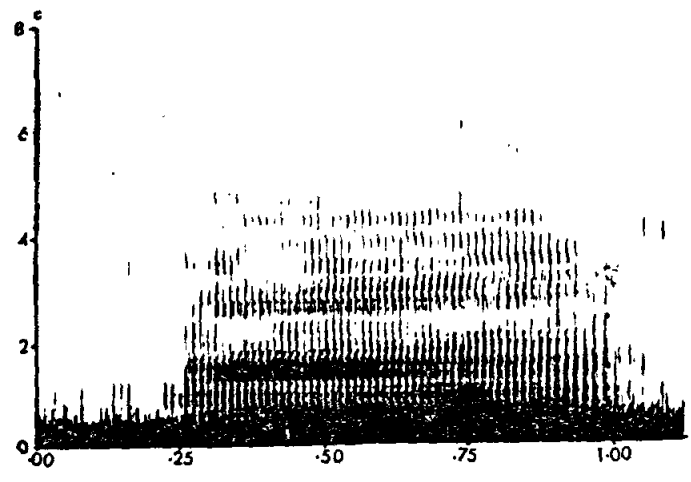
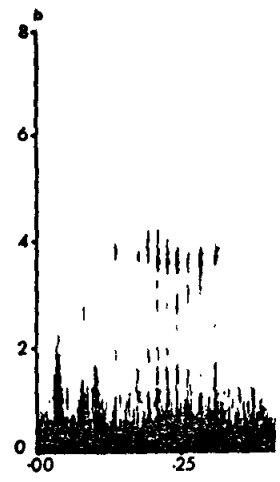
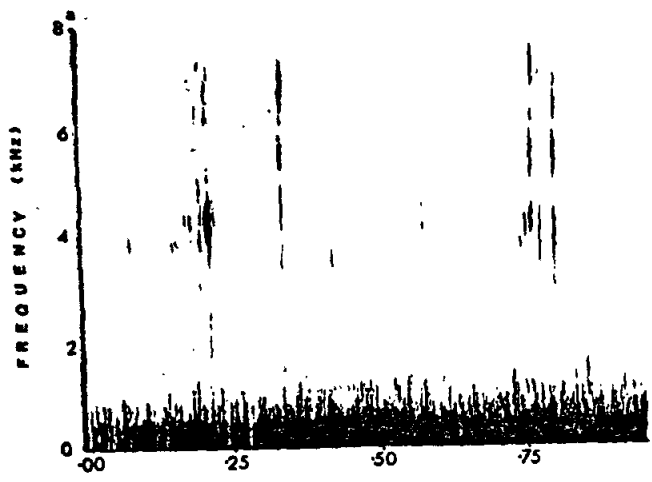
<u>Signal</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
"Moan" - "wail"	Spontaneously after a long separation from the dam. The louder, open mouthed sections of the spectrum are usually preceded by the more muted calls.	Calf.	Dam.	Calf wishes contact with the dam; in particular, to suckle.	Dam calls, approaches. Duet follows. Suckling eventually results.
"Click" - "moo"	As the dam licks the neonate calf (and almost continually immediately postpartum).	Dam.	Calf.	Assuring the calf of the dam's presence and position? Giving the calf an auditory "imprint" of the dam?	The calf may orient itself towards the call, or stop its movements, depending on the situation (see chapter 7).
	As the neonate calf begins to move with some degree of coordination away from the dam.	Dam.	Calf.	Locating the dam for the calf?	The calf may stop its movements away and orient itself towards the dam if she continues calling. It may also call.
	As the cow returns to the lying out place or the creche after some hours.	Dam.	Calf.	Alerting the calf and giving the cow's location.	The calf calls and the two converge. Suckling follows.
	As one adult joins another (rare).	All classes, but usually a bull in rut.	All classes, but usually a cow in rut.	Alerting the recipient? Giving the caller's location? Conveying a desire for a closer approach? Reassuring the recipient?	The recipient looks towards the sender, but does not respond.

<u>Signal</u>	<u>Situation</u>	<u>Sender</u>	<u>Recipient</u>	<u>Message</u>	<u>Response</u>
	In captive animals, just before feeding time (rare).	Only cows observed in this situation.	The keeper?	Anticipation? Desire for a closer approach (to be fed)?	
Bark	On an animal detecting something outside the group usually the observer.	All classes over 18 months usually adult cows.	The rest of the group.	Warning? Alerting?	If the group is wary, flight follows immediately, otherwise looking in the same direction as the caller, or ignoring it.
			The animal outside the group?	Informing it that it has been seen? Attempting to disturb it or cause it to move and identify itself?	
"Belching grunts"	During bouts of interactions at licks, food troughs etc.	Dominant adults?	Subordinates?	Warning?	To move away?
	During normal movements within close groups?	Dominants?	Subordinates?	Warning?	To move away?
Bellow	As one animal charges another, usually after a sudden move by a subordinate in defiance of normal dominance relations.	Dominant animal. Adult.	Subordinate.	Extreme aggression?	Flight.

Figure 31. Adult female contact calling to calves at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. Repeated "clicks".
- B. A "choked" moo.
- C. A full moo, preceded by several clicks.
- D. A "choked" moo, followed by two "grunts".
- E. A full moo preceded by two clicks, a choked moo, and a grunt.
- F. A full moo.

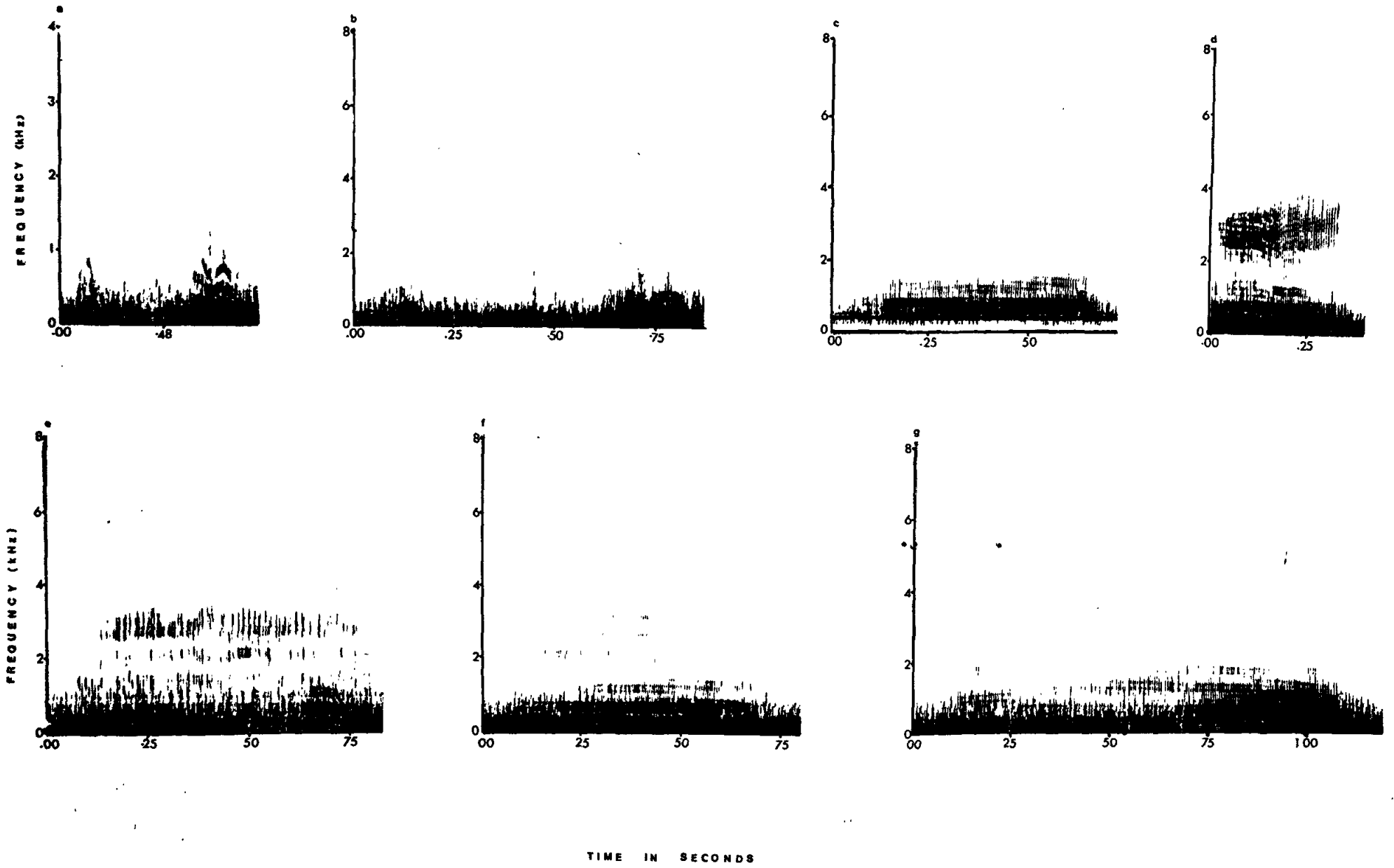
A, B, C and F are from one cow, while D and E are from another.



TIME IN SECONDS

Figure 32. Calf contact calling, spontaneously and in response to cow's calls, at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. Two "whimpers" as a calf approaches its dam to suckle.
- B. The same calls on the same time base and bandwidth as the following recordings.
- C. A "wail".
- D. A "bleat" from the same calf.
- E. A "moan".
- F. and G. Calls from two other calves showing parts of the moan/wail spectrum.



shows that the calls is in fact quite similar to the eland "moo" in structure. Although adult female contact calls were apparently a continuum (Fig 31) there were distinct elements which could be picked out. These were: a "click", a "grunt", a choked sounding "mm" syllable and a voiced portion corresponding to the "enh" part of the Bos calls shown in Kiley (1969 : 190). The sounds were usually heard when cows were waiting outside the paddocks to feed their calves. The normal sequence was for a cow to detach herself from the group, walk to the paddock fence, occasionally giving a "click" or a "grunt", then stand looking in at the calves and give a call which contained several or all of the elements. I had the impression that the earlier parts of the call were emphasised early on during the bout, while the end elements (which were much louder) did not appear until the cow had made several calls i.e. presumably when she was more highly motivated. The "low motivation", part of the calls sometimes disappeared completely at high level.

The corresponding calf calls were more variable, possibly to prevent habituation in the mother and to keep her attention (Scott 1968), and it was not possible to isolate particular component elements. There were, however, several forms which occurred more frequently than others, again representing various portions of a continuum (Figs 31, 32). These calls also seemed to show a tendency to be longer and louder with increased motivation. Often one would hear a duet between dam and calf, starting with a click from the dam and a low moan from the calf, then proceeding to the higher intensity calls, which they might give for several minutes before one partner failed to respond.

Calf calls were often very quiet, especially the "whimper", and it is possible that this particular call was given in many situations but not heard. In fact, this call was only heard when the calf was getting near to its dam prior to suckling (two or three metres apart) or else sometimes when it was approaching other calves (nose to nose).

Since it was difficult to hear calf calls under any circumstances, field observations of calf calling are limited. The

calls appeared to be elicited mainly in situations similar to those observed in captivity i.e. during approach to the dam prior to suckling. The calls, usually wails, were also heard several times when the calf group was moving in the occasional "stampede". Another instance where calling (again a wail) was elicited was when one six month old calf was being held in order to give it medication: while struggling it gave a bawling call which was only observed that one time, then as it stopped struggling it gave a very loud wail. The latter two instances suggest that the whimper-wail sequence may serve as a distress call, but it seemed to serve normally to locate the calf for the mother prior to suckling.

The adult contact call was observed in the mother-infant context and also in several other situations. The most frequent observation was of bulls giving the click-choked mm section of the call, when approaching females. This happened several times when free-ranging bulls approached the paddock and looked in at the cows. The call was also heard more rarely from cows joining a group: one occasion I was with a group that I had seen frequently over the last few weeks when a cow who had not been with them in that time appeared. She stood some distance from them and was apparently unaware of their exact position; for she looked around, called, walked a short distance, called again, and eventually made her way to the group; there was no apparent response to her calls or to her joining the group. The call was also heard in the paddocks just before feeding time from cows, sometimes two or three months prepartum.

Kiley (1972) records a similar range of situations evoking the "mm" call in Bos species, and remarks that in most artiodactyl species calls are not situation specific but depend on the "stimulus interest" of the situation. Increase in interest (or frustration) is marked by an increase in the larynx opening and call length, producing longer louder calls with higher frequencies. This description would certainly seem to apply to the range of eland contact calls, from the very short, stifled, low motivation sounds to the loud "voiced" full calls of high motivation levels.

ALARM BARKS

These calls were gruff, deep, penetrating sounds. Walther (1964) represents the very similar greater kudu female call as "bauw" and compares it with the "schrecken" calls of deer. The eland's calls were much rarer than in kudu. The call apparently had only one form, although it was heard on so few occasions that I cannot generalise about this. Barking was heard from adult females and subadults of both sexes. The head is thrown up during the bark, in the same way as in dogs: the posture is otherwise concentrated attention.

On all but one occasion, it was the sight of myself which stimulated barking, but the reactions of the barking animal and others nearby varied considerably. In one instance in dense bush, the nursery herd contained half a dozen tame adult cows who were between me and most of the rest of the herd. As the herd grazed towards me, one of the more wild individuals suddenly looked at me in the "concentrated attention" posture and began to bark. Although some animals looked up, and one or two calves trotted some distance in "scanning" postures, the tame cows paid no apparent attention, continuing to graze. The cow continued to bark for ten minutes before moving away to join some animals who had grazed on in a normal fashion. Other individuals remained, undisturbed. It seems that after the first call, which attracted the attention of the rest of the herd, and was then apparently discounted as an alarm, the cow continued to call to see if she could get some sort of reaction from me, in a similar fashion to reedbuck whistling (Jungius 1971). This was borne out by observations of animals at the lick beside my hut, when one yearling cow was licking. She could not see me through the gauze of the window, but was apparently uneasy, since she looked up to the hut every half minute or so, barked, and returned to licking until finally she looked up, gave a bark and immediately leapt away, her suspicions confirmed (her companions had paid no attention). I have seen a cow barking several times a minute towards a stimulus invisible to me for half an hour while the rest of the nursery herd grazed peacefully around her. Where the whole group was already uneasy, or where barking produced some obvious movement from me, immediately flight was the normal reaction of the herd.

AGGRESSIVE VOCALIZATIONS

"Belching grunts" were heard within the captive group and were given mainly during the jostling and rapid changing of positions at the troughs. Whether these were voluntary or involuntary resulting from jostling and rapid movement is unknown. Both Abbott (1968a) and Astley-Maberley (1937) noted these calls in comparatively peaceful groups. Abbott (1968a) interprets them as threat warnings.

The "Belching grunt" was not apparent as a call until I heard two other calls: an "urrrr" sound given as a warning from one cow to another, and a belching bellow given by enraged animals, particularly bulls. All of these calls had the same "forced" quality which gave the impression of belching and were clearly related, presumably in the same continuum fashion as the contact calls. The belching grunts were thus part of the normal, stable dominance interactions; the "urrrr" call was longer, had more voice and was heard in a newly introduced cow who had taken a place near the top of the hierarchy and was having trouble with another aggressive cow; the bellow was prolonged, modulated and heard during fights or prior to a charge.

NON VOCAL AUDITORY COMMUNICATION

Most activities have sounds which are produced characteristically (e.g. breaking bushes, urinating, moving through grass or bush) and which are capable of giving other eland information. In most cases the sounds are not exploited either by the sender or the receiver, and are therefore not ritualised into signals. In other cases, the potential for communication is present and, apparently, important.

Sounds of movement and feeding, especially branch breaking apparently serve to inform one animal about others. I could hear eland branch breaking over distances of more than 250 m in densely bushed, hilly ground, and on several occasions located a group in this way. Within the group dominant animals, on hearing branch breaking, would go to the subordinate animal and displace it. In one instance the captive group were lying in the paddock towards the end of spring. They had finished off all of the available tree-



level browse some weeks before, and were living mainly on grasses at that time. Suddenly a branch with much green foliage, weakened by a storm the previous day, broke with a loud crack and fell to the ground. The eland were on their feet and running to the tree - about 50 m away - before I had located or identified the sound. They fed avidly on their windfall and there was considerable aggression. The sound of branches breaking therefore had considerable significance for them.

Urination sounds i.e. the splashing of the jet of urine from a cow - attracted interested bulls (and other classes) to test the urine. In other cases, it stimulated others to follow suit. This may be the reason for the difference in rates of flow of urine - a cow urinating is both visually and auditorily distinctive from a bull, who stands in an almost normal posture and dribbles urine out slowly and silently.

When adult animals move around at a walk, they produce a characteristic "click" from their forelegs. This sound occurs as the leg finishes its pace or as it is being brought forward. It comes either from the carpals or the "knee" joint (Posselt 1963, states that the click definitely comes from the knee). The basis of the sound is uncertain at the moment. I have forelegs from only one animal which was known to produce this sound, and this animal showed extensive ossification of the lower foreleg, which may have been the cause of the sound. However, the skeleton of an old bull in the Zoology museum at Pretoria University did not show this deformation, but did have the cartilage on the heads of the long bones of the forelegs so worn that the bones themselves were rubbing together, again a possible source of the sound. In either event, knee clicking is widespread amongst old cows and almost invariably found in bulls over the age of six years, suggesting that if damage is associated with it, the loss in fitness is compensated for by some other gain. The sound itself is a regular one which is easy to locate and often individually characteristic. It is found in animals which are, because of their age, highly dominant. It would not be surprising to find that it has communicatory significance, possibly in interactions at night or in keeping groups together, but this remains to be proven.

Schaller (1967) notes that when gaur perform a leap at the beginning of flight, they produce a loud thump which is apparently a warning signal. Eland sometimes also leap at the beginning of flight and the sound as they hit the ground sometimes carries for 10 m or so, but, with my sparse data on leaping, I cannot say for certain whether this has any significance for other eland.

INDIVIDUAL RECOGNITION BY SOUND

Calves apparently recognise their dams by sound, responding to their calls from a very early age. The occurrence of duets suggests that cows are also able to recognise the calls of their own calves (otherwise duets would break up or be between any dam and any calf). The difference in adult cow calls is easily perceptible to the human ear, although calf calls are less easy to distinguish. The full "moo" call for two different individuals is shown in Fig 31. The reactions of one cow to imitated calls is described in Chapter 7. The cow was an experienced mother (up to seven previous calves), but reacted to the subnormal stimulus provided by my imitations until she had had prolonged experience of other calves calling at the same time as her own. This suggests that the mechanism of recognition is very plastic in its early stages and is refined by continued contrast with similar calls. A similar mechanism presumably operates for calves learning their dams calls. Adult to adult contact calls were rare, and I was unable to tell whether they involved individual recognition.

The "knee clicking" of old cows and bulls was often characteristic of the individual. When in the paddock with the animals at night, I was able to identify several individuals as they moved around, purely on the basis of the clicks.

Other calls and sounds were too uncommon to allow comparison, but seemed to be less individually characteristic. Alarm calls are relatively independent of the identity of the individual calling for their meaning, while aggressive calls are usually given at such close quarters that olfactory and visual recognition have probably already taken place.

CHEMICAL COMMUNICATION

There seem to be two main forms of chemical communication involving short term influence on behaviour patterns in eland: the senses of taste and smell. In addition, there is the possibility of chemicals acting directly as physiological controls (Fraser 1968, Estes 1972). Only smell, as a releaser of specific behaviour, was obvious during field observations, although cases where taste or physiological triggering could explain behaviour occurred.

OLFACTION

The presence and distribution of specialised scent glands in eland is uncertain. Pocock (1910, 1918) denies the presence of facial glands, although some earlier writers e.g. Sclater (undated) quoted in Pocock (1910) and Lydekker (1894) and Stevenson-Hamilton (1947) mention facial glands. Pocock only had a limited number of skins to study and considerable individual variation may occur within species: both Lydekker (1894) and Stevenson-Hamilton (1947) describe the glands as "small" and they may therefore be being lost through evolution.

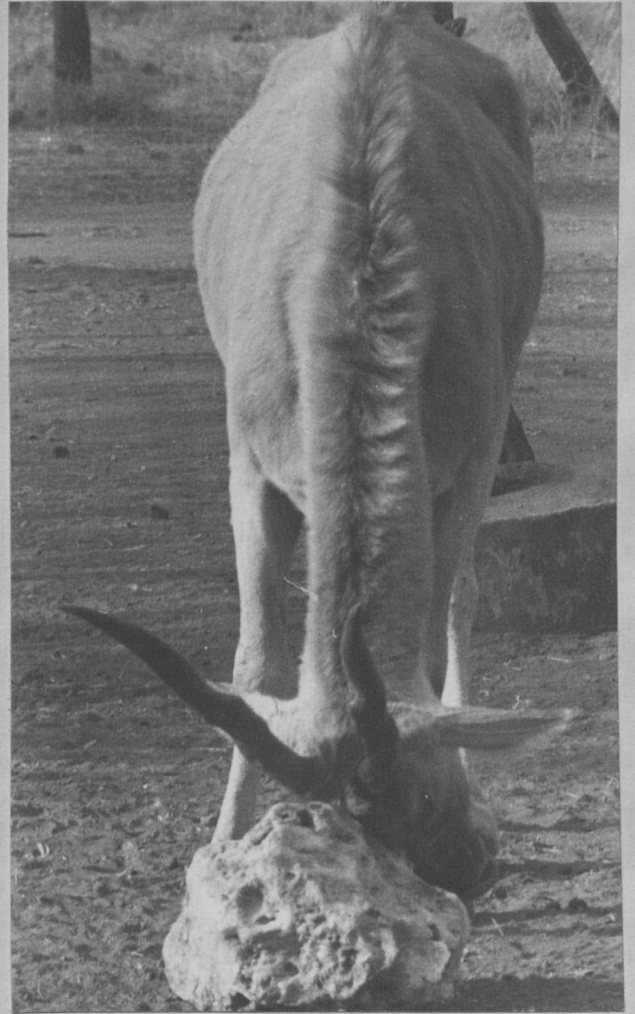
The false hoof gland, typical of all tragelaphines (Pocock 1918), gives off a sweetish odour in eland which resembles the smell of the rest of the body, but is much stronger. I detected a similar scent on the forehead brush of an old bull (the oldest at Loskop and possibly sexually inactive): the hairs themselves were distinctly oily, and this oil came away on my fingertips, which were then also scented. This suggests that some secretion from the base of the hairs had impregnated the brush. Astley-Maberley (1937) states that two bulls at Ngorongoro smelled ".... strongly!" to him when he was 80 m downwind, although I never noticed such a powerful scent at Loskop. Shortridge (1934) notes that the sweet scent may linger, and that areas used by eland may be detected by it.

The face and various parts of the body are rubbed on objects in the environment (Fig 33), including other eland, but this was usually as a part of grooming bouts or social interactions (e.g.

A

Figure 33. Rubbing as a possible means of scent transfer in eland at Loskop Dam Nature Reserve June 1972 - May 1974.

- A. Forehead rubbing on salt lick
- B. Eland would use any suitable object as a scratching post.



B



chinning) and there was rarely any sniffing or licking of the areas rubbed. Calves commonly rubbed one another with the chin or cheek region. However, in adults this was seen only as part of sexual behaviour. Since bulls could always be driven from cows by a more dominant animal, marking a cow by rubbing against her seems unlikely. My impression was that the only thing that bulls attended to in a cow was whether she was receptive.

Although the above would suggest that eland do not mark their environment to any great extent, the adults and young of both sexes marked themselves by rubbing their foreheads in urine and, to a lesser extent, other liquids such as mud or small pools of water. One cow also rubbed her forehead on a block of rock-salt (Fig 33A). Many ungulates show components of this behaviour in sexual activities, e.g. bison rub their faces in the ground before wallowing (McHugh 1958); Lichtenstein's hartebeeste males mark the ground with preorbital secretions then horn at it (Dowsett 1966); elk males in rut make a wallow which contains both urine and ejaculate and lie and rub their neck and face in it (Struhsaker 1967); territorial wildebeeste bulls urinate and defecate on their "stamp", rub forehead and facial glands in the stamp and roll in the result (Estes 1969). The actual process described in chapter 2 seems, however, to be unique to Taurotragus.

Since the behaviour was performed by both sexes, it seems unlikely to be purely sexually based, and since there was competition for other's urine it is equally unlikely to be a simple case of individual-scent marking. The activity was performed irregularly, and was rarely seen during winter. During summer rubbing was sometimes seen almost every time an animal urinated. Rubbing was seen both pre- and postpartum in cows in captivity, but less frequently in all cows in the wild. Animals always sniffed the urine before face rubbing, and sometimes sniffed it without rubbing, suggesting that there is some specific scent in the urine which is involved. I therefore assume that it is associated with some physiological state which is variable throughout the year, which is found in both sexes under some conditions, and which is possibly heightened by crowding or prolonged use of the same area. The nature of this

physiological/.....



physiological state is unknown, but would probably repay investigation. It may be linked with the physiological priming effects noted below.

Naso-nasal and naso-anal sniffing were important in identifying individuals and in checking the physiological state (e.g. oestrus, disease) of others. Naso-nasal sniffing is sometimes the result of a compromise, where each animal attempts to get its nose as close to the other as possible while keeping the rest of its body away - this would automatically produce a head to head orientation (see Figure in Jungius 1971 : 75). The strained looking posture of one or both members of the pair underlines this. In this case, the facial or breath scents may be of secondary importance to positional requirements, or they may have evolved to facilitate exchange of information in the "compromise" position. In other cases, naso-nasal sniffing seemed to be specifically directed towards the nose of the other, in order to smell the partner's breath: there are indications that each can identify what the other has been eating by this sort of exchange. Also, cows seem to use naso-nasal sniffing to get a final check on the identity of calves (see ontogeny), suggesting that the breath (or the facial glands?) is individually characteristic. In naso-anal sniffing, the reactions of the individuals involved suggest that this serves to augment information gained from naso-nasal sniffing.

Eland were often aware of where other eland were, even if there was no sight or sound of them. Beregrund (1974) records a caribou bull trailing cows over a distance of more than one kilometre apparently by scent alone, and while I did not see any similar feats in eland, they were certainly capable of scenting each other over considerable distances. The false hoof glands are apparently better formed for diffusing scent through the air than for scent deposition (Estes 1974). These may facilitate location between animals who, because of their feeding and movement habits, often become widely separated in areas which may not be well known. The glands may also provide an individual scent (Estes in litt.).

TASTE

Taste probably supplements olfaction in most circumstances. Young eland investigating strange objects or individuals almost invariably attempt to lick the object after a prolonged period of sniffing. Possible opportunities for gustatory communication include mutual grooming; sexual licking of genitalia; lapping and drinking urine; dams licking their neonates' birth fluids; dams drinking calves semi-liquid faeces; calves licking the dam's underside while locating the teat.

PHYSIOLOGICAL PRIMING

Estes (1972) has suggested that pheromones transmitted via urine may serve to synchronise breeding activity in ungulates and this view has some support from other studies (reviews in Fraser 1968, Gleason and Reynierse 1969). In the case of eland and other species, bulls are often found away from cow groups during most of the year (Abbott 1968a, b, Roth et al. 1972, this study) and are only found regularly with cows during the breeding season. If an effect similar to the Whitten effect (reviewed in Gleason & Reynierse 1969) exists in eland, this would automatically tend to keep the cow's calving periods and receptive periods in phase with the presence of bulls (bulls themselves are probably sexually active throughout the year - Skinner, van Zyl & Oates 1974). Support for the existence of this effect in eland is found in the prolonged breeding seasons found in zoos, where bulls are often kept with cows throughout the year; also, the cows at Loskop showed no signs of coming into oestrus when confined together without a bull, even though some were kept several months postpartum (other explanations can, however, be found for these phenomena-Chapter 7).

Estes (1972) suggests that the priming mechanism is mediated by flehmen, which informs the bull of the general state of females about him as well as of the particular females he is testing. This is not necessarily a complete explanation of eland flehmen. Apart from urine, there are several other stimuli which produced flehmen, some of which can be attributed to Estes' (1972) proposed vomero-nasal system. The scent of blood at close quarters, the taste of

garlic/.....

garlic, the scent of cheese and other strange olfactory or gustatory cues were seen to elicit flehmen. In addition, animals were seen to flehmen after having received a sharp blow on the nose; they were also seen to flehmen apparently spontaneously, on three occasions when standing doing nothing, and twice to flehmen in response to some stimulus undetectable to me, when sniffing upwind.

Testing and flehmen were seen throughout the year in all age/sex classes, although bulls in the rutting season performed it most prominently. This would fit in with Estes' (1972) suggestion that testing and flehmen are parts of both a physiological priming mechanism, synchronising sexual physiology within the population, and also part of a specific behavioural trigger for mating activity. However, from the previous observations it would seem that flehmen is also associated with other olfactory stimuli.

A physiological priming effect which is much more solidly supported for ungulates is the role of olfaction in the early bond formation of dam and calf (reviewed in Hersher et al. 1963b, Fraser 1968, Lent 1974).

TACTILE COMMUNICATION

Direct physical contact between individuals was limited to only a few situations. Apart from calf/calf, mother/infant and sexual interactions, any action which involved contact, or which implied that contact would follow, seemed to make the receiving animal uneasy. Even in the observed instances of social grooming between adults, the animals involved were often tense or uncertain and were easily distracted from grooming. Some cows actually seemed to use this uneasiness to displace their superiors from licks and troughs by licking and nuzzling at the superiors' anal region. Sometimes this caused the recipient to move, sometimes to turn and threaten, and sometimes there was no apparent response except for an irritated swish of the tail. The most striking example of this is the use of chinping to drive other animals about (see Chapter 5).

The use of nuzzling and chinping in sexual situations, apart

from/.....



from perhaps calming the cow and stimulating her to receive mounting, may promote oestrus in domestic cattle and may also have this effect in a wide variety of other bovids (Fraser 1968). Physical stimulation may presumably also play a role in maternal care and milk giving although whether any of this (except perhaps calf "bunting") can be regarded as signalling is doubtful.

Overall, the highest frequency of physical contact between individuals is in the form of aggression. This normally takes the form of a light tap with the horns, or a nudge with the head in young calves, and is certainly symbolic. As with most other forms of tactile communication in eland, the contact is first preceded by intention movements (approach, perhaps threat). Tactile signalling therefore usually acts to supplement and heighten the effect of previous signals, as might be expected from the effective ranges of the various senses.



CALVING AND ASSOCIATED BEHAVIOUR

There are several previously published records of the events immediately preceding and following parturition in eland (Walther 1958b, In Kirschoffer 1963, Stainthorpe 1972, Roth et al. 1972), but all of these are either not detailed or else deal with slightly abnormal births (Kirschoffer 1963 records parturition in a primiparous female and also in a multipare who had to receive aid). Records of calving seasons in eland are available for a variety of habitats and management regimes (Jarvis and Morris 1961, Brand 1963, Skinner 1967, Fairall 1968, Skinner & van Zyl 1969, Dittrich 1970, Spinage 1973, and Skinner, van Zyl & Oates 1974). There is little detailed description of eland behavioural development except in the management - oriented works of Posselt (1963) and Roth, Kerr and Posselt (1972) in Rhodesia, and Treus and Kravchenko (1968) and Treus and Lobanov (1967) in Russia. The following two chapters describe the birth and early development of eland calves in ethological terms. Appendix 6 gives a detailed description of a single birth, to help to integrate the descriptions and diagrams given in the text. The majority of records are drawn from the small group (N = four to nine) of captive cows observed over a period of 20 months, supplemented where possible from field notes.

DATE AND TIME OF CALVING

The study period covered two August - October calving peaks. Some records prior to this were also available (Table 18). The herd was introduced in 1963 as calves and since the age of eland cows at puberty is just over two years (Skinner 1967), records prior to 1969 are from the herd founders, their first offspring not reaching puberty until 1968. First generations were raised in the wild and were shyer than either herd founders or their original offspring. Tame cows and their calves were sighted more readily

than/.....

Table 18 : Number of eland calves born each month at Loskop Dam Nature Reserve during 1966 - 1973. Records prior to June 1972 from the reserve monthly reports.

	1966	1967	1968	1969	1970	1971	1972	1973	Total
Jan	-	1	-	-	?	2	-	-	3
Feb	-	-	-	-	?	-	-	-	-
Mar	-	-	-	-	?	-	-	-	-
Apr	-	-	-	-	?	-	-	-	-
May	-	-	-	-	?	-	-	-	-
June	-	-	-	1	?	-	-	-	1
July	-	-	-	-	?	?	1	-	1
Aug	-	-	7	6	?	?	7	7	27
Sept	-	6	5	3	?	?	7	5	26
Oct	1	1	-	-	?	?	4	7	13
Nov	8	2	-	-	?	?	3	1	14
Dec	-	-	-	-	?	?	-	-	-
Total	9	10	12	10	?	2	22	20	85

? - No records available.

than others and birth dates were therefore usually only known for the herd founders. Table 19, therefore, mainly shows the calving seasons of an ageing group of thirteen contemporaries, and, to a lesser degree, those of their first offspring.

The time of calving is known for 11 births (Table 20). Evidently calving may occur at any time but is concentrated around sunrise. The probability of a concentration of five or more births out of eleven in a given four hour period is 0.024, (binomial test, Siegel 1956).

Table 19 : Calving peaks for eland in the wild and in captivity

	Skinner & van Zyl 1969		This study	Brand 1963	Morris & Jarvis 1961	Dittrich 1970
	<u>Bushveld</u>	<u>Highveld</u>	<u>Bushveld</u>	<u>Captive highveld</u>	<u>London zoo</u>	<u>Europe Generally</u>
<u>Calving peak</u>	August - October	November - January	August - October	July - November	March - June	February - August
<u>Daylength (hours) at conception</u>	13-14-13	13 - 11½	13-14-13	13-14-13	16 - 14	-

Table 20 : Calving times for 11 eland at Loskop Dam Nature Reserve
June 1972 - May 1974

<u>Time</u>	<u>Number of calves</u>
00h01 - 04h00	1
04h01 - 08h00	5
08h01 - 12h00	1
12h01 - 16h00	1
16h01 - 20h00	1
20h01 - 24h00	2

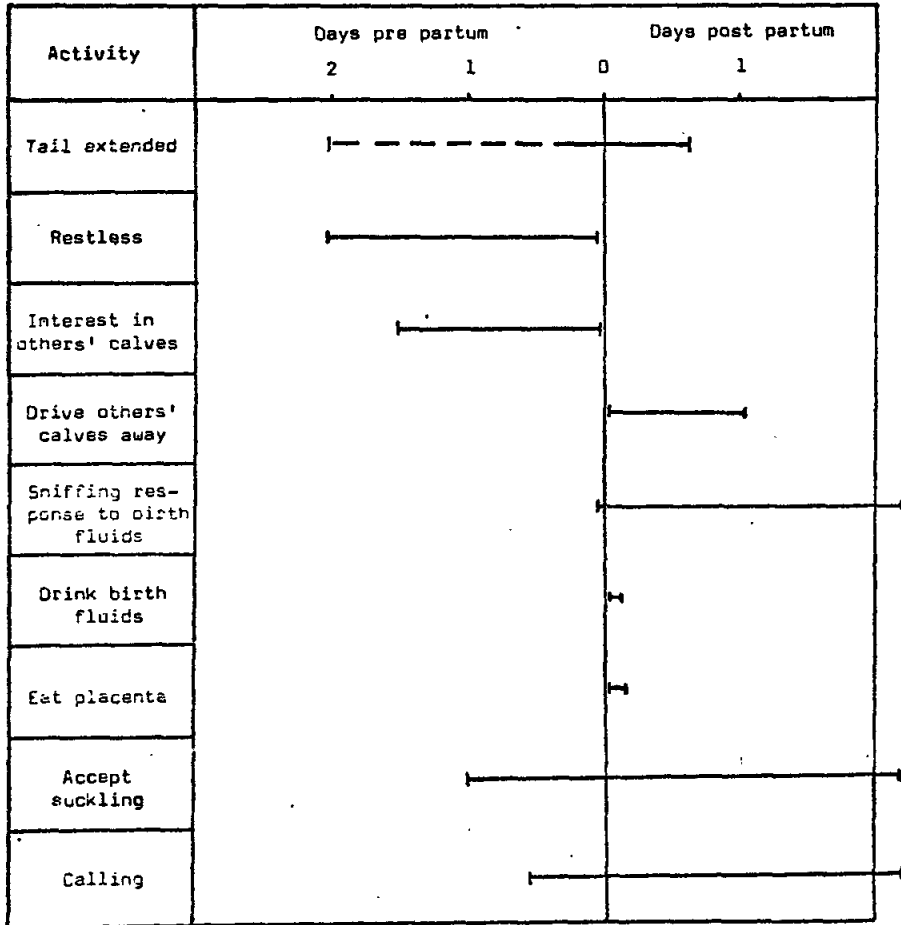
CAPTIVE GROUP BIRTHS

These are summarised in Figs 34 - 37 the actual birth process being similar to that in most ungulates (see Fraser 1968). Several incidents throw light on maternal behaviour and are therefore described in greater detail below.

i) For several days this individual (a high ranking adult female) "worried" the light wicker gate of the smaller inclosure once she had finished eating at the troughs within. On the night of parturition I left her for about an hour in the evening. During this time she succeeded in breaking down the two gates giving access into the larger paddock and in breaking a gate in that paddock which gave out into the reserve. The latter gate was never used by the eland. She gave birth that same night and returned with her calf four days later. Both were lured inside with food. She was the only individual to escape in this manner.

ii) In 1972, the low ranking female T was the first to give birth. Her calf (T's) was ten days old when the preparturient cow F started to follow it and sniff at it. When it attempted to suckle,

A



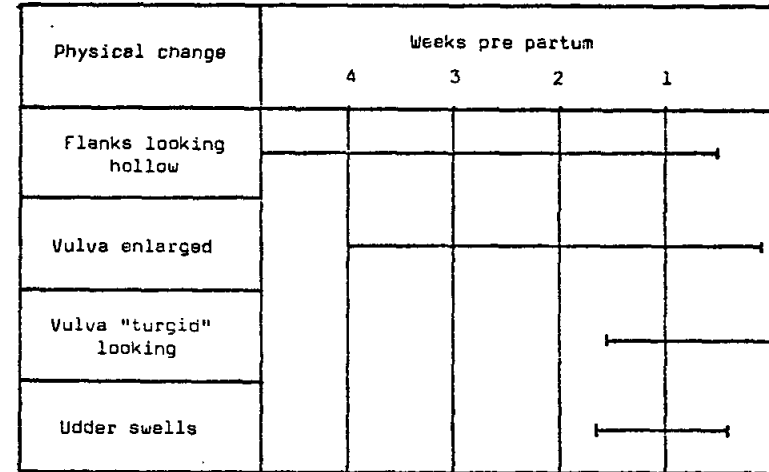
— = period covered by that phase of the behaviour

| = continues beyond 2 days post partum

--- = single observation

N = 6-9 pregnancies, 7 individuals

B



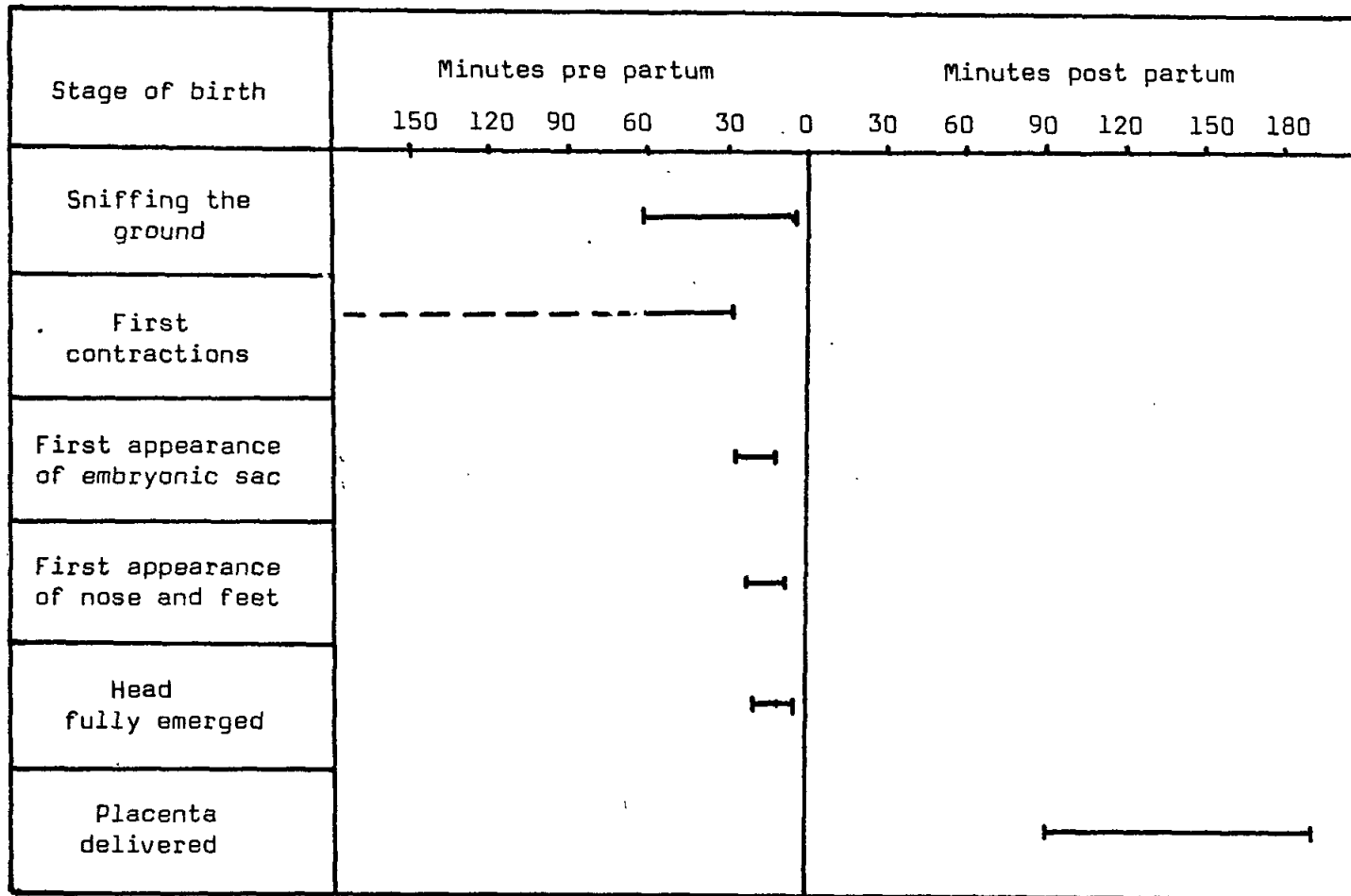
— = range covered by the earliest & latest appearance of the change

N = 13 pregnancies, 8 individuals

Figure 34. Behavioural and physical changes associated with calving in eland at Loskop Dam Nature Reserve.

A. Behavioural changes

B. Physical changes



| | = Range of appearance
 - - - = single observation
 - miscarriage

 N = 6 deliveries, 4 individuals

Figure 35. Progress of birth in eland cows at Loskop Dam Nature Reserve. June 1972 - May 1974.

Figure 36. The birth process in eland at Loskop Dam Nature Reserve
June 1972 - May 1974.

- A. The cow stands and sniffs the ground between early bouts of contraction. Restlessness and escape attempts may still be seen at this stage. The embryonic sac is visible.
- B. The cow lies for most of the contractions. The calf's foreleg and nose soon appears.
- C. In successive contractions, the calf's head is slowly forced out. Here the nose, the base of the ear and the eye are clearly visible.
- D. Once the head is free, the rest of the body is expelled only five minutes after "C". The whole of the body was forced out following a single, casual-seeming contraction.
- E. The cow grooms the calf and eats the embryonic membrane.
- F. Two hours later, she produces and eats the placenta. This may take an hour or more.

A



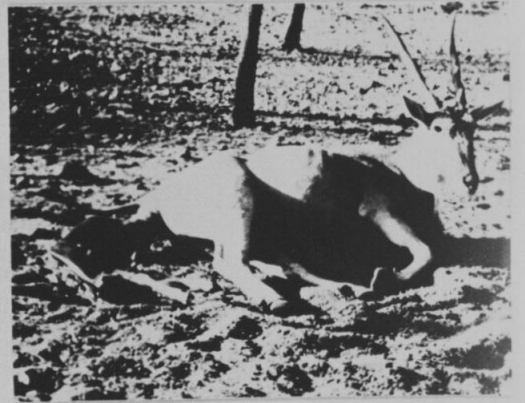
B



C



D



E



F



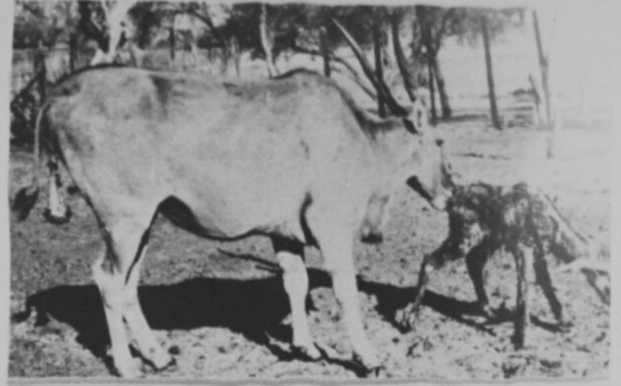
Figure 37. Early behaviour of an eland calf at Loskop Dam Nature Reserve. September 1973.

- A. As the dam, attracted by the calf's initial standing attempts, grooms it, the calf turns its head towards her.
- B. When the dam grooms its anal region, however, the calf freezes and shows no orientation to the dam.
- C. The dam stands as the calf nuzzles along her underside and licks the inside of her hindleg.
- D. Once the calf is suckling, she licks its anal region.
- E. and F. were both taken within one hour of birth, when the calf was approaching almost any large object, including the observer, and moving independently of the dam.

A



B



C



D



E



F



F at first brought her hind leg forward, preventing it. Later that same day, she allowed it to suckle for just over one minute before stepping away. The next day, she allowed it to suckle for over five minutes, actually driving T away to obtain access to it. She showed all the maternal behaviour patterns, including the licking response to its wagging tail as she nursed. Two hours after this, F gave birth. This birth was not observed, but F's subsequent behaviour showed that she had considerable confusion over the identities of the two calves. She would at first accept either of them, provided the other did not attempt to suckle. If it did, she would sniff the noses of both before horning one aside (not necessarily T's). She would lick both anally with no apparent discrimination. On occasion a calf had only to approach for her to check the one suckling, indicating that she had some awareness of the situation. This continued for two months, with T's suckling eventually being completely rejected. Several factors may have reinforced the situation, in particular, T's calf was actually more persistent in trying to suckle F than was F's - she had learned to shoulder F's aside at the teat (Fig 38) so that F was grooming her own calf, but T's was actually suckling. On one occasion after T's had been repeatedly attempting to suckle from F and rejected by mild threats and kicks, F suddenly whirled and charged not T's but T, who was feeding nearby. This was probably a case of redirected aggression, since T was the nearest adult at the time and the only one lower in rank than F.

iii) The following year F miscarried, probably as a result of some injury sustained in dominance interactions at the troughs. The calf was about one month premature and born dead. F, however, showed intensive licking and grooming reactions to the still calf, calling continually with the full repertoire of maternal contact vocalisations. When separated from it, she sniffed the ground where it had been and watched it being moved away. Four hours later, she was released into the second paddock, where the body was, went straight to it, and again groomed it. She continued to call for several days (3+) following final separation. She did not, however, show any interest in the other calves except to investigate

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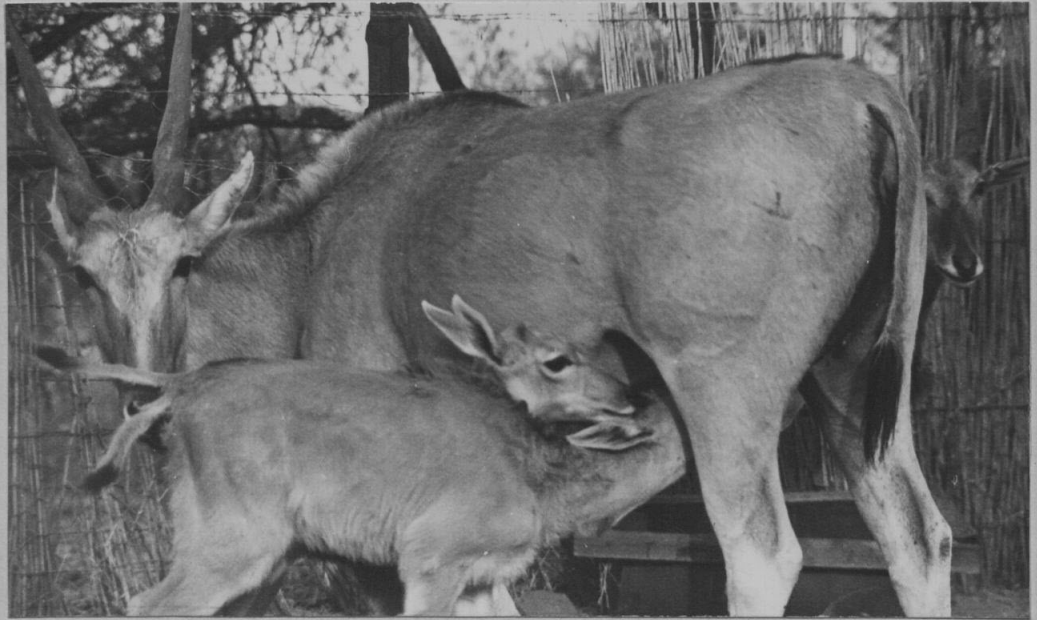


Figure 38. Milkstealing in captive eland at Loskop Dam Nature Reserve. September 1972.

and reject them. The birth was very much longer than the others (3+ hours from first contractions) and seemed to give her a great deal of pain. The placenta was not delivered for several days and she did not eat it, although she drank the birth fluids.

iv) When separated from her 1 week old calf in 1973, T showed similar signs of distress, returning repeatedly to the calve's paddock and calling but showing only investigatory and rejection responses to strange calves. Although her milk yield had been low, her calf-seeking behaviour persisted for more than a week, after which she moved out of the area and was not seen for several weeks.

v). The cow M bore her 1972 calf in the veld and was a frequent visitor to the paddocks, apparently just to drink in the nearby bay and to lie near to the captive cows. When her calf was a month old, it was stricken with heart-water fever. Her response to its weakened state was to approach it, repeatedly calling, groom it extensively, especially on the neck, then move away in the direction of the rest of the group, eventually circling back. She was in good condition and seemed to be greatly troubled by not being suckled, ducking and nudging at her udder and at one point reaching round and apparently suckling herself. The calf died shortly after this and she was taken into the paddocks but would not accept any of the calves present, despite her continued and probably painful milk production. She was in the area when her calf was being skinned, and repeatedly attempted to approach the corpse although she showed no signs of aggression or disturbance at what was going on. Once the calf had been skinned she ignored the corpse and went to the skin, nuzzling it with clicks and grunts before giving a pronounced flehmen and walking off to look into the paddocks at the other calves and call to them. She too continued to vocalise to the calves for at least one week before moving out of the area with two bulls.

vi) The cow A (high ranking, aggressive female) gave birth twice in captivity, both occasions being recorded and showing a remarkable similarity in their timing. In 1972, she calved soon after dark and allowed me near enough to touch her calf before she could lick

it (in fact, all the captive females would probably have allowed this). As she groomed its hindlegs and chewed up the membrane still sticking to its body, I smeared the fluids from the outside of the membrane onto my face and arms. When she got to the same end of the calf, she transferred her attentions from it to myself; after she had licked most of the fluids from my face, she preferred to lick my hair, even though no fluid had been put there. This response waned after about fifteen minutes, presumably after all of the fluid had been removed. During that fifteen minute period, she swung to and fro between the calf and myself, apparently in response to movements on our part. About ten minutes later, she drove two inquisitive calves away by charging at them, then turned and charged at me when I moved: my status had obviously changed. When I returned to my former position, however, I was ignored, even though I was if anything closer to both calf and mother.

CALLING

While vocalisations are considered in detail elsewhere, there are one or two instances which are of interest when considering the formation of the mother-infant bond. When the cow L had her second calf in the paddocks, in 1973, she was the only individual nursing. I found that I could elicit her approach by imitating the moan/bleat part of a calf's spectrum of calls (see Chapter 6), although her response to this waned on repetition in any single session. After one or two calves had been born into the group and were also calling, her response was much more specific and she would only approach or reply to her own calf's call. When 'A' also had her second calf in captivity, in 1973, it approached me during one of its exploratory dashes from A; I found that when I imitated the choked moo/grunt part of the adult females' contact call, the calf would freeze if it were moving away from me at the time, and that when it turned back to me, A herself began calling and caused the calf considerable confusion - it stood between us for several minutes before finally orienting itself towards A and, a little later, going to her. In this second case, my imitation was very poor, since the call had a strong fundamental in the 50

Hz. range. The calf's response was therefore a very generalised one. Older calves seem to be more specific in their response, since I could only occasionally elicit orientation from them, and never approach. Unfortunately, I was unable to use recording and playback techniques to confirm these observations.

DIRECTED AND GENERAL MOVEMENTS IN THE NEONATE CALF

Early orientation could be divided into two phases:

- (i) Before standing and movement from one place to another were possible.
- (ii) Following the appearance of standing and voluntary bodily movement (see e.g. Fox 1970, Lent 1974).

In the first phase, the first directed movements were in response to the mother's licking - the calf would turn its head towards the place being licked and follow the dam's grooming movements, usually also licking. Before this, calves made general, apparently undirected, nose-thrusts into the air, but the first definite orientation was to the tactile stimulus of being licked. "Seeking" seems to follow this initial orientation: the calves would struggle furiously when their dams stopped licking them, but would stop immediately when grooming was resumed. Later, grooming reduced the movements but did not stop them completely. While these early movements seemed to be in response to tactile stimuli (or their absence), the calf was also receiving at least two other types of stimulus. The cows made low level contact calls at frequent, irregular intervals as they licked and, as calves followed their dam's licking, they must also have seen her head, which made repetitive, small movements.

The calves became increasingly active with time and a dam's licking had proportionately less effect, unless she was returning to it after several minutes absence. The first definite purely visual orientation, coupled with a physical attempt to follow, was seen as dams turned away after a licking bout. At this stage, nose-thrusting was still seemingly undirected. While the respon-

siveness of the calf to the dam changed rapidly at this time, the changes were apparently quantitative rather than qualitative ones, probably because the stimulus/response possibilities were restricted. The major stimulus was the dam's grooming, while the calf's responses were orientation of the head, calling, trying to move it's body, and freezing.

Once the calf could stand, or could move itself from place to place by partly successful standing attempts, the simple responses seen when lying were sometimes accompanied by bodily movement from place to place. Dams usually responded to this movement by licking the face and anal region of the calf, then turning back to lick up the birth fluids. Calves would freeze when the dam licked them, but would move again when she stopped, as in the earlier phase. The bodily movement which followed, however, was not usually directed to the dam, but was simply "forward", regardless of where it led the calf. Head movements towards the dam were, however, more frequently seen in response to both her movements and her grooming.

At this stage, various natural experiments showed that other things besides tactile stimulation could provoke or inhibit orientation or generalised movement. As calves gained more control over their movements, these responses were superimposed on bodily approach or withdrawal. Almost any localised visual stimulus seemed to be enough to elicit orientation, approach and nose-thrusting, for example, or marks on the fences, the wires of the enclosure or corners. Isolated objects, such as trees or bushes were even more effective, while most response was shown towards moving ones (other eland or myself). Heat and/or light induced approach and investigation. The dam's calls and licking induced freezing, calling and orientation, as did any light, persistent touch on the face or anal region. The calves movements resembled a series of approaches at that time, rather than a sequence of approach/withdrawal, so withdrawal eliciting stimuli were less easy to determine. One characteristic which eventually caused withdrawal was a lack of change in the object being approached (c.f. Andrew 1964). The only time other eland caused immediate withdrawal was when they attempted to mount the neonate; even kicks

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and horning caused freezing rather than avoidance. When investigation and licking by others had been continuing for some time, however, calves would often jerk themselves away and move on. The "avoidance" response was, nevertheless, very strong in some circumstances, especially when the calf's movements were restricted by being held firmly or on being mounted by other calves.

These rather general responses appeared within the first two hours of life, by which time a definite sequence of head orientation, approach, and nose-thrust was seen. This sequence was seemingly directed towards all of the visual stimuli mentioned above, and formed the basis of suckling and following. Nose-thrusting was also seen independently of the approach behaviour and was usually directed towards objects presenting a horizontal profile at nose level.

THE FOLLOWING RESPONSE

The onset of following is indistinguishable from the early orientation and approach behaviour of the calf (see above). During the first hours of life, calves directed their actions increasingly with reference to other eland. This presumably represented developing species recognition. The movements were usually either directly towards or directly away from other animals. This was seen most clearly in the exploratory dashes made by three or four hour old animals, where they often ran from their dam, to another eland and back again. The restriction of the range of objects eliciting approach and following to eland was effectively finished within the first day of life for the captive animals (their only other regular choices were inanimate objects and humans). Walther (1964a) details nine stimuli eliciting approach and following in the young of Tragelaphus species; similar stimuli seem to apply for eland. The most usual situation for the eland calves was that of a larger animal moving past or away from the calf, faster than the calf itself.

From their first oriented movements (see Appendix 6) the eland calves showed a tendency to follow almost any object larger than

themselves/.....

themselves. Later, they would usually only follow conspecifics, but the size was still important. When a small group of calves was temporarily associated with a single cow, and moving at an uninterrupted walk from one place to another, they usually fell into single file with a progression of size from the largest to the smallest going to the rear, with the cow leading. Observations on wild and captive calves showed that they would follow any larger conspecific, but that the mother was by far the most frequent adult to be followed. Whether this is due to some additional mechanism or the fact that the mother was the adult who was most frequently in contact with the calf, and therefore most frequently in a position to be followed, is uncertain. On occasion the mother used this following response to lead the calf to a suitable lying up place, but generally it seemed to act to keep the calf in contact with its mother or its peers during the daily movements.

The normal position of the calf during following is to the rear of the cow either beside her hindleg or else up to one metre behind her tail. This position may vary, especially during flight, when the calf may move up alongside the cow or even in front of her.

The following response is particularly affective in maintaining the unity of the crèche group. Calves always follow the lead of another in approaching or withdrawing from an object, so that group movements were often ruled by either the boldest or the most timid individuals. This habit quite often led to stampedes in the nursery herd, when one of the calves suddenly took fright for some reason and dash amongst companions, these would respond by an immediate flight reaction, which might stimulate the adults to follow. Such stampedes were easily identified, since the crèche group would be in the lead, whereas in normal flight, the leading group was usually the sub-adult portion of the herd.

THE LICKING/CHEWING RESPONSE

This response, seen mainly in calves but also in sub-adults and adults, occurs in a variety of situations and may form the basis of

several/.....

several more complex behaviour patterns (see below). It consisted originally in all cases of a simple repetitive licking of an object. If some part of the object was brought into the mouth as a result of the licking, the calf would bite with its incisors, then sometimes work the object round to the side of the jaw; but the most usual pattern seen was licking, then repetitive biting and chewing with the incisors.

The stimuli initiating this response where varied but they had some common visual characteristics, being either small and distinct from their background (e.g. eland droppings, stones, a camera, teats, leaves, a brightly coloured pencil) something with a "loose" appearance or texture (hair, grass, fur) or else some combination of the two (e.g. the tip of a conspecifics tail, ears). These stimuli seemed to be the basis for the adults trying out new foodstuffs, since the tame animals would sniff and nibble at loose pieces of cloth, straps, or anything with a similar appearance on my person. Licking also occurred when the calves were being scratched or groomed, and they directed it towards objects with the same characteristics.

During ontogeny, this response occurred in connection with three major behaviour complexes: the calf's initial suckling attempts; social grooming; and feeding. It also occurred, although less prominently, in the initial orientation movements of the calf and, presumably, formed the basis of self grooming.

Licking/chewing underwent development in several ways. In teat seeking it disappeared completely once the calf had learned the position of the teat. However, it reappeared following rejection or some other frustration, and also just after suckling, when the calf would lick the mother's flank, tail and dewlap.

In adult mutual grooming, the areas eliciting grooming in the calf were almost completely ignored (e.g. the tip of the tail, the ears, the dewlap). This was partly the result of the emergence of other elements of the adult's social behaviour, such as a tendency to avoid approaches by a superior and to groom only following an invitation approach or a grooming demand. Both of these latter interactions involved "head-on approaches" and were easily disturbed. The "preferred areas" in the adults were therefore the ones

which/

which were most easily accessible, and the stimuli dictating the calf's preference were overruled by other considerations.

In the feeding context, licking/chewing was at first elicited by almost all objects in the environment filling the criteria listed above, although other preferences also played a part (e.g. stones, although common, were relatively rarely licked). The facilitation provided by another animal feeding in the same spot also affected which objects were most frequently licked (see also Leuthold 1971b, Altman 1956). With increasing age, the licking/chewing response was seen much less frequently as a means of testing objects as food, probably because other criteria (e.g. scent, colour) also become important. Nevertheless, the tame adults did sometimes seem to use only the original criteria in deciding what to eat.

TEAT-FINDING AND SUCKLING

The initial suckling attempts of the captive calves involved the integration of at least three distinct behaviour patterns seen in the neonate. These were the approach response, nose-thrusting, and the licking/chewing responses. The relevant stimuli and the calves' responses are given below.

- (i) "Something at nose level" giving approach, thrusting and licking, e.g. profile of belly;
- (ii) "Something resistant" eliciting thrusting e.g. a tree, the udder, a wall;
- (iii) "Something recessed or at a junction" eliciting movement in that direction e.g. between the legs, the shoulder/dewlap junction, top of human legs, a corner;
- (iv) "Something loose" eliciting licking e.g. tail, teats.

The initial suckling attempts of the captive calves were merely nudging motions which became increasingly directed towards particular stimuli, especially to horizontal profiles and to junctions at nose level. Once the calf in Appendix 6 had begun to direct its nudging and licking to its dam, it quickly found the teat and began to suckle. The other calves observed directed these actions to

their/.....

their dams much sooner, but, once there, took longer to locate the teat itself and to suckle. This suggests that the first calf's coordination had improved with time, despite the fact that it was directing its approaches to non-maternal stimuli (trees, fences).

In general, calves would nudge along the underside of the dam's body, occasionally concentrating on particular points and licking them intensively. The first licking or suckling bouts were directed towards the dewlap or the base of the throat, probably because the female is usually standing with these points nearest to the calf when it begins its attempts. The underside of the dam's body was the usual object of these attentions, although the actual requirements for eliciting thrusting seem to be "something at or just above nose level". The nudging and licking responses, once located along the belly-line, led the calves quite quickly to the teat area, although they then often spent some time licking the inside or outside of the cow's hindleg or even her tail. The teat actually seemed to be licked into the mouth initially, although once it was there, the calf butted and sucked vigorously immediately - usually with the effect that it lost the teat and once more resorted to licking. The first successful suckling may not actually yield much milk, since the teat is so frequently lost and has to be re-found each time. Subsequent sucklings are more productive, although the calf may continue to have trouble locating and maintaining contact with the teat for some days. The initial stimuli continued to be important in teat location for the first few bouts, and one week-old calf was seen to use them several times.

On only one occasion did I see a cow helping a calf towards the teat by nudging it, and that was when one cow was showing a maternal interest in another's neonate. The calves do, however, seem to follow the swing of a cow's head after she has naso-nasally checked them. This movement causes the calf to move towards the rear, where it usually has little difficulty in locating the teat.

Even the youngest calves tail-wagged frantically while approaching and especially while suckling. This may have stimulated the cows to lick the calves' anal regions (Fraser 1968). The effect of pressure in that region is to cause the calf to freeze and lift aside its tail. The freezing response may be important in helping

the calf to locate the teat, since cows appeared to "freeze" their calves' movements in this way mainly when they were in roughly the "normal" suckling position, which would increase the calf's chances of teat-location. The reflex is very strong since I myself managed to elicit freezing by touching the base of a neonates tail with my finger. The calf remained standing with its tail to one side for several minutes until I "released" it by removing my hand.

SUCKLING AND WEANING

The development of suckling from the first day until the end of the fourth month is given in Fig 39. The dam was most receptive to the calf's suckling up until the end of the first month. Although there was a high proportion of rejections in the first week, this was mainly because of the even higher proportion of suckling attempts. After this time rejections of suckling attempts steadily increased, until the fourth month, when all suckling was rejected. The length of individual suckling periods also reached a maximum towards the end of the first month, and shorter suckling periods became more frequent after the first month ($P < 0.01$, extension of median test, with a median for whole period of 8 min 10 seconds and a range of 1 min 15 seconds to 20 minutes).

Milk stealing was observed, but these attempts were rarely successful (Figs 38, 39a). Rejection of foreign calves was usually either by means of a threat or a mild horning action or else by moving away. The calves may also have been sensitive to rejection implied by females completely ignoring them. For example, a calf would make a tentative approach to an adult female and stand three to five metres away from her with its neck outstretched, head slightly lower than shoulders and ears forward, as if sniffing towards her but unwilling to go any closer. If the female continued with her ongoing activity, the calf would turn away, while if the female turned her head towards it, nose out, the calf would trot forward, often with a "whimper" and naso-nasal sniffing would follow, then suckling attempts.

In the captive group, weaning probably occurred earlier than in free-ranging calves, since the cows were separated from their calves

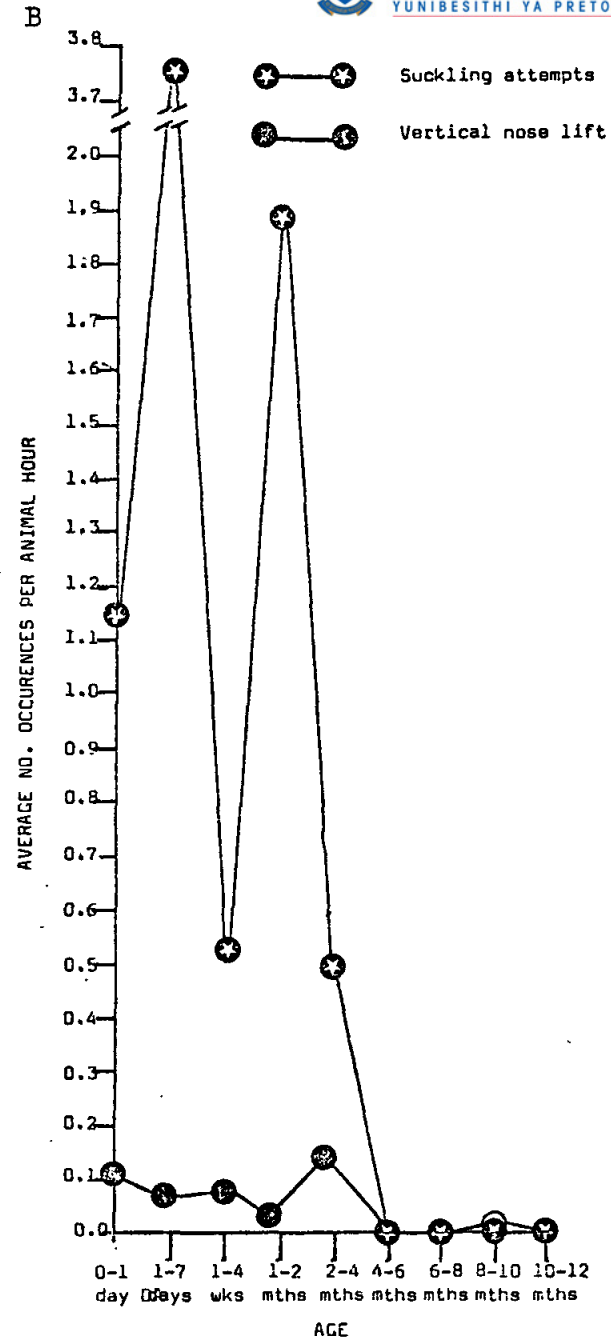
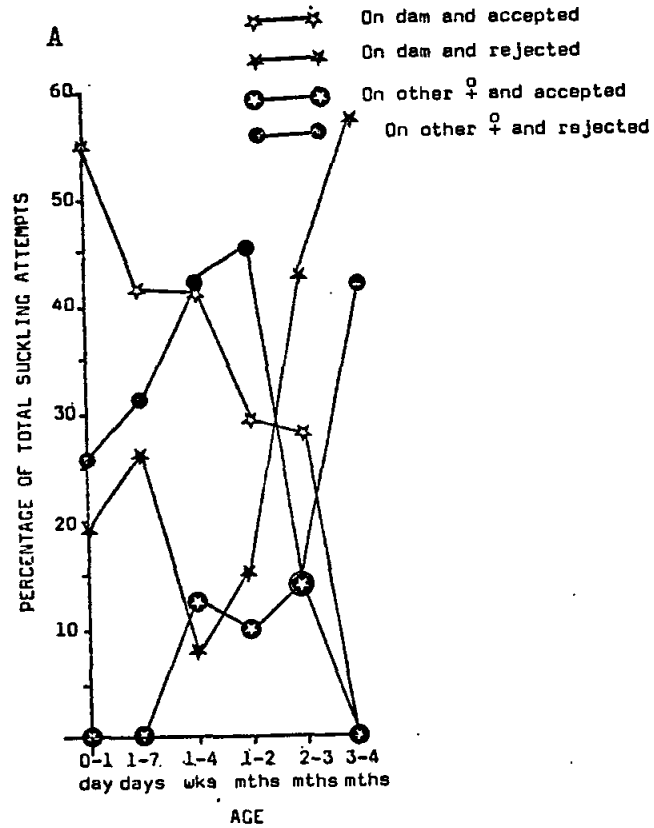


Figure 39. The development of suckling in captive eland calves at Loskop Dam Nature Reserve June 1972 - May 1974.

- The proportion of successful and unsuccessful nursing attempts on the dam and on other cows.
- Variation in the frequency of suckling attempts with age.

during the day. The optimum suckling frequency was probably greater than this regime allowed, since the dams would sometimes cluster around the paddock quite early in the afternoon, and begin calling to their calves two or more hours before they were actually allowed to suckle (but compare Joubert 1970). In addition, the cows had only the calves to return for once the rains had begun and some of them did not touch the supplementary food at all. In the wild there are several factors (e.g. social tendency, similar foods etc.) keeping cow and calf in more continual contact which probably facilitates extension of lactation. The process of weaning in the captive calf group was probably an exaggeration of what normally occurred, since the cows returned to the calf at increasingly greater intervals until they finally failed to return altogether. In the wild, cows began to move away from the nursery herd for short periods and to forage separately from it during the second month of the calf's life. As the summer went on and the winter approached, the two fractions were more and more independent in their movements until during the winter proper, the central calf group was almost all that remained of the nursery herd.

DISCUSSION

SEASONALITY AND TIME OF CALVING

The timing of the calving season in eland is less precise than in many other antelope e.g. impala. In spite of this, all wild population records show a stable calving peak. Records given by Skinner (1967) show a wide range of gestation periods between populations: 256 to 285 days. Within populations, however, the range is much more limited. The inter-calving interval is even more variable, both within populations (Roth et al. 1972, give 283 - 553 days) and between them: eland in Rhodesia (Roth et al. 1972) averaging 334 days, while South African eland average 371 days (Skinner 1967).

Skinner and van Zyl's (1969) average of 271 days for the gestation period gives a conception peak of mid-November to mid-February (for the two years covered by this study). (The majority

of the August calves were born from the end of the second week onwards). The peak may be determined in part by nutrition. Skinner & van Zyl (1969) find a difference in calving dates between bushveld and highveld animals at the same latitude, and Brand (1963) records a calving peak for highveld eland on the same latitude in captivity which is comparable to the bushveld calving peak. The only apparent difference between the two highveld populations is nutrition. There are indications of some influence by photoperiod (Spinage 1973), which are partly confirmed by data from Jarvis and Morris (1961). These show a concentration of births around the months with maximum photoperiod in London (Table 19). On the other hand, Spinage's (1973) records show a wide diversity of calving periods with latitude, and Brand (1963) records a similar variety of seasonality in different southern African habitats. There are, therefore, probably factors besides daylength and nutrition determining conception and parturition seasons e.g. temperature (Fraser 1968).

Within a population, additional factors may determine calving dates. Apart from the effect of low nutrition and temperature (Fraser 1968) on the sexual drive of males, Skinner et al. (1974) report a annual variation in eland sexual physiology which is probably partly connected with fluctuations in body mass. Nursing may also effect conception, since the semi-captive females in my study ceased to visit their calves about the time they conceived again. However, cows kept with their calves, or artificially milked, continued to lactate and nurse well after conception (Treus and Skinner 1967, Treus and Kravchenko 1968). The conceptions at Loskop in 1965-6 occurred considerably later that year than subsequently. These conceptions were the first for all cows, and presumably represent the earliest dates of fertile ovulation. Following years show a "homing-in" onto the present, apparently fixed, season. Puberty itself may be delayed by poor nutrition (Skinner 1967), and if there are many such heifers in the population, their delayed first calving may affect the calving peak.

The Loskop cows were introduced from Giants Castle Nature Reserve, but it is unlikely that the "homing" of the calving date

is due to an adjustment to the local ecology. They were introduced at the age of about one month (first conception about 28 months later) and the calving period at Giants Castle is very similar to that at Loskop Dam (Abbott 1968a, b).

This seasonality, in many Southern African populations, brings the calf into the world a month or so before the end of the dry season (Roth et al. 1972, Fairall 1968, Brand 1963, this study). Fairall (1968) remarks that grazing is at its worst during calving, but feeding activity records obtained in this study show an increase in browse in the diet in June-August with the pre-rains flush in woody plants. The calf is thus born as the mother's forage begins to get more nutritious and it continues to suckle until well after the first rains, so that it is weaned onto growing vegetation, particularly grasses (as with hartebeeste: Gosling 1969). Calves younger than six months are unable to exploit the same winter browse since their horns are not long enough to be used in breaking down branches, so that a later calving season would reduce the resources available to the young the following winter. Also, the eland is essentially an opportunistic feeder and has a variety of foods available throughout the year (see Chapter 3); the load of carrying and nursing a calf in winter is therefore probably less than for an equal sized, water dependent animal with a restricted diet. Apart from the direct nutritional aspects, there is also a possibility of pheromones producing synchrony in calving and conception (see Chapter 6).

The time of birth shows a significant concentration in the dawn hours (0400 to 0800) and most births took place in the dark. This is probably a period of low activity for the eland, and so corresponds with Slijper's (1960) observations but Lindahl (1964) reports the reverse for ewes in which peaks for the onset of parturition were also during hours of darkness.

There are several possible explanations of this. Firstly, the calf is born into darkness or semi-darkness, and thus has a low visual stimulus input. This is possibly at an optimal level to favour following in a naïve calf which might otherwise be distracted or prevented from following altogether by too high a level of stimulus contrast (Andrew 1964). The daylight which soon follows then

allows/.....

allows more rapid learning to take place, with the basic level of acceptable stimulation (or stimulus contact) being raised by the calf's pre-dawn experience. Secondly, the calf would normally be isolated except for its dam, and therefore she would be the only available stimulus for orientation. Appendix 6 shows, however, that the calf could easily be led some distance by stray moving objects while the mother rested. Darkness during the initial postpartum phase may thus reinforce the isolation mechanism, by reducing the probability of an encounter which would lead the calf away. Finally, pre-dawn calving may protect the calf against the weather, since the calf is at least half dried and lying up before the heat of the day. Time spent lying and moving while still damp in the chilly spring night is also reduced to a minimum.

It is unlikely that pre-dawn births are a predator defence mechanism, since the species most likely to take eland young (hyaena, hunting dogs, leopard, lion) all show peaks of hunting activity in this period (c.f. Schaller 1972, Kruuk 1972). Kirschoffer (1963) reports that of six eland births in Germany, all occurred during the day, but with a concentration of 3 "am frühen Morgen", while Roth et al. (1972) report that the majority of births in Rhodesia occurred "at night", with the rest occurring early in the morning or else late afternoon. All populations therefore tend to concentrate births in the dawn/dusk periods, while the early afternoon is uniformly low in births. The figures are, however, sufficiently at variance with those from Loskop to suggest that there is some local or racial adaptation involved.

COMPARATIVE ASPECTS OF THE BIRTH PROCESS

At Loskop, prepartum indicators of birth (Fig 34) were highly variable inter-individually, but birth indicators for any individual were more consistent. Roth et al. (1972) and Kirschoffer (1963) also found wide variation within samples and Roth et al. (1972) remark that some cows show no external signs of pregnancy until a few days before giving birth. Roth et al. (1972) and apparently Kirschoffer (1963) are reporting on a different race, which may account for some differences, e.g. Kirschoffer's animals

gave birth in the standing position. In Rhodesia, pre-parturition ~~physical~~ changes appeared sooner than at Loskop but the restlessness seen up to two days prior to parturition at Loskop only appeared four hours before birth in Rhodesia.

Among other ungulate species, indicators of imminent parturition, such as isolation, seem to be rather similar (Fraser 1968, Lent 1974). These may however vary in extent and cause according to species. Lynch (1974) reports that preparturient blesbok were probably segregated from others by differing food requirements, and caribou may become separated by group movement (Lent 1974); other species will actually seek isolation e.g. impala (Jarman and Jarman 1974). Generally isolation is distinctive and is associated with a "hiding" period in the calf (Lent 1974).

There is usually little preparation for birth, apart from segregation, in ungulates Lent (1974). Once contractions had begun, the Loskop eland would often sniff and move around over a limited area, as in domestic sheep (Smith 1965). There might be a flow of fluid at this stage, but I never saw a cow lapping it. Spinage (1969) reports the preparturient waterbuck as being very aggressive, which might be regarded as a preparation of the birth area, and I found that, while eland cows would show a great interest in other's calves, they would sometimes be highly aggressive towards adults and yearlings. Interest in young is well documented (see Hersher et al. 1963a, Lent 1974), although actual stealing of young may be a result of high planes of nutrition and would not occur under natural conditions (Fraser 1968).

Labour in eland was in the form of convulsive waves of contraction passing over the whole body, which appears to be the same for other antelope (Kirschoffer 1963). Other animals reacted characteristically to the female, as in bison (Fraser 1968). Cows' vulvae were sniffed and nosed by others during birth, but they strongly repulsed such approaches if they could.



RECOGNITION OF THE CALF BY THE DAM

The recognition of the calf by the mother probably has a much more clearly defined sensitive period than the reverse situation (Lent 1974, Fraser 1968, Scott 1968). In domestic stock, if the birth and aftercare is allowed to take its normal course, the dam will become attached to the neonate very rapidly, e.g. goats in five minutes (Klopfer and Gamble 1966). In sheep and goats attachment of the dam to calf depends on maternal isolation and the maintenance of contact between offspring and dam (Hersher et al. 1963b) and is probably similar for eland. F's "adoption" of T's was probably the result of T's being present at F's birth and providing similar stimuli to the neonate.

Hersher et al. (1958) conclude that there are two stages in the maternal bond formation:

- (i) Learning of the calf's characteristics.
- (ii) Specification of the maternal bond.

Klopfer and Klopfer (1966) and Fraser (1968) suggest that the emergence of maternal behaviour and the specification of the bond is probably connected with the presence of oxytocin in the mother's bloodstream. This seems likely in eland, since maternal interest in calves is a very distinctive short term change immediately prior to parturition. The only early separation and reunion results available at Loskop were those from F and her stillborn calf. In this case, she very rapidly fixed her maternal behaviour to the calf and refused to nurse any other, so that it was not possible to distinguish the two phases, both of them occurring within half an hour. This compares with 20 - 30 minutes in sheep (Smith et al. 1966), 12 hours in mouflon (Tschanz 1962), 5 minutes for goats, 1 hour for caribou and 6 hours for pronghorn (Lent 1974).

Klopfer and Gamble (1966) conclude that scent is necessary for the specification of the bond, but not for the appearance of maternal behaviour. Neonate calves are frequently relatively scentless themselves (Lent 1974) but have the birth fluids and membranes attached to them which are probably individual-specific and which may be important in specifying the bond (Hersher et al. 1963b; Smith

et al. 1966, Tschanz 1962, Smith 1965). Eland cows would sometimes show the licking response to the rear of a strange calf, then sniff its nose and horn it away. If perianal glands are involved in individual recognition as in mouflon (Tschanz 1962), they are less important and less precise than the breath or the facial scents. Licking and chewing the birth fluids and membranes does not put the female into close gustatory and olfactory contact with the calf, but it seems that the fluids only provide the initial grooming and acceptance stimulus, as in goats (Hersher et al. 1963b). This stimulus may not be very specific for eland. For example, several females showed maternal behaviour towards Sally's calf (Appendix 6), even though most of them had calves at least one month old.

Scent is certainly the initial recognition factor for most ungulate mothers (Fraser 1968, Lent 1974), but the subsequent development of recognition may vary. Eland would check calves naso/nasally or naso/anally, occasionally leaving their own and sniffing a few others before returning. This apparent comparison of odours is also found in other species e.g. caribou (Lent 1966) and sheep and goats (Hersher et al. 1963a) but I never saw any definite trailing or long distance sniffing in eland. Visual recognition may also be important for eland. One cow, showed persistent approaches to a calf very similar to her own when it was suckling. The mother would step away and try to protect the calf, but the intruder would not leave until she had sniffed the calf closely, whereon she would horn at it and turn away (compare F. Smith 1965, and Lindsay and Fletcher 1968, for sheep). Espmark (1971) records that reindeer cows recognize their calves by calls, which eland also seem to do, but other species such as roe deer (Kurt 1968) seem to use the calls more as a general initial orienting stimulus, with recognition following on closer contact.

As noted earlier, the early separation of the dam from the group (in many species) is probably more important for the dam's attachment to the calf than vice versa. This separation is often reinforced by maternal aggression (Hersher et al., Fraser 1968, Lent 1974) or by actions such as nudging the calf into a position which restricts its movement. Neither of these activities were pronounced in the eland cows, except in the post-suckling stages.

Prior to this, the cows would sometimes keep near their calves by following them and occasionally be calling, but would also allow the calves to stumble off into the night within an hour of birth and to go at least 30 metres away, i.e. the length of the paddock, without showing anxiety. If the reactions of F to her stillborn foetus are representative, then attachment would be complete by the time the calf is standing, but the observations suggest that the behaviour of the eland is adapted to calving in isolation where there is little danger of a "distracting" stimulus affecting the course of attachment.

SPECIES AND MATERNAL RECOGNITION

Several authors have remarked on the similarity between imprinting as seen in nidifugous birds and the initial attachment of dam and calf (e.g. Hinde 1961, Hersher et al. 1963a, Schneirla 1966, Bateson 1966). In fact, Sluckin (1970) gives five criteria for classical imprinting, each of which is seen in the approach behaviour of the neonate eland: distress at separation; recognition at reunion; choice of the familiar object; "run-to-mother" when presented with strange objects; willingness to work for reunion. The analogy between ungulates and birds is not, however, complete, since calves have in suckling a powerful stimulus reinforcing the bond which is not found in chicks. Nevertheless, even after the calf is suckling regularly, its "following" behaviour is triggered by very similar stimuli to those most effective in eliciting approach in chicks (compare Walther, 1964a - with Bateson, 1966). Bateson (1971) remarks on the probable importance of multi-modal stimuli in classical imprinting, and it is interesting to note that the first oriented movements of the calf are in response to the dam when she is presenting the calf with three stimuli, each intermittent, at a fairly low level and characteristic of the dam (grooming, contact-calling, the sight and movements of the head as she licks).

The calf's initial active seeking behaviour was very generalised, in that apparently a general level of stimulation was sought. Calves struggled when not groomed, but would calm when their mothers licked them. After a while, grooming by itself was insufficient to calm the calf and presumably the level of stimulus sought by the calf had changed. If grooming was resumed after a pause

it would still stop the calves' movements, which indicates that they were probably seeking a particular level of stimulus contrast (Andrew 1964). This rather general concept describes fairly accurately what happened when the calf had only a limited number of responses and a restricted sensory input. Once the calf was on its feet, however, only the sudden termination of prolonged grooming bouts could be attributed directly to a lack of stimulus contrast. Otherwise, the increased repertoire and sensory capabilities of the calf prevented an accurate assessment of the contrast perceived.

In eland, early teat-seeking behaviour could not be distinguished from approach and following, and it was only after the second day of life that nudging disappeared from the sequence: orient, approach, nudge. After this, calves would still approach strange objects, but would only direct nudging and suckling to other eland. The range of stimuli eliciting approach also rapidly become restricted, although more slowly and to a lesser extent than in nudging. Orientation eliciting stimuli, if affected, were reduced even less than approach eliciting stimuli.

While the actual mechanism of this restriction (Fox 1970) is unknown, the effect is to rapidly limit the eland's social behaviour to other members of its own species. Species recognition seemed to be at least partially present by the end of the second day as shown by flight and grouping tendencies and by reaction to social approaches. This corresponds roughly with Gilberts (1974) critical period of the first 24 hours for fallow deer.

Species recognition, therefore, is highly analagous to imprinting in nidifugous birds. Maternal recognition, on the other hand, seemed to depend on the acceptance response of the female, as in cattle (Schloeth 1958), although calves were able to distinguish their dam's calls at the age of about one month (c.f. Espmark 1971).

SUCKLING AND THE MOTHER/INFANT BOND

As with roan (Joubert 1970), caribou (Beregrund 1974) and some other ungulate species, the mother/infant bond in eland is apparently very loose, since little interaction except for suckling occurs between mother and calf. This apparently limited interaction may, however be very important both for the mother and calf, as can be

seen from the reactions of mothers on separation from their calves (Fraser 1968, Lent 1974). Calves were more easily disturbed when separated from their mothers. A one week old calf was brought into captivity with its dam after living in the wild from birth onwards and at the age of one month it was still showing signs of panic when disturbed and separated from its dam, even though it was with a group of calves which had been in captivity for almost one year and which were completely untroubled by all human activities. If it could see her with other adults in the larger paddock, it would eventually work itself into a frenzy and hurl itself against the fence in an attempt to reach her; once the two were together, there was no sign of any unusual interaction between them, but the calf would be much calmer, would resume moving with the calf group and ignore human activities just like the others.

Suckling attempts are closely linked with mild disturbance in many ungulates, but Lent (1974) rejects the possibility of reassurance being gained from contact with the mother, since a disturbed cow would be unlikely to nurse. He concludes that the alert posture of the cow is similar to that of nursing and that this is the cause of suckling attempts. While this may be true of actual suckling, it would seem from the above that in the case of eland the calf is capable of being disturbed in its own right and of seeking out its dam (for comfort) (or possibly just an adult rather than calves) in a fashion similar to Harlow's monkeys (1959).

Young ungulates are apparently capable of very rapid learning in a general fashion (Moore 1958) and of modifying their "innate" teat-seeking behaviour as a result of experience (Selman, McEwan and Fisher 1970, Stephens and Linzell 1974). The possibility of attachment to the dam being connected with, or at least facilitated by successful suckling has already been mentioned.

In addition, with "hider" species (Lent 1974) the suckling rhythm is more pronounced and the space/time schedule of the dam and calf may be governed by this to such an extent that it forms the basis of all early socialization in the calf (see detailed descriptions in Bubenik 1965 and Joubert 1970, also Leuthold 1971a). The captive eland at Loskop had a fixed schedule imposed on them, but

the ease with which they adapted to it indicates that a very similar schedule probably applies in the wild, and this was borne out by the few observations on suckling made in the field.

As with Kurt's (1968) roe deer, suckling was very frequent during the "sensitive" period - in this case probably the first day or so for species identification (see Leuthold and Leuthold 1973). It therefore appears that, although other reactions may be involved in initial mother/infant bond formation, suckling and the regime imposed by it is very important in reinforcing and developing the relationship between the two animals, and that this influence is not limited to the actual rewards supplied by obtaining milk.

CHAPTER 8

CALF BEHAVIOURAL ONTOGENY AND SOCIALIZATION

LYING OUT

During the lying out phase, the captive group calves already showed highly social tendencies. If one calf was already lying out, other calves would join it either to lie out in the same place or else to lie there ruminating. There were several places in the paddock which were initially chosen for hiding by newborn calves but these were soon abandoned when the neonates began to follow the lead of others. The result was that all of the calves used one "traditional" lying out place (Fig 40). Although the conditions of captivity did not allow the lying out behaviour to appear in full, several subphases could be distinguished:

- (i) The first day or two, when the calf initiates lying out and selects the place according to purely physical criteria. It moves away from the group but once it has lain down will accept the presence of another individual.
- (ii) The calf begins to follow the lead of others more and more, both in leaving the group initially and in selecting a lying out place. In the captive group, this subphase overlapped with the following one and lasted until the end of the second week. In the wild, its appearance naturally depended on the presence of other calves in the group and their readiness to lie out at the same time as the neonate.
- (iii) The calf does not leave its peer group, but instead adopts the "lying out" sleeping posture within the group. The calf still sleeps for long periods, as in true lying out, but it is possibly using the herd as "psychological cover". This phase overlaps the previous one and merges indistinguishably into full participation in peer group activities. In the field it appears to begin in the second week of life if the calf is in a large nursery group; it may not appear at all if the group is small or if all the calves present are too old to share the lying calf's activity cycle and thus to provide a stationary "crèche" subgroup within the herd.



Figure 40. "Traditional" lying out in captive eland at Loskop Dam Nature Reserve. September 1972. The two nearer calves are less than four days old, while the furthest calf is two weeks old.

The neonate is therefore slowly absorbed into the herd as a result of its increasing sociality and possibly only secondarily as a result of a decreasing tendency to hide. The actual progress of the absorption depends on the calf composition of the associated group.

Since the dams did not have free access to the captive calves at all times, it was not possible to determine the importance of the mother in initiating or terminating a bout of lying. Even when the mothers were with the calves, however, it was the neonates which chose the time and place of concealment. Luring of the calf into a suitable place, as described by Walther (1964a) for the greater kudu, was observed, but generally there appeared to be no attempt at all by the mothers to determine the lying out place. Disappearances of the mother or companions triggered lying, as Leuthold and Leuthold (1973) found for lesser kudu.

Termination of the lying out bout, on the other hand, could occur at the initiative of calf or dam. Again, this depended to some extent on the physical and social situation. On occasions in the wild, a cow was seen to leave the nursery herd at the beginning of the evening move, go directly to her calf and stand over it, whereon it rose to suckle. She would not rejoin the herd during daylight (i.e. for up to another hour). It seems likely that the cows would not abandon their calves and travel the 1 - 2 km sometimes involved in the evening move. On the other hand, cows called to their calves from the stationary herd, and lying out calves also joined their dams spontaneously, so group movements only partly affected the termination of lying out. In addition, calves would sometimes terminate the lying period on being approached by conspecifics other than their dams, although probably this only occurred when the calf was ready to move in any case (c.f. Walther 1964a).

The mother would sometimes approach a lying calf, groom it for a while, then leave it again without the calf showing any response. Whether this behaviour tended to occur at the beginning of a bout of lying is unknown, but it is possible that this is a form of "testing" of the calf's willingness to lie, as described by Walther (1964a) in other tragelaphines.

The reaction of the calf to approach and contact when lying out varied with age. I could approach and touch neonates with impunity, but after the second day of life they would only allow me to approach and would not let me touch them. The flight distance increased with age and varied from one individual to the next. Lying in groups seemed to facilitate freezing, since even calves just leaving the lying phase allowed me to get to within 0,5 m when they had a younger companion.

The selection of the lying out place was apparently on the basis of very similar criteria to those given by Walther (1964a) for Tragelaphus species. They included:

- (i) "Something vertical" e.g. a tree, a fence, a corner.
- (ii) "Something shaded" e.g. an overhanging bush, tree or fence.
- (iii) Slope - most of the places selected were on the uphill side of the paddock.

In the field, the calves seemed to lie out at the fringes of thickets or of small stands of dense vegetation, or in grassland/woodland ecotones but this may be merely the result of the calf's criteria being easily satisfied in these areas with out necessitating much penetration into dense cover. Kurt (1968) found that for roe deer, cover actually seems to release lying out, but this is not certain for eland.

Cows were aware of where their calves were lying, and on one occasion, a cow left the nursery herd 300 m away to attack me when I was near her concealed calf. Leuthold (1971a) found that not only did lesser kudu mothers know where their calves lay, but also that place seemed to be very important in identifying the calf to the mother.

REACTIONS OF OTHER INDIVIDUALS TO THE NEONATE CALF (Fig 41)

Generally, the captive group calves showed intense and somewhat aggressive interest in the neonate, approaching (usually in groups) sniffing, and attempting to chin or mount it. These calves often suddenly jerked themselves away and trotted off from the neonate as

Reactions of other individuals to the developing eland calf

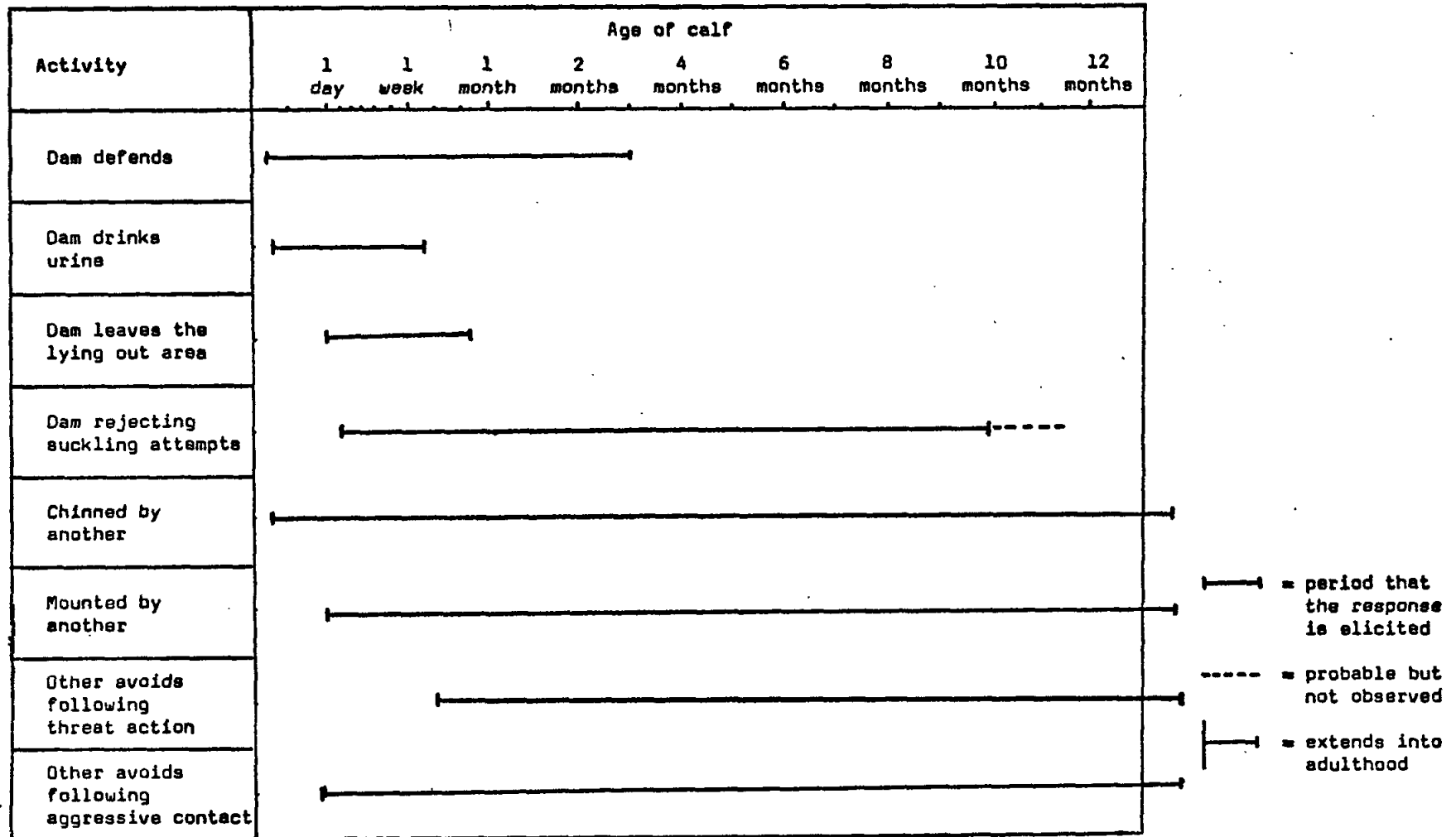


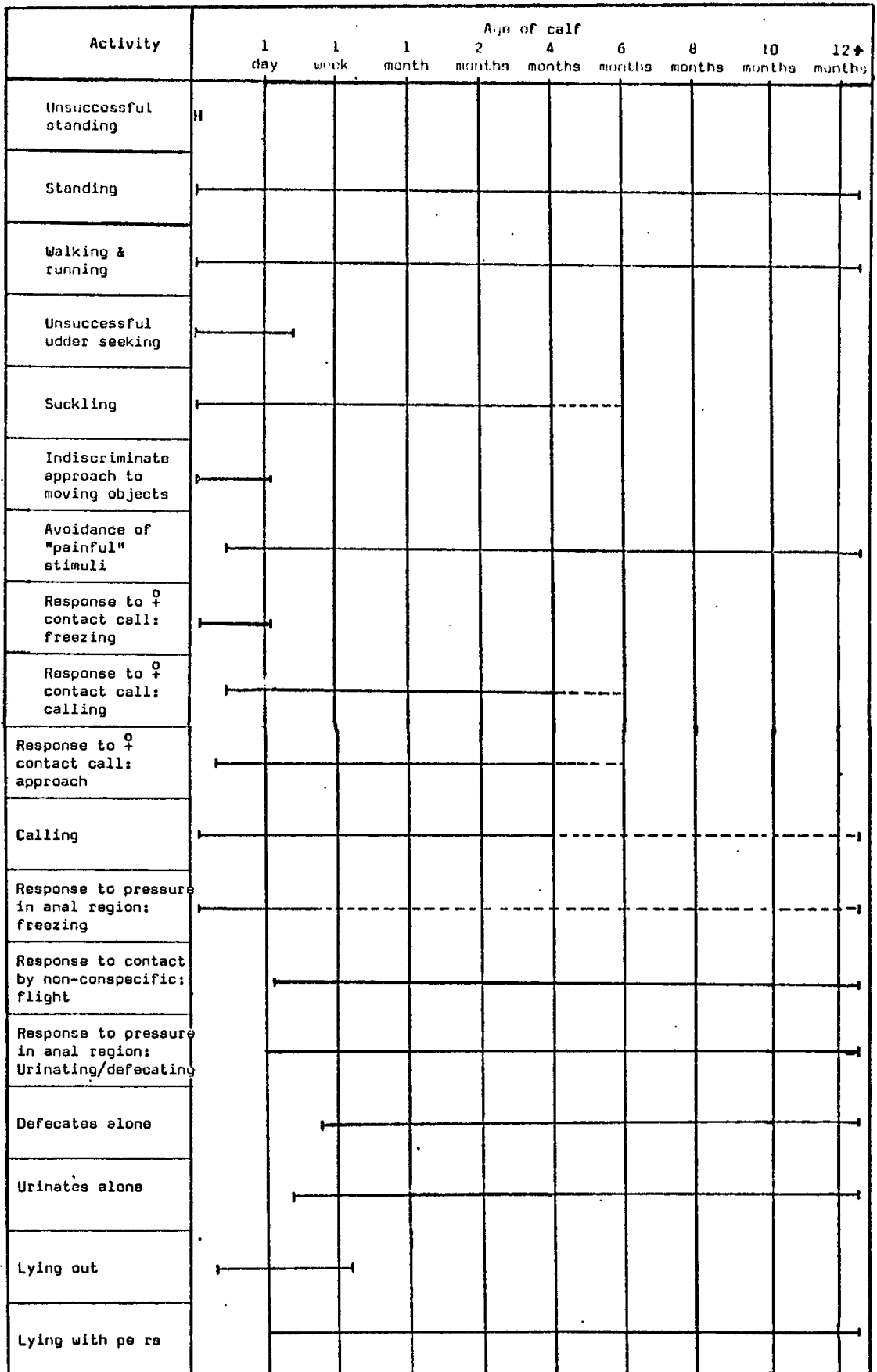
Figure 41. The reaction of other eland to the developing eland calf at Loskop Dam Nature Reserve. June 1972 - May 1974. The periods between the major time divisions (e.g. one day - one week) are linear.

if slightly afraid of its failure to respond to them normally. The most usual adult reaction was to approach and sniff the calf at least once, then to show varying degrees of rejection such as turning away, horning at it, or trotting off. A few individuals, usually with calves less than one month old, showed more positive responses, grooming or even nursing it although this was rarely seen for calves over two days old. Figures 42 - 46 show that the neonate receives very intensive social attention for the first day of its life, and that this rapidly diminishes during the first month. This attention comprises aggressive approaches e.g. sniffing and grooming. The aggressive component becomes more pronounced during the first week mainly as a result of the calf's rather indiscriminate suckling attempts. The calf seems capable of responding only to a threat which is very clearly directed towards it, and this continues for the first few months of life (Fig 46). Adult animals seemed more or less to ignore calves and to leave it up to them to get out of the way or else to be brushed aside. This was also recorded as contact aggression and contributed largely towards the high levels noted.

Grooming received from adult females is normally a mixture of maternal grooming patterns and normal inter-adult patterns. The face and forequarters are the main centres of attention, although the anus may also be licked. Calves groom each other and the neonate rather differently, concentrating on areas where there is either long hair e.g. the "mane", or else where there is a projection of some sort e.g. tail, ears, dewlap, and often chewing at them rather than licking. Olfactory investigation is mainly directed towards the calf's nose (Fig 44) although the adult cows, especially the mother, also showed interest in the calf's anal region.

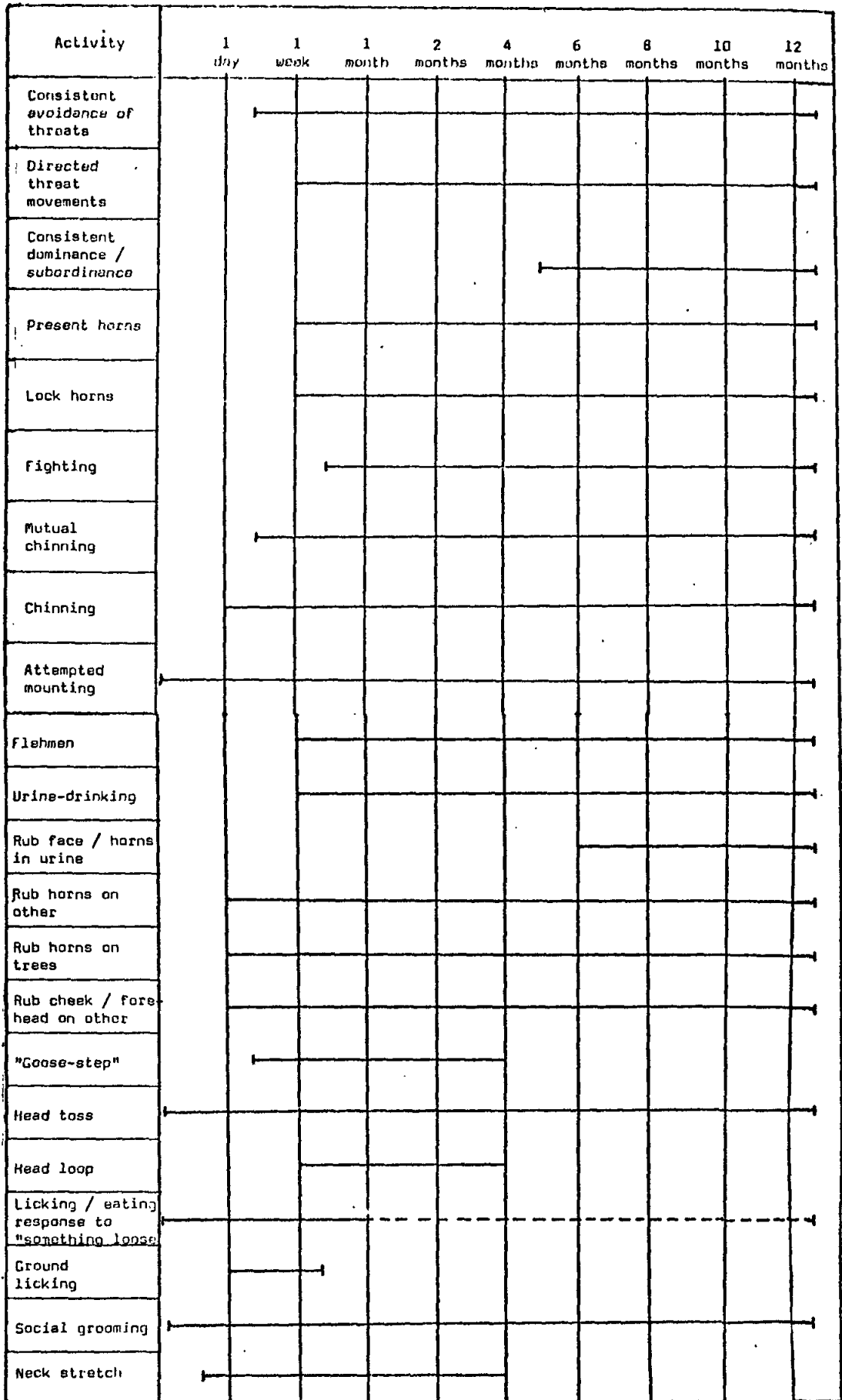
THE EARLY APPEARANCE OF "SEXUAL" BEHAVIOUR PATTERNS

Figures 42 - 46 show that several behaviour patterns associated with mating in the adult are among the first social behaviours shown by the developing calf. The most striking of these is mounting, but flehmen, chinning, a form of driving, and urine drinking all appear



— = period covered by that phase of the behaviour
 ----- = not observed but probable

Figure 42. The development of behaviour in captive eland calves at Loskop Dam Nature Reserve (i). June 1972 - May 1974.



— = period covered by that phase of the behaviour
 ----- = not observed but probable

Figure 43. The development of behaviour in captive eland calves at Loskop Dam Nature Reserve (ii). June 1972 - May 1974.

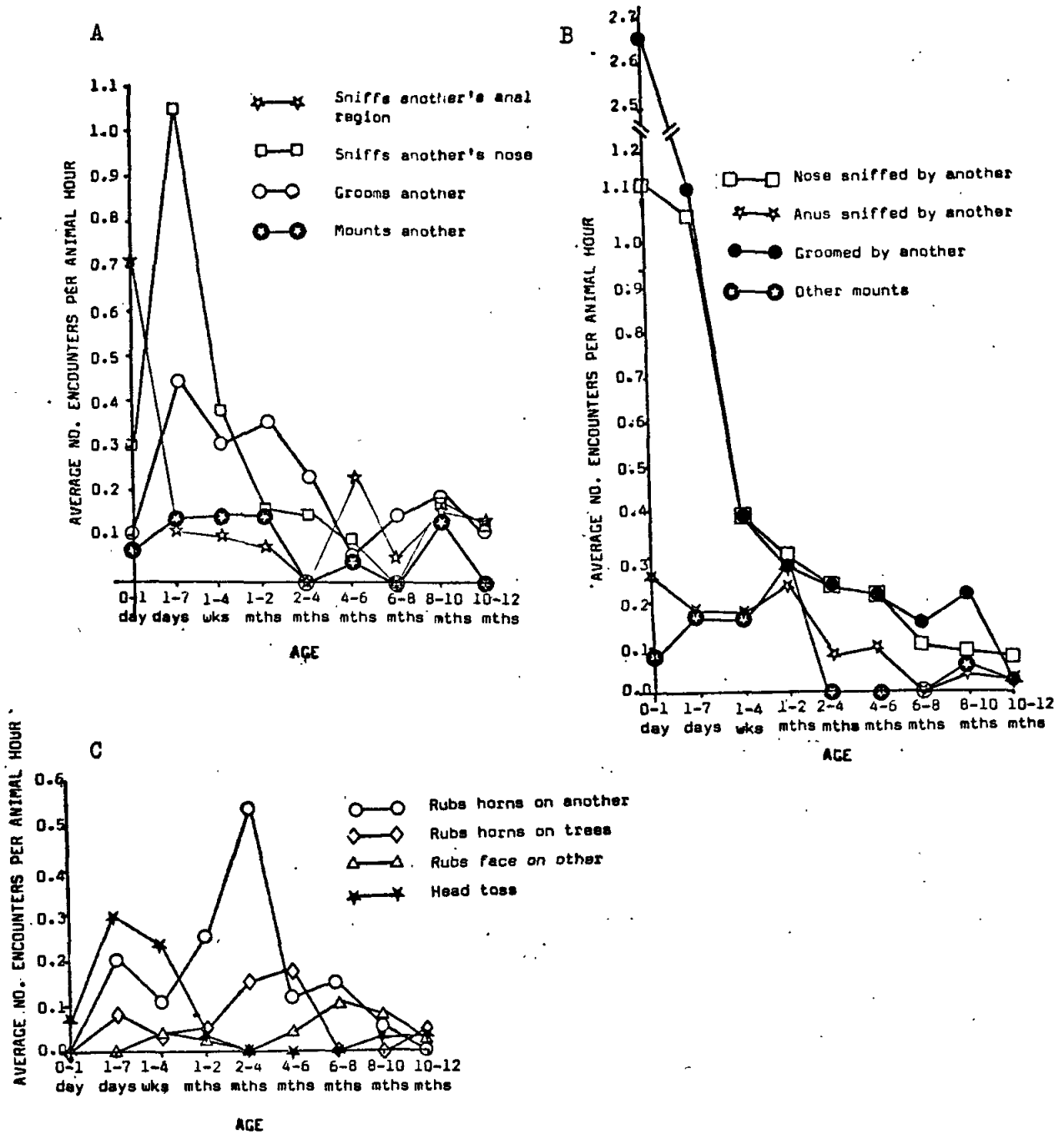


Figure 44. The development of general social behaviour in captive eland calves at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. Investigation and main forms of body contact with the calf as the active partner.
- B. Investigation and the main forms of body contact with the calf as recipient.
- C. The use of the head and horns by the calf.

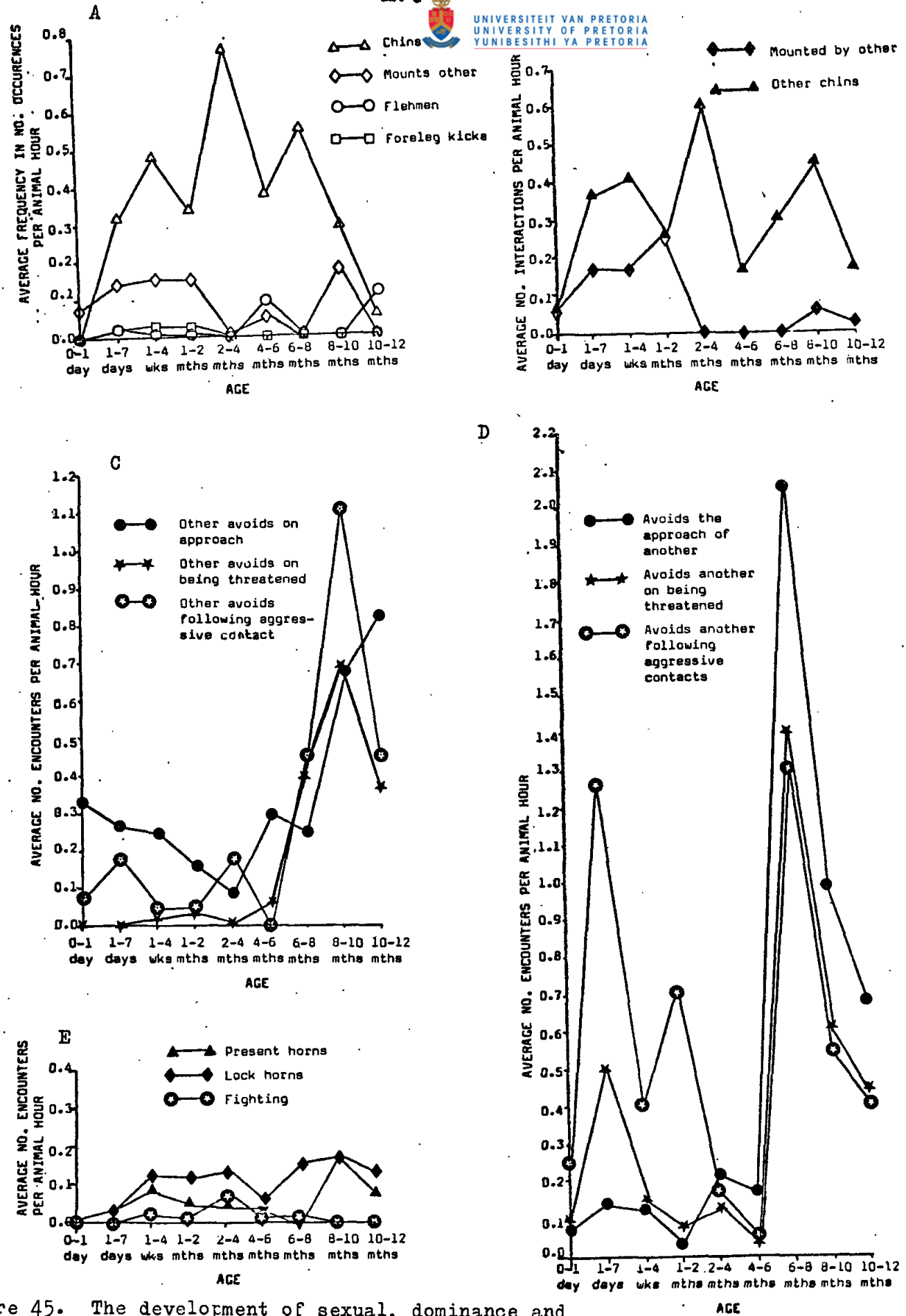


Figure 45. The development of sexual, dominance and aggressive behaviour patterns in captive eland calves at Loskop Dam Nature Reserve June 1972 - May 1974.

- A. "Sexual" behaviours with the calf as the active partner.
- B. "Sexual" behaviour with the calf as recipient.
- C. Dominance interactions with the calf as the initiator.
- D. Dominance interactions with the calf as recipient.
- E. "Challenge" activities by the calf.

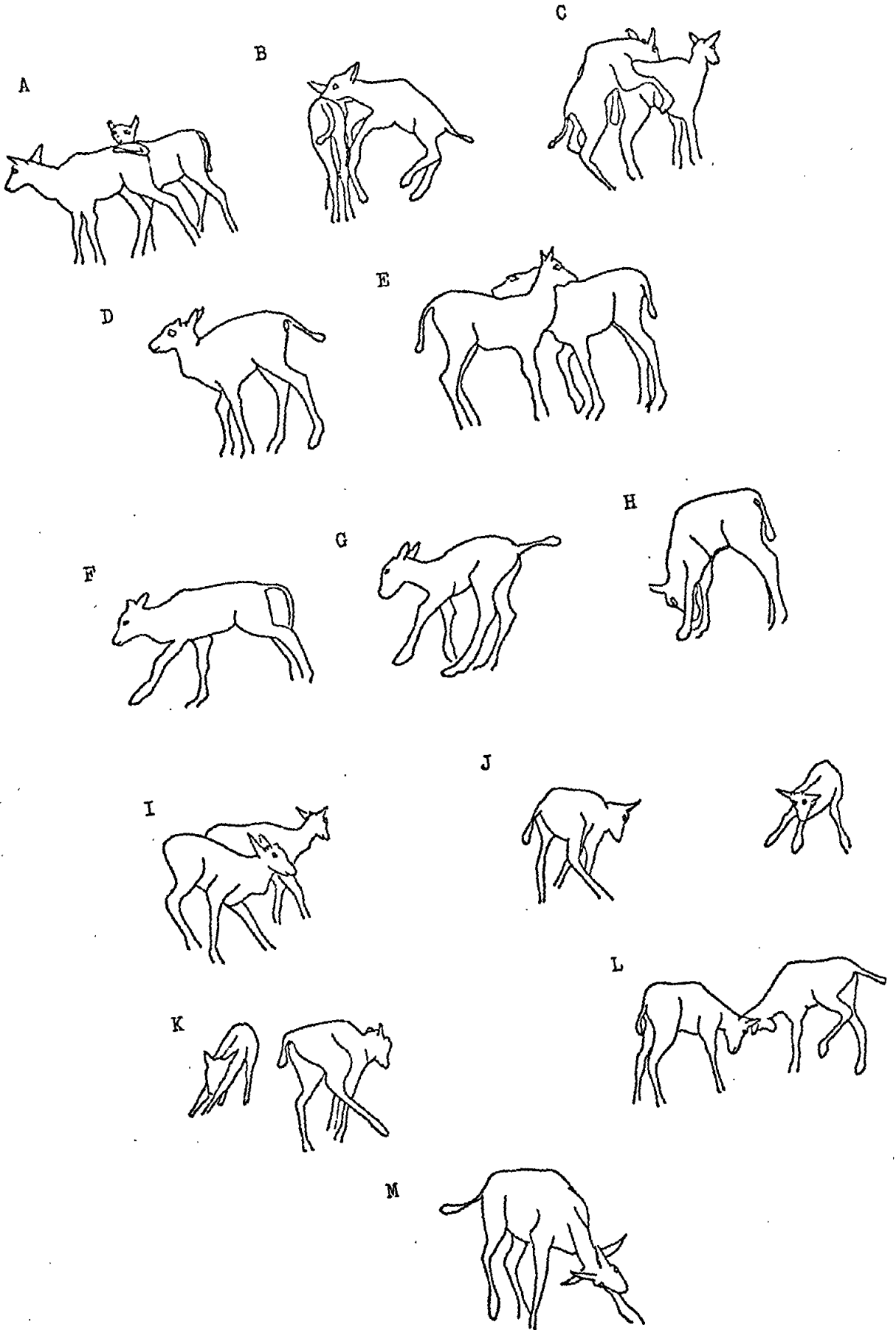


Figure 46. Early "sexual" and aggressive behaviour in eland calves at Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. One calf chins another's rump while watching the observer.
- B. Mounting from the side in a 12 hour old calf.
- C. Mounting from the rear ("correct" orientation) in a two week old calf.
- D. Chinning intention stance - often sufficient to cause the recipient to move.
- E. "Mutual chinning", resembling neck wrestling - the calves appear to push downwards with their chins. Not seen in adults.
- F and G. The foreleg kick, given spontaneously by calves of various ages.
- H. The foreleg kick combined with a horning movement. The kick is just finishing, while the head is still lowered.
- I - L. A play fighting bout in 6 week old calves.
 - I. The slightly younger calf dashes about, past the older one, kicking out at it with its hindlegs.
 - J. They square off after a period of chasing.
 - K. They dash towards one another and kick out with their hindlegs as they pass flank to flank.
 - L. A more normal horn engagement follows.
- M. Spontaneous horning movement in a 5 month old calf.

within the first week. Even in the adult, none of these is restricted purely to male/female relationships, but instead appear either without any obvious cause or else as a form of aggression. The description of these activities as "sexual" is therefore a convenient label and is not a motivational classification.

Flehmen appeared early in the second day in one bull calf, as a response to the scent of another (female) calf's urine. It normally occurred at a very low level in the captive group calves and it is not possible to say how typical this early appearance is. In one instance, it was evoked by sniffing fresh eland dropping, but otherwise it was limited to fresh urine; this is rather different to the situation in the adult where flehmen could appear in other contexts. The accompanying behaviour was highly variable but seemed to be basically the same as that in the adult i.e. approach the urinating animal with head and nose out, sniff the urine and drink it, stand rigidly with the head well up and nose above the horizontal, and flehmen. Apart from a single suspect case, I did not see a calf induce any other individual to urinate by chinning it and then to drink the urine and flehmen, which is the more complete adult bull version.

Chinning, involving lifting the chin over some part of the recipients' body and pressing downwards, was seen in a variety of circumstances but the response of the partner was usually to move away. The only exception, "mutual chinning", is treated separately. Chinning in adults occurred mainly, but not exclusively, in sexual preliminaries, but it had much more general application in the calves, who would apparently use it to drive the other individual away. Up to the age of six to seven months, the recipient's response was always either to step aside or else walk off, but after the dominance hierarchy had been established, the younger calves regularly used this walking response to obtain access to food by chinning their superiors at the food trough. At first, the superiors moved away, allowing access to the trough, but after a month or so the superior would move away from the chinning animal but retain the use of the trough, and would often threaten the other. This used chinning in a non-sexual context accounts for the high rates recorded in the first to eight months (Fig 45). Even the youngest

animal/.....

animals avoided chinning, and this persisted into the adult stage except for the special case of oestrous cows.

The preliminary stance for chinning involves lifting the head slightly up, and standing in a "hunched" posture as if to mount. This posture was not normally as pronounced as the pre-mounting posture, especially in older calves and adults, but was very distinctive (Fig 46D). It was sometimes employed by younger calves when they crowded up against one another, or else when they were in the midst of a group whose members were moving rapidly and closely together. One of the eliciting stimuli for pre-chinning intention movements seems, from these and other observations, to be the sudden presentation of a conspecific's rear or back very close to the calf and in its path.

Chinning retained its coercive character less successfully in another context. It was frequently used by weaning calves on their dams following rejection, when they would lift their heads and rub their chins along the cow's flank (Fig 47). This behaviour was apparently related both to chinning and to the soliciting/placatory vertical nose lift, since the calf had to lift its chin up into the vertical position in order to be able to chin at all. It was not very successful in inducing the cow to give milk, but it did lead to intensive bouts of calf/dam grooming.

Mounting and its preliminaries occurred in similar situations to chinning, except that the general level of excitement of the calf seemed to be higher, e.g. on the introduction of a stranger. As before, all animals moved away on being mounted, and would also move off from the pre-mounting stance after the first month.

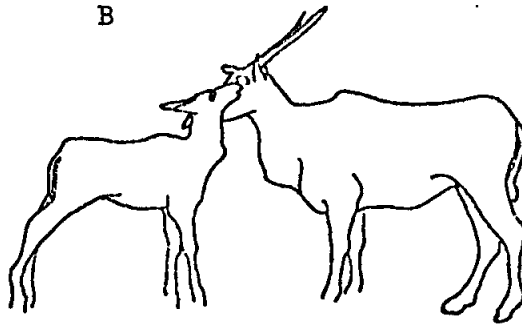
The orientation of both chinning and mounting was highly variable at first but soon concentrated around the rear of the recipient, i.e. the "normal" position. It was also affected by other factors, such as the relative positions of the two individuals when the behaviour was elicited, and the position of objects of interest - calves would move so as to be able to chin the partner and to watch these.

Apart from the situations where there was an obvious releaser for chinning and mounting, the calves occasionally chinned others and then followed in the normal calf single file when the recipient moved away. This movement usually led the calves to some focus of interest

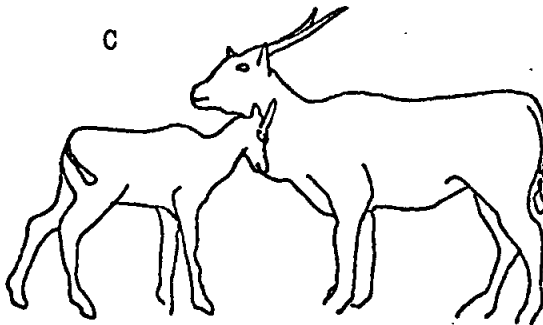
A



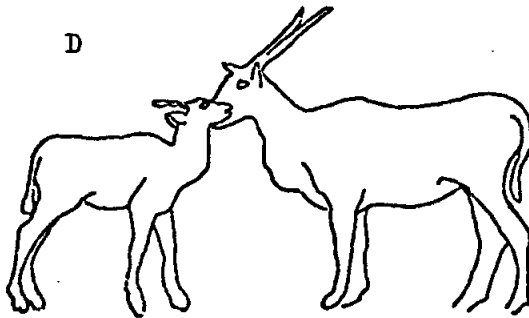
B



C



D



E



Figure 47. Reactions of eland calves to adults. Loskop Dam Nature Reserve. June 1972 - May 1974.

- A. Orientation to the dam's head as she feeds.
- B - E Interactions following the rejection of suckling.
- B. Rubbing the cheek on the dam's face.
- C. Rubbing the forehead and horns on the dam's neck.
- D. Licking the dam's face.
- F

which was apparently determined by the orientation of the lead calf when it was chinned, although whether the rear calf was driving the other towards this point is uncertain. Such behaviour was seen more clearly in the T. derbianus yearlings, and in this case the heifer drove the young bull towards people looking into the enclosure.

From all of the above, it may seem that infant chinning and mounting has very little connection with later sexual activity, but there were several instances which showed that even at this stage, these basically aggressive activities are also partially sexually motivated.

In one case, a yearling bull was feeding with the rest of the captive groups and a cow. Ignoring all other troughs, he went to the cow and stood behind her and sniffed her vulva then chinned her, causing her to urinate, and flehmened on drinking the urine. He then drove all the other yearlings away. When the cow had finished feeding at the trough, however, he went to it and fed, ignoring the cow completely. He had access to several other troughs at all times during this exchange, all of which contained the same fodder mixture.

In the second case, a four month calf was observed attempting to suckle on a lactating female. It was rejected, went round to the dam's rear, and rubbed its chin along the side and back of her body. The cow urinated and the calf drank the urine, gave a flehmen, then urinated in its turn.

In the first case, some mild sexual interest was probably involved in the exchange, as well as the desire to feed at that trough. In both cases, an incongruous sexual sequence was probably initiated by the use of mating activities (the "tending" position and chinning respectively) in an originally non-sexual context (c.f. Lind 1959).

DEVELOPMENT OF AGGRESSION

Apart from the aggressive use of mating activity components, the young calf also used a similar repertoire of threats to that seen in the adult. The basic movements involved in these threats (head lowering, nodding) appeared within the first few days of life and were sometimes treated as threats by other calves. The calf itself, however,

seemed/.....

seemed to perform these actions almost accidentally and often seemed surprised both at the action itself and the results. Behaviours which emerged in this way include head toss movements, a violent head looping movement resembling the horn sweep and head nodding. These actions were usually first seen without any noticeable eliciting stimulus, often when the animal was alone and walking from one place to another. In the older calves and the adults, the complete actions were also normally performed while the animal was moving from one point to another, but were directed towards a conspecific which was either in the way or which was trespassing in some other fashion. The eliciting stimuli for and the development of coordination of these behaviours is uncertain, but it is interesting that they constitute the basis of most of the threat actions seen in the adult eland.

Within the first week (Fig 44) the calves showed a tendency to rub their horns on trees and on conspecifics. This behaviour appears from the first to be a coordinated one and to be used by the calf mainly to ease irritation in the developing horns. The calves would often have bouts of scratching the horn bases against twigs, then going over to another calf and rubbing their horns against it. The conspecific appears to be a preferred object for this rubbing (Fig 44), but would be very unsatisfactory as a scratching post. The horn rubbing is directed initially to all parts of the other's body, but becomes localised to the head and neck region, which are presumably the most effective areas for scratching. Often, but by no means always, the recipient of the rubbing would turn its head to the other and they would stand head to head twisting their foreheads so as to bring the horns together. It was difficult to distinguish between low level play fights and horn rubbing at this stage, since the one frequently passed into the other.

My relationship with F's, a female captive calf, from the age of one month onward is of interest here. She initiated it by tapping me on the head with her forehead as I was sitting looking down at the ground. Subsequently she came to rub her horns on my legs several times before allowing me to scratch her between the horns. After this she would approach me in the normal calves' play and grooming posture (head low, nose forward, direct head-on approach), lower her horns into the "present horns" position, then stand while I scratched

the bases of her horns. If I stopped, she would place her horns against my legs and push and twist as if "fighting" with them, at the same time rubbing the horn bases up and down. If I resumed scratching, she would immediately stop, while if I did not, she would transfer her rubbing attentions to a conspecific and sometimes a play fight would result. On some occasions, she however, would not stop pushing when I scratched her and instead fought vigorously. It was not possible to determine which behaviour she would show when she first approached, and from the reactions among other calves to sudden onslaughts following a normal approach/invitation, they too were sometimes unable to tell what their companions intended.

She would also approach me and receive scratching calmly after going to several companions and presenting horns in the typical play fight invitation.

Horn rubbing both on companions and on trees drops considerably during the emergence of the dominance hierarchy at about 6 - 8 months (Fig 44, Table 21).

Coordinated adult fighting behaviour appeared as early as the first month (Fig 45). This was represented by the sequence: approach - present horns - lock horns - horn wrestle - turn aside, but was neither as clearly defined nor as vigorous as in adults. It was usually preceded by a head-out invitation approach rather than by a "proud" challenge. Sequences were rarely completed and quite often the "present horns" was not visible as a distinct posture but instead the approach slurred over into the horn lock.

Fighting continued at about the same frequency for the first fifteen months of life. After this time it became less frequent amongst heifers and the majority of aggressive interactions were limited to threat and submission actions. In the field young bulls showed interest in the pre-rut fighting at the end of their first year, often attempted to initiate fights with older bulls, and moved with the all male groups found at this time of the year; adult aggressive behaviour was therefore taken to be established by the age of 18 months for both sexes.

ESTABLISHMENT/.....

Table 21 : The Direction Of Aggression And Sex In The Eland Calf At Loskop Dam Nature Reserve
 June 1972 - May 1974.

Month	Number of times that an animal of the age class was involved in aggressive interactions with another calf	No times an animal of age class involved in "sexual" interactions with another calf	Frequency of aggression between calves in interactions/ animal hour	Frequency of sex * behaviour between calves in interactions per animal hour	Direction index for aggression	Direction index for sex
0 - 1	39	195	0.214	1.071	0.462	0.467
1 - 2	13	87	0.210	1.462	0.692	0.426
2 - 3	17	7	1.417	0.583	1.000	0.714
3 - 4	52	16	2.215	0.675	0.962	0.837
4 - 5	27	8	0.718	0.212	0.852	0.125
5 - 6	7	3	0.545	0.273	1.000	0.333
6 - 7	11	10	0.550	0.500	1.000	0.200
7 - 8	17	8	1.360	0.640	1.000	0.500
8 - 9	74	23	1.722	0.547	0.933	0.131
9 - 10	128	23	2.190	0.394	0.783	0.178
10 - 11	217	23	4.375	0.485	0.812	0.131
11 - 12	62	19	1.067	0.316	0.855	0.473
12 - 13	23	4	2.109	0.381	0.749	1.000

* ("Sex" includes only chinning and mounting)

ESTABLISHMENT OF THE DOMINANCE HIERARCHY

The direction index in Table 21 was obtained by dividing the number of interactions which followed the direction of the hierarchy (i.e. the ones directed to younger or subordinate individuals) by the total of all interactions of that type in that period. The index is therefore analagous to Rowell's (1966) "direction consistency index" except that here the criterion that at least 100 observations should be made for any one index has been abandoned, since the trends of the indices rather than the absolute values are important. Also, the rank order here was initially based on the ages of the calves, although this seemed to correspond only partly with the final dominance rankings of the yearlings.

Although aggressive interactions occurred mainly in one direction between given pairs of individuals after the first two months of life (Table 21) aggression between calves remained generally at a low level until about the seventh month, when calves began to use aggression in the same way as adults. Prior to this, access to resources was obtained mainly by chinning and mounting. This earlier phase was marked by a less possessive attitude on the part of the calf, with troughs and foodplants being freely shared and with the animals often feeding mouth to mouth.

Adult-like aggressiveness appeared very quickly over a period of about one month when the older calves in the population reached the age of eight months. It involved younger animals as well, insofar as they now began to receive aggressive attention from their elders, and this caused the high levels of aggression participation in the 2 - 4 month age classes and in the 7 - 8 month class. The structure of the group when the dominance hierarchy became effective was: two calves of eight months, (T_8' and F_8'), one of seven (A_7') and one of six (S_6') months; shortly afterwards, a two month old calf (T_2) was also introduced, together with L who was assigned the same age as T_8' and F_8' on the basis of his horn length and general size.

Figures 44 and 45 reflect the change in relationships between individuals. Not only is there an increase in the total number of interactions, but also the nature of the interactions change. For the first week or so of life, calves seem incapable of responding

to threats, and adults drive them away mainly by use of "contact" aggression - pushing, kicking, horning. The calf eventually responds to these actions by turning aside. Most aggression at this time is related to suckling (compare Figures 39 & 45 with Table 21).

The record for responses of others to aggression by the calf is similarly biased, since many animals, especially lactating females, may avoid a calf's approach regardless of what that approach is. The low levels of calf involvement with other calves' aggression in the first months is emphasised in Table 21. The post-weaning increase in showing aggression is spread over a longer period than receiving aggression, mainly as a result of the age spread in the group the younger animals received most aggression until they started to respond to threats and simple approaches, when less aggression of all sorts was directed towards them.

The dominance relationships established in this way were very consistent over short periods and seemed closely related to the ages of the animals involved. The heifer A¹ succeeded for a time in dominating L, who was a month older and considerably larger, but this period lasted for only one month before L was again the higher ranking animal. This disparity was probably due to the fact that L was introduced to the group after it had stabilised. He was also dominant to T¹ (the alpha animal) if he approached her from the rear, but after avoiding him she would frequently turn and horn at him frontally, at which he would move away and T¹ would be left with whatever caused the original conflict (she was also dominant in all interactions which began face to face). This latter relationship suggests that T¹ was not recognizing L as an individual, but was reacting to some cue (e.g. his confident approach, his general size) when he approached her with threats from behind. This was not true of other individuals and it may be that they all used slightly different cues in this situation.

This instability centred around L was the main source of low direction indices for the later months. When the relationships were examined more closely, however, it was found that the older animal was the one which frequently successfully showed aggression to the other. In every pair of individuals, even though the younger occasionally drove the other away. Because of the low values obtained for all interaction frequencies around the six month period (mainly because

of few observation hours), it is not possible to generalise much further from the figures. It was obvious from the effect of L, T's and F's on the younger animals that the social structure within a calf group depends very much on the age class composition of the group, and that the development of an individual calf is greatly affected by the stages of development of its companions - even a matter of a month's difference in age could completely change the basis of a relationship.

PLAY BEHAVIOUR AND "SPONTANEOUS" ACTIVITIES

As in "sexual behaviour", the term "play" is a general one of convenience only. It should not be taken to imply any particular motivational state on the part of the animals concerned, and it is used only because of the similarity of the actions and situations involved to behaviour described as "play" by other observers (see Looizos 1966, Ewer 1968).

As already indicated, infant fighting activities seem closely connected with scratching etc. of the growing horns. Fights which apparently began merely as a form of mutual scratching occasionally developed into what were termed "play" fights because the vigor and direction of the actions involved were no longer consistent with the relief of cutaneous irritation, nor were they appropriate to the stage of the horns' development as far as effective fighting went. These fights in fact resembled adult horn wrestling, both in the general postures of the animals and in the specific actions involved in twisting and turning the head. Dissimilarities were that the "defeated" animal immediately resumed fighting, that bouts of mutual grooming frequently alternated with bouts of fighting and that the initial approach was often the neck out, nose extended "invitation" rather than the head up, neck slightly back, "proud" looking challenge approach.

In addition to the normal adult fighting pattern, another form of play fight was seen on rare occasions, usually following a bout of spontaneous running activity in the calves. In this form of fighting, two calves would square off about two to three metres apart with splayed forelegs, (Fig 46) then race together, swerving to avoid one another and kicking out with their hindlegs as they passed. These kicks

were/.....

were powerful enough to be painful, but not to do any damage, as I found from personal experience. I saw no use of the hindlegs in either dominance activities or in serious fighting. Walther (1958a) notes that rear leg kicking is an interspecific fighting behaviour in antelope.

Apart from fighting activities, there were also occasional bouts of running and jumping, interspersed with horn presentations to conspecifics. The behaviour was not very contagious, although other calves would occasionally follow the running one for short distances. The calf would sometimes interrupt its racing to stop briefly before another in the present horns posture, then dash off again, and it was this which stimulated following on most occasions. Running also included the occasional bound, which resembled a leap over an invisible object and may have been triggered by slight irregularities in the ground.

Chinning and mutual grooming were also prominent in the calf groups, especially in the unweaned calves. As mentioned previously, chinning was often used as a mild form of aggression, but it also appeared in play sessions with no particular cue nor any apparent objective. One form of "chinning" which was peculiar to the play bouts was termed mutual chinning. This involved two animals standing facing in opposite directions and usually neck to neck. Each would rest its chin on the others shoulder and push down until one animal broke away. This was very reminiscent of Walther's (1964a) "Halskampf", but was not very energetic and would also take place with the two calves standing in the "opposite parallel" position chinning each others rumps again until one turned away. This activity was seen only between young calves and was restricted to "play" situations.

Occasionally when walking the calves would perform a variety of actions apparently spontaneously, and give the impression that the animal itself was surprised by the action. Several of these, for example head nodding and head looping, have already been mentioned in connection with the development of aggression. Another action, which often occurred with the head loop, was a kick out with the foreleg. This occurred as an emphasis of the normal forward movement of the leg in pacing and was termed "goosestep". It resembled



no other element of eland behaviour, either infantile or adult, and its nearest analogue (in appearance) in other antelope seems to be the "Laufschlag" of the gazelles.

Play was limited almost entirely to animals younger than sub-adults. Sometimes cows were seen to respond to fighting play in their calves by lowering their horns and allowing the calf to "engage" them and to push against them, but more often a cow would either stand ruminating as a calf for example pushed against her legs, or else she would move away (Fig 47).

In the captive group, play took place only at dusk, just after the calves had suckled and fed. In the wild, it was also restricted mainly to the dusk, usually appearing after the evening movement of the herd. It would, however, also be triggered by the joining up of two subgroups of the nursery herd. These groups may have been separated for a day or so and would usually meet by convergence on a lick, water or some other focal point. The animals (of all ages) would race forward, converging with many leaps and straight-legged bounds; once the groups had joined, vigorous and extensive play fighting would result, together with more sedate adult investigatory approaches, grooming and sniffing.

DEFENCE OF CALVES

Kruuk (1972) reports a group defence of eland calves against a spotted hyaena in which defensive actions by several eland cows were triggered by the sight of a pack of hyaenas chasing a single calf, while Drummond (1875) records a herd of eland tearing two dogs to pieces. There were no interactions with predators at Loskop and on the few occasions where defence was shown it was against my own approach. These occasions all involved single cows and the releasers for the attack were uncertain, since they would normally permit me to approach both themselves and their calves, together or separately, without doing more than walking away. One common feature of the attacks was that the cows were highly excited for other reasons - having been driven for some distance, waiting for food etc.; also the calves themselves were usually excited and dashing around or trying to hid behind the dam. The excitement of the calf was very obvious in Kruuk's (1972) case and this may be the normal trigger for

defensive/.....

defensive action. This is not the whole story, however, since parturition stimulates many ungulates to defend a space around themselves which may or may not include the calf, and this certainly happened in at least one instance (see "Information from other births").

Jarman (1974) regards group defence of calves as typical of bovine social organisation and to be expected in the socially convergent (Estes 1974) elands. While the extent of the general convergence will be discussed elsewhere, it is true that eland cows showed low level defensive reactions similar to the Bovinae, in particular an increased wariness with calves, a warning signal (also given by other members of the population) and a "mobbing" response, especially at dusk or after dark (c.f. McHugh 1958, Schloeth 1961, Fraser 1968, Estes 1974, Sinclair 1974). As noted earlier, eland cows have some difficulty visually distinguishing their calves at times, and when a calf suddenly appears, most lactating cows in the group react to it in some way, usually by visually or nasally checking the new calf or else by looking at or going to the calf pool. In Kruuk's case, mistaken identity may have contributed to the extreme (for an antelope) form of mobbing seen, although it would not explain all of the features given. From the reactions of the Loskop eland, it seems that the potential for mobbing and group defence is in their behaviour, but that at the present stage of development, it is represented by behavioural elements which only form the final complex when highly specific criteria are fulfilled for each element e.g. dusk, producing congregation and approach tendencies; the excitement of the calf, stimulating defensive reactions from females whose calves are similar to the one being attacked; one animal bold enough to initiate defense; and social facilitation strong enough to overcome flight responses. It would therefore be seen only rarely and probably would vary in its degree of integration and its frequency from one genetic population to the next.

FEEDING

There are two early behaviour patterns which are apparently important in feeding and in feeding and in the development of food preference - the licking/chewing response, and the tendency of calves

to/.....

to follow the heads and bodies of their elders. The stimuli eliciting licking/chewing (above) favour the intake of vegetation, while the calf's following tendency introduces it to stands of plants, if not to particular species.

The basis of adult feeding behaviour is apparently established very quickly in the eland droppings from a five day old calf were found to consist almost entirely of undigested fodder. The initial intake of food seems to be based on the tendency of the calf to follow its mother's head movements and to lick and chew at the same spot. This response has already been described as appearing almost immediately post-partum in the newborn calf with respect to the mother grooming its body. In the context of following the mother's feeding movements, it appeared as early as the first day. The licking/chewing response was seen equally early in this situation, and calves up to two months old sometimes seemed to chew twigs and grass stalks for the sake of the action rather than for food.

At the end of the first week, calves showed another behaviour pattern which was later introduced into the feeding technique. They twisted twigs and branches between their horns as adults sometimes do when breaking down branches otherwise out of their reach. No successful feeding resulted from this until an age of five or six months and, since domestic beef calves perform the identical action, it is probable that this behaviour was unconnected with feeding in the very young calves and was more immediately concerned with the relief of irritation in the growing horns.

The calves had the habit of orienting their grazing movements to the head of the nearest adult. This may introduce the calf to some of the larger food plants. "Education" may take place in another way, since one cow could tell what the other animals had been feeding on by sniffing their breaths in the normal naso/nasal exchange; if I had given calves extra food such as fruit, not available in the paddock, she would sniff their noses, horn them aside, and come directly to me for food. It is feasible that the more aromatic food plant species could be learned by the calf in a similar fashion.

In 1972, a group of four captive calves aged from one to three months was presented with a variety of food plants not normally ob-

tainable/.....

tainable in the paddock. All were taken regardless of palatability to adults, but some more readily than others, except for an Acacia karroo branch, which they tried but could not cope with because of the long thorns extending past the leaves. An Acacia caffra branch was, however, immediately stripped, including some of the young, green thorns. Adult tuition, or even innate criteria of palatability, therefore, does not restrict the food intake to "known" species.

DISCUSSION

EARLY SEXUAL BEHAVIOUR AND AGGRESSION

The early appearance of sexual behaviour patterns in eland is not unique. Joubert (1970) Altmann (1956, 1963) Sambraus (1970) Bubenik (1966) and Lynch (1974) all record sexual behaviour, usually mounting, as appearing in very young ungulates. Hinde (1968) suggests that newborn animals are hypersensitive to gonadal hormones and that this may account for the high levels of sexual activity seen in many neonates. The results found for the appearance and development of flehmen in eland (Fig 45A) would support this argument, since this activity shows a relatively high level in the first week of life before tailing down to zero in the fourth month. After this, the record becomes highly variable (this was mainly the result of the activities of the young bull L). The foreleg kick, tentatively classed as a sexual activity because of its resemblance to "Laufschlag" (Walther 1964b) showed a similar curve without the later irregularities. Chinning and mounting, on the other hand, showed high levels continuously for the first two months, with chinning increasing after that time and only decreasing well after consistent dominance relations had been established. It is my contention that chinning and mounting, initially stimulated by gonadal hormone effects in the neonate, come to serve a function in the calf's behavioural repertoire and are therefore present at high levels after the hormonal effects have ceased.

Walther (1964a) argues that tragelaphine infant mounting is primarily an aggressive action derived from phylogenetically old

fighting activities. However, Walther's (1964a) argument that the tendency of sitatunga calves to mount from the side was due to a flank attack rather than a misplaced mount is unconvincing since:

- (i) non-ungulate species also misdirect early mounting attempts; (Hinde 1966 : 382 - 3 and references, see also Sambras 1970).
- (ii) although aggression was obviously involved in some mounting in eland, both calves and adults mounted from the rear at all times once the "correct" orientation had been established, regardless of the apparent motivation.

From my own observations and those of others (e.g. Altmann 1956, 1963, and Bubenik 1965) it was clear that calves used mounting in situations involving mild aggression, but that the result of mounting was to coerce the other individual into moving in some way, rather than to attack it or challenge it. It is therefore likely that the mounting individual is making use of the tendency of sexually non-receptive animals to move away from sexual overtures (see also Chapter 5), and that the "primitive" forms of fighting supposed by Walther to have formed the basis of aggressive mounting in modern horned animals may in fact have also originally been derived from mounting.

"Chinning" in its extreme form resembled Walther's (1964a) "Auflegen" as described for greater kudu, although normally it involved less contact with the other animal, since the chin and the underside of the mouth were the areas placed on the recipients back, rather than the whole neck and the chin as in the kudu (see Chapter 5). The role of chinning as a coercive rather than a challenging action is even clearer than in mounting. Not only was it almost independent of rank (direction consistency index for inter-calf interactions -0.63), but also when it was used, the result was normally to drive the recipient towards or away from a key point which the chinning animal then approached. This can be seen particularly clearly in Figs 27 and 45. Although the behaviour was seen in adults, the most prominent use of chinning was by subordinate calves during the emergence of the dominance hierarchy. At this time, chinning was always oriented to the rear of the recipient and the intention posture, which also sometimes elicited movement, resembled that of

mounting/.....

mounting. The connection between these two (chinning and mounting) in the sexual ceremony of the adults is very strong. Since very similar aggressive situations elicit the two in the calf, it would be simpler to suggest that they are sexual patterns which are utilised by young animals rather than they are very different fighting and threat actions which have become closely associated in two completely different contexts (Walther 1964a, 1974 relates the extensive use of the neck and chin in horned ungulates mating ceremonies to symbolic neck fighting).

On a few occasions, chinning in the calf merged into form of driving resembling "Trieben" (Walther 1964a), in which both animals walk along with the rearmost pressing down on the base of the tail of the leading individual. This apparently resulted from chinning being continued, as the foremost animal walked away and was again seen in "coercive" situations.

So it would seem that calves originally use "sexual" activities in a rather general fashion and later initiate movement with them. Since the recipient always moves away at this stage, it is impossible to say whether an attempt at intromission would follow (or rather, behaviour associated with intromission), and whether the sequence chin - mount - intromission is innate and the result of the recipient of a calf's early mounts moving away is to teach the calf that mounting can be used to dislodge a conspecific who cannot as yet be threatened or forced aside. This explanation is, however, open to experimental proof.

FUNCTIONAL ASPECTS OF LYING OUT

The most prominent part of the calf's behaviour in the first month is the lying out phase; this activity presents the calf with a series of very strong social stimuli separated by bouts of very low stimulus levels, both social and non-social. From Hinde's (1966) and Sluckin's (1972) remarks on the effects of stimulus rich and limited environments, it would seem that lying out must have a considerable effect on the future social behaviour of the calf. One striking thing about almost all ungulate species is the rapidity with which they form attachments to individuals of their own age class (e.g. Schloeth 1961, Joubert 1970) despite the fact that these are considerably different

to the mother in size, conformation and behaviour, and this is particularly noticeable in the eland, where the calf seems to prefer its peers to its mother almost from birth. From the interactions which occur between calves, as opposed to those occurring between adults and calves, it seems likely that it is the higher level of social activity in the other calves, as well as the fact that they are less capable of eliciting withdrawal responses (e.g. by effective threats, by contact aggression, by use of physical strength to push the other away), which is important. Follower calves are in contact with animals other than the dam almost from birth (e.g. McHugh 1958), so that there is no strangeness about a young conspecific. Lying out species, however, must frequently encounter their first peers after the flight response has appeared - this certainly happens in eland. In spite of this, hidlers show as much, if not more, preference for a peer as do followers.

It would therefore seem from the above that the optimal stimulus seeking of the eland calf, modified by lying out, has the effect of reinforcing peer group bonds and, as a result of this, affecting the course and speed of the social development of the calf. As the calving season proceeded at Loskop, the eland nursery herd grew larger and calves joined it at a much earlier age, which may have been the result of the higher social stimulation received by the calves when joining their dams to suckle in or by the herd.

Lying out seems to be slightly anomalous in the eland, since Lent (1974) notes that "follower" types are more typical of migratory or nomadic species, and also that following appears to be a better defence strategy for open habitat species. The persistence of lying out in the eland may be due either to its phylogeny - it is recently derived from a family of species which has very strong preferences for woodland - or else because of some special value of lying out which does not affect other highly mobile, open habitat species, such as the wildebeeste. In fact, comparing the length of the lying out period in eland (maximum length observed, three weeks) with that reported by Walther for greater kudu (45 days before lying out is completely lost) it would seem that the period is much reduced. This compares with other open habitat types which show lying out - e.g. springbok for one to two weeks (Novellie pers. comm.) - rather

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than the extreme values sometimes seen in species utilising habitats with very dense cover (see Lent 1974 for records). It is therefore likely that lying out has some value for the eland, but that the advantages of moving with the herd rapidly come to outweigh those of lying out.

Lying out is generally accepted as a defence strategy (Lent 1974), but the value of some of the behaviour patterns associated with it are less certain. Anus licking and consuming the calf's faeces and urine by the mother is more characteristic of lying out species than follower species (Lent 1974), and the termination of the lying out period often marks the end of this behaviour (e.g. Joubert 1970). It is probable that the scent of the calf is reduced in this way, but Spinage (1969) remarks that the waterbuck calf's lying out place may be strongly marked by the adult's scent so the importance of calf scent is uncertain. Altmann (1963) reports an elk cow trailing her calf by scent, even though coyotes seemed unable to do this. The value of scent removal or reduction, and of lying out generally, therefore probably depends on the sensitivity and persistence of the predators and is not an absolute protection.



CHAPTER 9

DISCUSSION

FEEDING AND SOCIAL ORGANIZATION

Jarman (1974), in relating feeding to social organization in antelope, predicts that eland would have a large, fixed home range with large herds of fairly stable composition, which may split into subherds during the dry season. This splitting, however, should not normally cause a great change in average group size. This is mainly due to the wide range of acceptable food coupled with low competition. In its annual cycle of movement, group size and association, the Loskop eland rather resembles group D species (according to Jarman, 1974, pure coarse grazers) in that it forms a seasonal superherd. The herd in group D species is, however, the reverse of that in eland, since "D" animals "may live in such superherds throughout the year, the superherds being temporarily split into smaller herds only for breeding." (Jarman 1974 : 233). Also, D species typically aggregate during the dry season into large groups seeking local abundances. The reverse happens in the Loskop eland, and even migratory eland seem to split into smaller groups rather than form large, cohesive herds (see e.g. Sidney 1965 : 266).

The reason for this is probably the eland's feeding style. It retains the browsing preference of its tragelaphine relatives, but has adapted to its larger size, following the Jarman-Bell principle, i.e. by taking more continuous, low value food types. While it is capable of taking grasses, these act as a supplement to its browse. During summer, forbs (and young grasses) are probably the major part of the diet. In winter, these would become more discontinuously distributed and have a lower food value. The eland apparently responds to this by switching to the larger, although very discontinuous, browse species (evergreen shrubs and trees), using grasses to maintain a basic level of nutrition which would be impossible for a ruminant of the eland's size feeding only on dry season browse. Browse, however, is

still/.....

still an important part of the diet and its increased discontinuity would have a disruptive effect on the herd. Animals must forage further apart from one another (Jarman 1974), and this would quickly result in independent subgroups (see Chapter 4). Figure 14 and Tables 3 and 4 give an indication of the effects of food value of forage on group size and structure, and on the feeding style.

From Chapter 3, the above discussion and from Hoffmann and Stewart's (1972) classification of the eland stomach structure as that of a preferential browser, it seems that eland feeding is an adaptation of style "C" feeding to compensate for increased body mass. Adaptation is also seen in the time spent ruminating, which is much higher than that in greater kudu, a style "C" browser (Owen-Smith pers. comm.). Whenever eland are part of a functional ecological unit (Grzimek and Grzimek, 1960a; Fraser-Darling, 1960; Stewart and Zaphiro 1963; Pienaar 1969; Foster and Kearney 1967, In: Schaller 1972), they occur at very low densities and biomasses - an exception is Ngorongoro crater for which Kruuk (1972) gives a population of 400 in 260 km². This suggests that this adapted style "C" is only capable of supporting low numbers of eland, possibly because of limitations in the amount of suitable browse.

Although Jarman's (1974) predictions on the social organization and feeding habits seem at first glance to be inaccurate, they become more acceptable when viewed in the light of the eland's evolution. The eland is a recent derivation from the basic tragelaphine stock (E. Vrba, pers. comm.), which is otherwise represented today by woodland browsing species. In moving into more open habitat and utilizing the browse there (which may have induced a size increase - see Geist 1966, 1974b), the eland would almost necessarily have had to supplement its browse with graze. The niche thus exploited, that of a mixed feeder preferring browse, is a very narrow one. Hoffmann and Stewart (1972) list only two other species, steenbok and Grant's gazelle, having the same characteristic stomach structure: these two differ considerably in size from one another and from eland. This means that intra-individual competition is potentially high even at low biomasses and small group sizes. The eland's ability to utilize low value foods reduces this competition, favouring aggregation since they are in an open environment. Group sizes are therefore only

seriously affected by competition when the food value is very low i.e. in winter. This mechanism would supplement the food dispersion factor described above. Thus, Jarman's (1974) feeding style effects operate within limits defined by the evolutionary history of the species and by its present ecology. There is a continual interplay between these which makes it impossible to distinguish cause and effect with the limited information available.

It should also be noted that, in African antelope where feeding sets a limit on population size, it is usually the winter distributions and nutrient values of foods which are the determining factors. Similarly, the winter food value of forage will determine the individual's general feeding styles. Summer feeding is often good enough to support animals with weights and styles which are inefficient for the local vegetation structure (e.g. migratory populations). An animal can therefore support a body weight or social organization incompatible with its feeding style if it can reduce the effect of winter scarcity, as e.g. by laying down fat. Von La Chevallerie, Erasmus, Skinner and van Zyl (1971) record the weights of eland bulls shot throughout the year (Table 22). Although the sample was small (one bull every two months for a year), there is obviously a great loss in weight which only picks up after the highveld rains have begun. For this to be a valid explanation of the eland's body weight/feeding style contrast, confirmatory records should include yearly female weight changes in several free-ranging populations.

THE ELAND MATING SYSTEM

The basic eland male mating system seen in this study was a dominance hierarchy, where several mature bulls might be sexually active within a herd at the same time. Rank is apparently determined in three manners; from the life-long experience of the bulls in fighting each other; from the results of fights prior to and during a particular rut; and from immediate indicators of rank e.g. size, colour and confidence. The hierarchy apparently tends to limit access to females to higher ranking bulls (Chapter 5). The degree of limitation seems to depend on: the availability of receptive females (see Chapter 4); different females, the degree of confinement; the familiarity of bulls with one another; and the reinforcement of the

dominance/.....

Table 22 : Seasonal effect on body composition of highveld eland.
 From von La Chevellerie et al. 1971.

Date shot	May	July	Sept.	Nov.	Jan.	March	Mean.
Live weight (kg)	496.0	487.8	294.4	320.0	368.0	484.8	408.5
Kidney fat (kg)	1.8	1.0	0.1	0.2	0.3	1.7	0.85
% Fat in buttock	3.9	2.2	2.1	1.0	2.7	2.5	2.4

dominance hierarchy by e.g. feeding encounters (c.f. Lott 1974).

Recent reviews of ungulate social systems (see e.g. Geist and Walther 1974) have emphasised the uniqueness of the eland's mating system. The Tragelaphini in general, and the eland in particular, may resemble the Bovini, Capridae and Cervidae in having rank dominance rather than the territoriality characteristic of other African antelope (Estes 1974, Leuthold 1974). Estes (1974) explains the hierarchy in African antelope as the result of high mobility coupled with high sociability. This mobility is probably caused by feeding strategy (Chapter 4), while the sociability results from anti-predator adaptations - cover-seeking, coordinated defence - to open habitats (c.f. Hamilton 1971, Vine 1971, 1973). These considerations, however, probably define group size and composition rather than the mating system: within these limits time, energy and genetic investment strategies probably determine which system occurs e.g. by sexual selection (Owen-Smith 1974).

In antelope in general, the male investment in a calf is probably very low compared with that of the female. There is, therefore, a tendency for polygyny where conditions permit (reviews in Campbell 1972). With an equal sex ratio at birth, the male's energy should be invested in competition with other bulls to maximise inseminations.

In eland, this investment is in: growth beyond sexual maturity; intra-sexual fighting; maintaining the tending bond at the expense of feeding; and increased mortality.

Growth beyond sexual maturity is to be expected in species where reproductive success is size-dependent (Gadgil & Bossert 1970). The factors governing this size-dependency in male eland are fighting prowess through increased weight and strength, and dominance displays linked with this. Size, being both age and condition linked, may then be important to a cow in indicating two alternative desirable features in a father to one of her limited number of offspring. Firstly, the probability of her male calves competing successfully with other males of the same age (indicated if size depends on condition). Secondly, the possibility of her male offspring surviving to an advanced age and fathering offspring each year (if size depends on age). The latter may be important, since "old" males are distinguished from equal-sized younger males by colour, and seem to have priority with females (Chapter 5). Intersexual selection would then reinforce intrasexual selection for dominance attributes (c.f. Orians 1969, Selander 1972, Trivers 1972).

While there is probably a differential mortality between sexes at Loskop (Chapter 2), mainly through bulls' higher tendencies to accident and disease, the vulnerability of bulls at different ages is unknown. If there is a high mortality from these non-social causes in the early adult phase, then the model proposed in Appendix 3 becomes very likely. Increased male mortality is in effect an investment of fitness (or reproductive effort) in an attempt to obtain a potentially high reproductive success in the face of competition from other males (see e.g. Trivers 1972, Orians 1969). When males compete and non-social mortality in adults is low, as probably the case in eland, then energy/fitness investment in social encounters will be high, particularly in defence of females. Size and colour in relation to age are again important, since older animals are likely to fight more vigorously and to sacrifice more fitness to defend their position (Gadgil and Bossert, 1970; Parker 1974b): they should therefore be avoided by younger males. This latter is probably the key point in determining the eland mating system. Only where it is profitable to a young male to allow an equal but older animal to retain



a female will such a system exist. The profit may result from alternative females being close by, as in a densely herding species with a limited breeding season and therefore many simultaneously available females. It may also result from a long potential life expectancy combined with a high risk of death or injury in an all-out fight. The former condition certainly fits eland, while the latter is highly probable - Hofmeyr and Lenssen (1975) report a wild eland cow calving at 20 years: male life expectancy may be somewhat lower, but would still be high for an antelope.

COMPARATIVE ASPECTS OF SOCIAL BEHAVIOUR

The comparative behaviour of ungulates in general, and antelope in particular, has recently been extensively reviewed (Geist and Walther 1974, Jarman 1974, Geist 1974b). I can add very little to these comparisons except to note that, for an animal which exploits a considerably different habitat to that of its nearest relatives, the eland's behaviour is very typical of the tragelaphines (c.f. Krumbiegel 1954, In: Geist 1974b). Where it differs from its relatives is in the frequency of social interactions - eland seems to rely on a continual awareness of what is going on around it rather than on social signalling or stylised exchanges. This is particularly remarkable, since the eland is a highly social species at some times of the year. In this, (Estes 1974) it resembles the gaur. It also resembles gaur closely in other aspects of its biology: sexual size dimorphism, adult male colour dimorphism, lack of territoriality and casual group formation. Casual group formation seems to be the key here, since animals who are repeatedly coming into contact with different, but probably familiar, individuals cannot be continually fighting or displaying (see Chapter 6). Low rates of social interaction are therefore probably a secondary adaptation to feeding and predation pressures, which govern the size and nature of groups (Chapter 4). The conservatism of the social signals which were seen is in correspondence with Edinger's principle (Edinger 1948, In: Geist 1974b), which states, amongst other things, that signal structures normally tend to be highly conservative in evolution. A comparison of such visual displays found in this study with those found in other tragelaphines is given in Appendix 5.

The Tragelaphini as a whole differ from other antelope in lacking strict territoriality, although for bushbuck there is some debatable evidence for territoriality (e.g. Jarman 1974, Leuthold 1974, Jacobsen 1974). Another characteristic is the relative lack of the specialized skin glands normally associated with territoriality (Pocock 1918, Ralls 1971, Johnson 1973). These and other characteristics seem to indicate that the Tragelaphini and the Boselaphini have evolved independently of other antelope for some time. Also, that this evolution has emphasised male dominance and fitness to breed in terms of personal characteristics (e.g. size, scent, possibly courtship behaviour) rather than the possession of a territory.

The reason for this emphasis can only be speculated on, since it may depend for its origin on specialised circumstances now lost. Curiously, it is easy to see why the rather typical eland should rely on a hierarchical system (see Estes 1974; Jarman 1974: and "Eland Mating System" above) but the species which are more typically tragelaphine in size, conformation and ecology are less understandable at present. One possible explanation is in the availability of females, since when oestrus females are well dispersed or come into oestrus unpredictably, a hierarchical rather than a territorial system is favoured (Goss-Custard *et al.* 1972). All tragelaphines either have an extended or continuous breeding season (Ansell 1960, Wilson and Child 1964, Owen 1971, Allsop 1971) or else have ruts in winter, when groups are at their smallest and most dispersed (see e.g. Fairall 1968, Simpson 1968, Spinage 1973).

One would expect seeking out, tending and defence of females by individual dominance characteristics to be most distinct when there is a great pressure on females to wander: this would occur when they are rather large for their browsing style. Thus the lesser kudu and the sitatunga have adult body-weights of 55 - 104 kg and 45 - 205 kg respectively, while all other style b feeders tend to have weights in the region of 40 kg, with the maximum of 54 - 77 in reedbuck. Part of this difference is, of course, due to sexual dimorphism, which in turn is due to dominance i.e. there is a danger of circular argument. It is, however, noteworthy, that the bushbuck, also probably style b, has a lower range of weights (32 - 77 kg) than the other two tragelaphines in this style and is also probably the most territorial in its behaviour

records/.....



(records from Jarman 1974). It is basically feeding style and food dispersion versus female body weight which is important here, as it probably also is in the eland. In this context, it would be particularly interesting to know the feeding style, the nature of female movements and the breeding system in the bongo, which is a very large antelope compared to other forest-dwelling species.

Life expectancy of breeding adults is also important here, since a territorial male sets himself up to take all comers with a possibility of no return. Geist (1974b) notes that where predation is heavy, it pays a male to gamble much of his physiological life expectancy (i.e. if there were no predation) against the chances of fertilising many females quickly. He suggests this as the reason for the tendency to territoriality in African antelope, while northern ungulates with low predation tend to rely on the long term returns from the extended growth past maturity found in dominance systems. Again, the fact that the tragelaphines are often rather large for their general feeding style is important, since they will be better able to defend themselves from predators than their competitors. There are few records of life expectancy in the wild for tragelaphines, but it is possible that their potential and average life expectancies are considerably higher than for comparable antelope.

MANAGEMENT IMPLICATIONS

The suitability of the eland for domestication has been widely commented on and several authors have collected information relevant to this (see e.g. Huygelen 1955, Posselt 1963, Skinner 1966, 1971, Littlejohn 1968, also references in Briand-Petersen and Casebeer 1971). It may, in fact, have been utilised at one time by bushmen (Woodhouse 1971). Hale (1962) lists 14 characteristics desirable in domestic species, such as promiscuous matings and precocial development, all but one of which - limited agility - eland possess if managed correctly. Tame animals rarely use their agility if they are used to fences, but all important fences should be over 2.5 metres and built to prevent their being pushed over or picked to pieces with horns.

Although the eland potentially has useful characteristics, considerable management may be necessary to realise these. When eland



are free-ranging, they are very shy even when frequently encountering man. However, when forced into close, continual proximity with man, they quickly lose their fear and flight distance becomes very short (Hofmeyr and Lenssen 1975). For this reason, if wild animals are introduced into confined quarters, or if calves are being reared in captivity, they should be exposed as much as possible to the sight and sound of people - still being careful not to panic them with e.g. too much noise, too rapid movements or too fixed a gaze.

Most herds would be established with a small number of animals, especially bulls. It is therefore important to the manager to allow as many animals as possible to contribute to the initial genetic pool, although he may later wish to breed selectively. The male hierarchy system can prevent all but one bull from breeding for several years. It is therefore necessary to rotate bulls, keeping the more dominant animals away from the cows to allow the others to breed for part of the season. The bull's aggression at this time of the year may present problems and all separating fences should be strong and high. Once the herd is established, a breeding herd structure of 22 adult cows, 3 subadult and yearling cows, 1 3-7 year old bull and 1 subadult and 1 yearling male as proposed by Roth et al. (1972), should maximise production while reducing conflict.

If a herd is to be used as breeding or for milk production, such contact with humans is important; herds for meat production can be less tame. Calves can be reared on domestic cow's milk (Posselt, with reservations, 1963, Stainthorpe 1972), which gives an opportunity to tame them and to get them used to being handled e.g. by massaging their udders (Treus and Kravchenko 1968). Cows can be let out to feed in the day and will return to give milk at night. Even if the herd is not to be used immediately for milking or breeding purposes, it is good policy to raise calves in captivity, since calves born in the wild are very shy, regardless of their dam's behaviour. Bulls should be separated from the heifers as soon as possible, since they are particularly dangerous in the breeding season if they have no fear of people or vehicles.

If the herd is to be utilised for meat, it will compete best with cattle, in terms of productivity, under extensive veld grazing conditions (Skinner 1971, and references). Animals to be removed should

therefore/.....

therefore be separated from the breeding stock as soon as possible and introduced into the veld. However, young eland use their rations more efficiently than their elders (see Skinner 1967) and if young calf mortality is high, as it is in most cases (Roth et al. 1972), it may be worthwhile to raise them in captivity for the first few months. This will also have the advantage of making them less shy later and may enable them to be easily driven into camps and then transported, rather than being shot on the farm. Once in the veld, it may be desirable to give them supplementary rations from time to time. They will be dominant to all other antelope; horses and zebra, two possible companions, may be dominant to smaller animals, but not to mature bulls. Eland will therefore use such supplements with little fear of competition.

While very adaptable feeders, eland are apparently utilising a very narrow niche under most conditions in the wild and their biomass is usually very low. This niche is apparently present in most South African ecotypes so that eland may be found there or be introduced successfully in small numbers. It does, however, mean that animals will have to be carefully watched and possibly given supplements if they are confined to relatively small areas. All studies of eland in semi-domesticated conditions, except Stainthorpe (1972) fail to state how important their food supplements are to their confined populations. Stainthorpe (1972) in one year kept 52 animals in a 500 acre unit (26 per km²) and fed them on winter rations, mainly lucerne, which average out to 4.4 kg/animal/day. In addition, the animals fed for two hours a day on a high quality, prepared winter pasture. In summer, however, rations were unnecessary. His animals were therefore almost completely dependent on their supplements during the winter, but would achieve densities comparable with cattle on high quality pasture in summer. From the previous discussion, it is clear that winter food availability is particularly important to eland populations, especially those in confined areas (see "Feeding and Social Organization", above). However, from the same discussion, it seems likely that a relatively small amount of high quality food supplement may make a considerable difference to the carrying capacity of winter veld, if all members of the population are fed. To date, eland have been treated as cattle for management purposes (e.g. food levels), and



I would suggest that a series of experiments on the carrying capacity of veld with different winter supplement levels be carried out.

Since eland are such broad spectrum feeders, the effect of their feeding is well distributed over the various levels of vegetation. Prolonged intensive use of an area does, however, mean that overstocking could cause severe damage, since all the vegetation available will be disturbed to some degree. This problem is normally reduced by the nomadic habits of the eland, but even at low densities breaking branches for food may present a problem (see Fig 10). In the winter, up to 20% of tree/shrub browse and 8% of all active feeding was off broken branches at Loskop. It was a fairly constant proportion of the total tree/shrub browse, and since such browsing is mainly a response to low grass and forb nutrient levels, excessive branch breaking is a useful indicator of overstocking. High quality supplements should reduce tree damage by reducing the dependency on high level browse, but will not prevent it completely. Such supplements would also increase local tree damage around the food, because of the tendency of eland to concentrate in these areas. Rations locations should therefore be well dispersed and changed regularly.

The comments so far have concerned management of highly restricted population although some are applicable to more natural circumstances. For large populations where only limited management is carried out (e.g. in reserves), there is little to add, since I have only indirect information on mortality, predation pressure, emigration or recruitment. Also, the eland's flexibility in feeding means that the annual cycle seen at Loskop, while probably typical of bushveld areas, may not be seen in other vegetation complexes. The same principles should, however, apply, since the basic feeding style would be unchanged. In choosing an area to establish a large eland herd, care should be taken to include large areas of winter food species, since these will probably define the range of the population and put an upper limit on numbers. The size of these areas will vary according to the vegetation type, and it may be advisable to run a pilot study with a few tame eland to discover their winter feeding habits in that area, before finally drawing up boundaries and introducing the main herd. From Stainthorpe's (1972) herd and from my own observations, it is clear that summer feeding

area/.....

area can be a fraction of the size necessary for the winter range, although it should, even in dry years, be able to take the maximum number of animals permitted by the winter areas. These two carrying capacities will almost certainly have to be determined separately for each of the major vegetation types found in Southern Africa.

SUMMARY

Because of its size and vulnerability to hunting and disease, the South African eland is virtually extinct where unprotected. Despite this and the eland's meat potential, little is known of its general ethology or ecology apart from a few specialist studies on captive or "semi-domesticated" animals. The present study describes the ethology, social organization and ecology of a small population of eland at Loskop Dam Nature Reserve in the Eastern Transvaal; with some comparisons to captive Giant eland at the National Zoological Gardens, Pretoria.

The structure of the Loskop eland population, derived from the proportions of each age class in groups sighted, shows a high calf mortality, which probably affects males more than females. The sources of this mortality were uncertain, probably being very general and including predation, accident and disease.

Basic activities were divided into: "inactive", "grooming", "ruminating", "walking," "grazing", "browsing" and "other activities". The proportion of time spent on each varied seasonally, feeding being the major activity throughout the year.

Feeding style and food preferences varied continually. These affected daily and seasonal movements, although the population's limited range and the heterogeneous vegetation prevented detailed analysis.

Groups split and reformed easily and were open to newcomers. Group size varied seasonally, as did group composition. The latter was affected mainly by breeding during the spring and summer, but may also have been affected by food requirements during the dry season.

Most observable dyadic interactions were dominance or aggressive exchanges. Stable dominance was enforced by a series of threats and symbolic attacks derived from the charge. Dominance challenges, seen mainly between bulls in the rut and in calves, were head-on approaches followed by horn engagements which rarely escalated into serious fights. Dominance apparently ruled access to all resources except in very young calves. In bulls, dominance was linked to mass which was in turn linked to age; old bulls could be distinguished by both their bulk and their colour.

Courtship is apparently less elaborate than in other tragelaphines: even giant eland showed a much more elaborate ritual than was seen at Loskop. Access to females was determined by the bull's dominance rank, but the importance of inter-male competition may vary considerably with circumstances. Behaviour normally associated with courtship, mainly chinning and mounting, was also observed in several non-sexual contexts. Visual signals apparently depended mainly on context for their meaning; this was illustrated by the grooming activities seen in various situations. The majority of visual signals seen could be considered as a basic message which was modified by the age/sex class of the sender or recipient and other factors.

Auditory communication was limited, being confined to three basic continua of calls, only one of which, contact calling, was other than rare. Contact calls occurred most frequently between calf and dam, but were also heard from bulls approaching cows and from captive cows awaiting food. Alarm barks and aggressive vocalizations were the other basic calls. Other possible forms of auditory communication were: clicks coming from the knees and sounds accompanying routine activities, particularly feeding.

Detectable chemical communication was limited. Self marking with urine was seen, but its function was obscure. The facial glands and the false hoof glands produced a body scent, but they were not obviously used to mark the environment. Olfaction and taste were probably of prime importance in the initial formation of the dam/calf bond. A long term physiological effect may also have been involved.

Calving was observed in captive cows and the development of the bond and the general behavioural ontogeny of the calves were recorded. Calving was seasonal, peaking between August and November, with isolated births throughout the year. The majority of births observed were in the early morning. The birth process itself resembled that seen in other ungulates. For the dam, the birth fluids were important in forming the initial bond, while the calf relied on a few general responses to visual and tactile stimuli. Orientation, the following response and the licking/chewing response, were the main forms of early behaviour and formed the basis of much of the calf's later activities. Teat-finding initially depended on general cues, although teat position was quickly learned. Suckling was lengthy

and took place at long intervals. Weaning was gradual and took place between four to six months.

The true concealment phase was short and apparently terminated by an increasing tendency to mix with other calves. The reaction of other animals to the neonate was that of interest in a stranger, combined with some wariness. Amongst the early social behaviours seen, those associated with sex in adults were most obvious. While their cause in the neonate was uncertain, they quickly came to serve a signalling function, usually causing the recipient to move in some way. Aggressive behaviour patterns were also seen at an early age, usually in the form of play. Consistent dominance relationships were not seen until about the sixth month, and even these were not as stable as in adults.

Feeding preferences were apparently based on learning, very general cues being enough to stimulate eating in the neonate.

The general social organization of eland can be interpreted as an adaptation of a large preferential browsing animal to variations in the quality and dispersion of its food supply. The eland mating system is unique amongst antelope in that bulls' access to females is determined purely on the basis of dominance rank. This can be explained as an adaptation to nomadism and to the large groups necessary as anti predator defence in open country.

OPSOMMING

As gevolg van sy grootte, blootstelling aan jag en siektes het die Suid-Afrikaanse eland bykans uitgesterf in onbeskermdes areas. Met die uitsondering van enkele gespesialiseerde studies op die aanhou of „semi domestikasie“ van die diere is baie min bekend aangaande die algemene gedrag en ekologie. Die huidige studie omskrywe die etologie, sosiale organisasie en ekologie van ’n klein elandpopulasie by Loskopdam Natuurreservaat in die Oos Transvaal en vergelykings word getref met die reuse eland van die Nasionale Dieretuin te Pretoria.

Die samestelling van die Loskop elandpopulasie soos afgelei uit die verhouding van ouderdomsklasse in waargeneemde groepe dui op ’n hoë kalfsmortaliteit wat moontlik meer manlike as vroulike individue raak. Die bron van hierdie mortaliteit is onseker. Dit is moontlik baie algemeen en sluit aspekte soos predasie, ongelukke en siekte in. Basiese aktiwiteite is ingedeel in: onaktief, liggaamsversorging, loop, grasvretend, blaarvretend en ander. Die hoeveelheid tyd aan elk bestee, varieer seisoenaal, met voeding die hoofaktiwiteit gedurende enige tydstep.

Voedingswyse en voorkeur varieer gedurig en beïnvloed daaglikse sowel as seisoenale bewegings. ’n Gedetailleerde analiese is verhoed weens die populasies se beperkte tuisgebied en die heterogene vegetasie.

Groepe split op, kom weer maklik bymekaar en is oop vir nuwelinge. Die grootte van ’n groep varieer seisoenaal net soos groepsamestelling. Laasgenoemde word gedurende lente en somer hoofsaaklik deur voortplanting beïnvloed, maar mag ook beïnvloed word deur voedselbenodighede gedurende die droë seisoen.

Die duidelikste waarneembare interaksies tussen pare diere was dominante en aggressiewe wisselwerking. Stabiele dominansie word bewerkstellig deur ’n reeks dreigemente en simboliese aanvalle. Uitdagings om dominansie tussen bulle gedurende bronstigheid en by kalwers is trompop konfrontasies gevolg deur horingskermtuselings wat selde lei tot ernstige gevegte. Dominansie beslis skynbaar toegang tot alle bronne behalwe by baie jong kalwers en bulle. By bulle is dominansie

gekoppel aan massa en laasgenoemde aan ouderdom; ou bulle kan onderskei word aan beide hul grootte en kleur.

Hofmakery is skynbaar minder uitgebreid as by ander *Tragelaphinae*; selfs die reuse eland toon 'n meer uitgebreide ritueel as wat by *Loskop* voorkom. Toegang tot koeie was bepaal deur die bulle se dominansie rang, maar die belang van intermanlike individue kompetisie mag aansienlik varieer weens omstandighede. Gedrag normaalweg geassosieer met hofmakery, soos rus van die ken op die koei se romp en bestyging, is waargeneem tydens verskeie nie-geslagtelike gebeure.

Sigbare tekens is waarskynlik hoofsaaklik afhanklik van hul verband vir hul betekenis, soos geïllustreer deur liggaamsversorgingsaktiwiteite gesien onder verskeie omstandighede. Die meeste waargenome sigbare tekens kan beskou word as basiese boodskappe gemodifiseer deur onderdom/seksklas van die sender of ontvanger asook ander faktore.

Auditoriese kommunikasie was beperk en wel tot drie basiese reekse roepe waarvan net een, kontakroep, nie uitsonderlik was nie. Kontakroep was meer algemeen tussen kalf en moeder, maar het ook voorgekom wanneer bulle koeie nader en van koeie wat in gevangenissskap wag op voedsel. Alarmroep en aggressiewe vokalisasies is ander basiese roepe. Nog moontlike vorme van auditoriese kommunikasie was klapgeluide van die knieë en die klanke geassosieerd met roetine aktiwiteite, veral voeding.

Waarneembare chemiese kommunikasie was beperk. Selfmerking met urien is waargeneem, maar die funksie is onseker. Gesigskliere en vals hoefkliere produseer 'n liggaamsreukstof, maar hulle is nie ooglopend gebruik om die omgewing te merk nie. Reuk en smaak was moontlik van grootste belang in die aanvakklike vorming van die moeder/kalf verhouding. 'n Lang termyn fisiologiese effek mag ook betrokke wees.

Geboorte is waargeneem by koeie in gevangenissskap en die ontwikkeling van die band en die algemene gedragontplooiing van die kalwers is opgeteken. Die diere kalf seisoenaal en toon 'n kalfspiek tussen Augustus en November met geïsoleerde geboortes gedurende die jaar. Die meeste geboortes is waargeneem gedurende die vroeë oggend. Die geboorte proses self stem ooreen met wat waargeneem is by ander *Ungulata*. Vir die ma is die geboortevloeistof belangrik vir die vorming van die aanvank-

like band, terwyl die kalf berus op enkele algemene gebeure soos visuele en gevoelstimuli. Oriëntasie, die volgende reaksie en die lek/kou reaksie was die hoof gedragsvorm van die jong dier en vorm die basis van baie van die kalf se latere aktiwiteite. Speenvind het aanvanklik berus op algemene aanwysings, hoewel die speenlokaliteit vinnig aangeleer was. Soging was lank en het met lang tussenposes plaasgevind. Spening het geleidelik plaasgevind tussen vier tot ses maande.

Die werklike fase van verstekingsgedrag was kort en termineer waarskynlik deur met 'n verhoogde neiging om te meng met ander kalwers. Die reaksie van ander diere teenoor die nuweling is dié van belangstelling in 'n vreemdeling gekombineer met 'n mate van waaksaamheid. Onder die vroeë sosiale gedragsaktiwiteite gesien by jong diere is dié geassosieerd met seks by volwassenes die mees opvallendste. Hoewel die rede vir hierdie gedrag by jong diere onseker is, dien dit gou as 'n funksionele teken wat veroorsaak dat die ontvanger beweeg op een of ander manier. Aggressiewe gedragspatrone is ook gesien op 'n jong ouderdom, gewoonlik in die vorm van spelerigheid. Bestendige dominansie verhoudings is nie waargeneem voor ongeveer ses maande ouderdom nie en selfs dan was dit nie so stabiel soos by volwassenes nie.

Voedingsvoorkeure was skynbaar gebaseer op aanleer met baie algemene aanwysings voldoende om die jongeling te stimuleer om self te eet.

Die algemene sosiale gedragsorganisasie van die eland kan beskou word as 'n aanpassing van 'n groot dier, met 'n voorkeur aan 'n blaardieët, by veranderings in sy voedselkwaliteit- en voedselverspreiding. Die eland se paringsstelsel is uniek onder antlope daarin dat die toegang van bulle tot koeie suiwer op dominansierangorde gebaseer is. Bogenoemde kan verklaar word as 'n aanpassing tot 'n nomadiese bestaan en die groot groepe nodig as 'n verdedigingsmeganisme teen roofdiere.

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APPENDIX I. THE USE OF
MOTORCYCLES IN FIELD RESEARCH

Since, as far as I know, motorcycles have not been used as main transport in a field study of this nature, it may be worthwhile noting some of the main considerations which arose. There were, in fact, two machines used during the study, with widely differing success. The first of these, while efficient as a cross country machine, required continual maintenance and spares were frequently unavailable. The second was equally effective and much more reliable. Both presented logistics problems, since they were the only transport easily available and even minor breakdowns (e.g. a thorn badly ripping an inner tube) might be irreparable in the field. There were many other drawbacks, whose validity would vary from area to area. There was a limit on the amount of equipment which could be carried, since bulky or heavy packs interfered with control and manoeuvrability. Some animals became used to the sound, but most were much shyer of this than of cars (the noise could, however, be cut down by special silencers); the exposed position of the rider would have been dangerous had there been major predators around - as it was, ostriches would attack the machine at times. Also, while most travelling was done at fairly low speeds, accidents could be serious if e.g. an impala, bemused by the slightly ventriloquial sound of the exhaust, jumped into the path of the machine. Equipment and the rider also had to be strong enough to take the occasional, inevitable, fall in rough country; rainstorms were much more serious than when using a car.

On the credit side, the machine could go almost anywhere the eland could, given sufficient skill in the rider. It was also a much cheaper form of transport. All-round visibility was better than in a car, although eye level was lower than in e.g. a Land Rover. General cross country capability was the equal or the better of a four-wheel drive vehicle, but was slightly different - a very narrow passage could be negotiated and the machine could always be manhandled if necessary, but deep, fine sand and dense thorn brush presented problems. My general

feeling/.....

feeling is that a motorcycle is very useful secondary transport for field studies, but that its range between major overhauls and its working lifetime probably prevent its being the sole transport in out-of-the-way areas.

APPENDIX 2

CLASSIFICATION OF GROUPS

The classification of groups sighted presented some difficulty. Groups were by no means uniform in composition, either with respect to age/sex class or to individuals. Also, there was occasionally difficulty in defining the group itself. Animals were sometimes so scattered that I doubted whether they could readily sense each other (up to 0,5 km from the next eland) but they would eventually rejoin the main group. These animals were treated as temporary groups split off from the main herd, since they fed and moved seemingly independently for several hours or days at a time. This division was necessary, since casual sightings and sightings in the denser habitats could not be expected to yield accurate records if the complete group was assumed to include all such outlying individuals.

Groups which could not be accurately counted were divided into five types: nursery herds: all adult male groups; all adult female groups; adult male/adult female groups; and mixed groups. Nursery groups were arbitrarily defined as those with at least six members, a third or more being younger than subadults. The other groups are self explanatory and included solitary animal sightings.

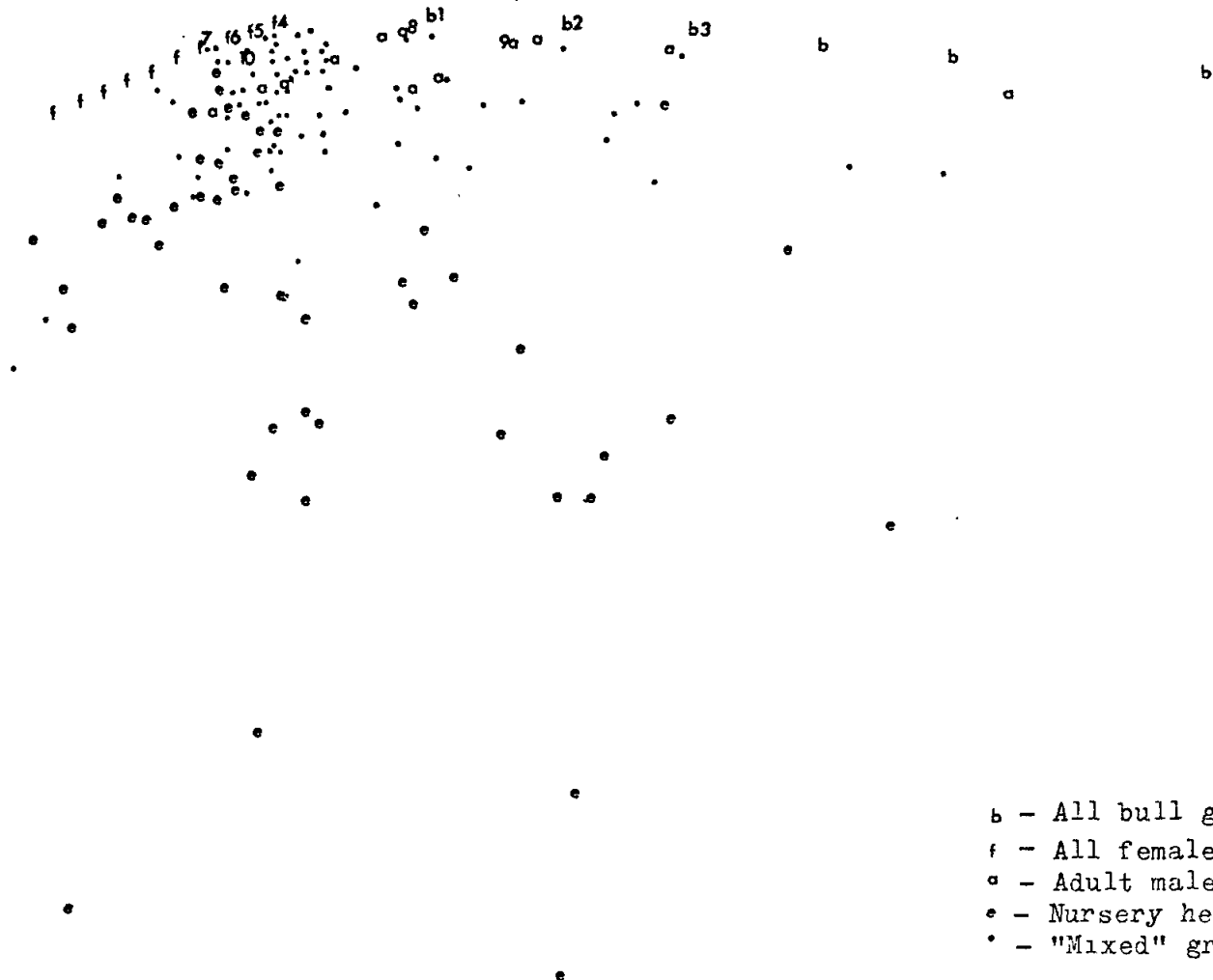
This division worked well in practice and seemed to correspond to the nature of the groups seen in the wild. However, when groups with known age/sex class composition were subjected to principal components analysis (as in Penzhorn 1975, except that the attributes were age/sex classes instead of individuals), a different picture emerged (see Fig 47). Although the classes used did correspond roughly to sections of the distribution of the first two components (cumulative component = 65,005), the " / " and the "mixed" classes were less clear divisions than the others. The limited number of subadults in the population made this necessary - the few observations which included subadults were very heterogeneous and I could not include them with adult animals; all sightings which involved subadults (except nursery herd records) were therefore listed under "mixed".

Other contributions to the "mixed" classes were sightings which included low numbers of young animals. There seems to be a real differenc

between/.....

Points repeated five or more times

- (1) One bull 32 sightings
- (2) Two bulls 13 sightings
- (3) Three bulls 7 sightings
- (4) One cow 36 sightings
- (5) Two cows 38 sightings
- (6) Three cows 14 sightings
- (7) Four cows 7 sightings
- (8) One bull,
three cows 7 sightings
- (9) Two bulls,
two cows 6 sightings
- 10) Two cows,
one calf 6 sightings



b - All bull groups
 f - All female groups
 a - Adult male/adult female group
 e - Nursery herd
 c - "Mixed" groups

Figure 48. The sorting of groups produced by principal components analysis and the original classification of group types at Loskop Dam Nature Reserve. June 1972 - May 1974.

between groups which contain more than two young animals (in which case the young are usually the major class and the herd is classified as a nursery herd) and herds which have two or less young, (when the young are usually very much a minority no matter what the size of the group).

A revised classification which would probably be more generally applicable to other eland populations would therefore include provision for considering groups with subadults either a group type of their own, or else as part of the adult age class (the distinction is not possible from the present group records). It would also include a category for groups with small numbers of calves (the major part of the present "mixed" category). From seasonal records, although not from the P.C.A. diagram, a distinction between nursery herds with no adult bulls (mainly August - September) and the same herds with adult bulls (October - February) also seems to be necessary.



APPENDIX 3

SUBADULT SEXUAL STRATEGY

In the case of the strong subadult male and subadult female association, shown by the very high correlation coefficient in Table 6, I suggest that this is at least partly based on the subadult male's sexual strategy.

For a tending animal such as an eland, the time budget for tending and fertilization is related to its energy resources by the optimum relationship.

$$\frac{Tr}{Tn} = \frac{ex_n}{ex_r} \cdot \frac{fr}{fn} \quad (\text{adapted from Parker 1974a})$$

Where Tr = the time spent on sexual activity in the receptive female "domain".

Tn = the time spent on sexual activity in the non-receptive female "domain".

ex_n = energy cost per fertilisation in non-receptive female's domain

ex_r = energy cost per fertilisation in receptive female's domain

fr = frequency of encounter of fertile females in receptive female domain

fn = frequency of encounter of fertile females in non-receptive female domain.

Assumptions

- (a) It is possible to divide females into two domains where they are normally receptive or normally non-receptive.
- (b) Other energy demands do not affect the amount of energy available for sexual activity.
- (c) Other essential activities do not restrict the amount of time available for sexual activities.

Within/.....



Within the normal rutting season for eland, dominant males will achieve the majority of fertilisations within the nursery herd and their energy expenditure per fertilisation will increase sharply with the end of the female receptive peak and the splitting of the majority of females into smaller subherds spread over a wide area. Since a dominant male is then more or less assured access to any cow he encounters if he is himself unaccompanied by a more dominant male, it becomes more advantageous to him to abandon the competitive herd and to tour the total home range alone, conserving energy and feeding freely, and to rely on random encounters to produce receptive females if any occur at all. This tendency would be augmented by the fact that there are increased demands from other sources on the bulls time and energy outside the breeding season. For young bulls and especially subadults, the situation is different: during the normal rut, they have very little opportunity of fertilising any female and their energy expenditure per fertilisation will be very high, mainly because of the presence of dominant bulls. Once the majority of adult females and the dominant males have left the central herd, this energy demand has been relieved and any females which now come into oestrus will quite possibly be fertilised by a subadult for less expenditure of energy than during the peak of the rut, even although the energy requirements of remaining with the herd, and of non-sexual activities generally, may otherwise be higher. As the number of available females and the frequency with which they come on heat drops, one would therefore expect that increasingly lower ranking animals would leave the central herd until only a nucleus of calves remains. Subadult females tend to come onto heat at Loskop later in the season than adult females, and it would be to their advantage to remain with the main source of actively competing bulls i.e. the nursery herd, far longer than the adult females, which would have been fertilised and moved out long before the subadults' first fertile oestrus. It is therefore mainly the subadult bulls which would fertilise these cows if this argument is true. The age at first oestrus of eland cows is highly variable, even under controlled conditions, and heifers may therefore come onto heat at any time of the year. It would therefore probably be advantageous for subadult males and females to remain together even when food competition has caused them to separate from the nursery herd calves.



The whole argument for divergent sexual strategies rests on the fact that no matter what the subadult's energy expenditure during the rut, it is almost impossible for him to achieve an insemination, and that because of this if he is to achieve any fertilisations at all he has to put himself in a situation outside the normal breeding season where he has the maximum opportunity of encountering fertile females, even if this means an energy expenditure which would be prohibitive to an adult dominant male. This energy expenditure should not, however be high enough to seriously prejudice the bull's chances of future fertilisations when adult.



APPENDIX 4

INTERACTION PREFERENCES

As Altmann (1968a) points out, in order to understand the preferences of one age/sex class for another in interactions, it is necessary to know how available each is in relation to other potential partners. In calculating this availability, both he and later Shank (1972) took what amounts to the total animal time ("Monkey years" Altmann 1968a) that each age class was under observation, then divided that by the total number of animal hours from all age/sex classes. This gave an "availability" index for each age/sex class, and the probability of interaction between two classes on a random hypothesis is the product of the availability indices of those classes. (Shank's derivation is somewhat different, but the qualities being manipulated and the final result are identical).

In fact, this probability of interaction as it stands describes the whole population and in interpretation one cannot separate the mechanisms governing group formation and those governing interactions within the group. The process of group formation, group size and group companion selection are probably more influenced by ecological factors than are short term interactions within groups, and I attempt to deal with these separately for eland. In order to analyse the results of interaction frequencies on this basis, it is necessary to obtain a measure of intra group availability for each age/sex class with respect to each other age/sex class. This is especially important in species which have distinct group types consisting of a particular age class - if the "availability" of this class is included in a measure such as that used by Shank (1972) one might get a high probability of interaction between two classes when in fact they may never meet.

In order to allow for this, it is necessary, when calculating the probabilities of an interaction occurring on the random hypothesis, to calculate the availability of each age class for each other on the basis of group companionship. Thus:



$$A_{i,j} = \sum_{k=1}^Q n_i \cdot n_j \cdot T_k$$

Where $A_{i,j}$ = the intra group availability of the class i and the class j to each other.

n_i = the number of individuals of the class i in the k^{th} group.

n_j = the number of individuals of the class j in the k^{th} group.

T_k = the time that the k^{th} group was under observation.

Q = the number of groups.

$A_{i,j}$ may then be expressed as animal hours of intra group availability of class i for class j, and vice versa.

The probability of interaction is then

$$P = \frac{A_{i,j}}{C}$$

Where C is the total of all age/sex class hours of availability. The probability matrix is then set up as in Altmann 1968b.

This formula is only of use when observing the activity of all members within a group. If one is following the interactions of single individuals, the formula becomes:

$$A_{i,j} = \sum_{k_i=1}^{Q_i} n_j \cdot T_{k_i} + \sum_{k_j=1}^{Q_j} n_i \cdot T_{k_j}$$

Where $A_{i,j}$ = the availability of class i to class j.

Q_i = the number of groups where an animal of class i is being followed.

Q_j = the number of groups where an animal of class j is being followed.

n_i = the number of animals of class i in the k_j^{th} group.

n_j = the number of animals of class j in the k_i^{th} group.

T_{k_i} = the length of time that the k_i^{th} group was observed.

T_{k_j} = the length of time that the k_j^{th} group was observed.



According to both Shank and Altmann, the probability of interaction within an age/sex class should be weighted to allow for the fact that each member of a group containing animals of a particular class have only $n-1$ individuals of that class to interact with. Following Shank's suggestion,

$$A_{i,i} = \sum_{k=1}^Q (n_i - 1) n_i T_k$$

For the purposes of this study, an additional correction was made. On examining my results, I found that although there were some unknown animals included in sightings where interactions were observed, these animals were almost never recorded as having shown any interactions. "Unknown" was usually recorded as a result of an animal being sighted briefly between two trees and not being seen again during observations on that group. To cancel the weighting of these in the animal hours recorded, only known animals were included in the class counts n_i, n_j for the purposes of these calculations. This was particularly important, since the "group" might be spread over half a square kilometer of dense woodland, while my area of effective observation would be limited to a few square meters. This method has its dangers (see Altmann 1974), but is more accurate than including uncritically all group "members", since it effectively limits my recorded observation time to animals that I could get at least one good look at.



Table 23 : A comparison of eland expressive behaviour with that (Appendix 5) of other tragelaphines.

	<u>Taurotragus</u>		<u>Tragelaphus</u>				<u>strep - sisceros</u>
	<u>oryx</u>	<u>derbianus</u>	<u>scriptus</u>	<u>spekèi</u>	<u>angasi</u>	<u>imberbis</u>	
<u>Threat</u>							
Nose vertically upward	?? ⁽¹⁾ [?]	exc	+	++		++	++
Symbolic snapping in females	- [+]		+	++	++	+	++
Head shaking	+ [exc]	+	exc	exc	exc	exc	exc
Head nodding	+ []		+	exc	+	+	+
Downward sweep of head or horns	+			-	++	-	
Medial presentation of horns	++ [+]	+	+	++	++	++	+
High presentation of horns	? []			-	?	-	-
Low presentation of horns	+ [++]	++	+	+	++	+	+
Head low posture	++ ⁽³⁾	++ ⁽³⁾	++	+	++	+	++

From Walther 1974 for Tragelaphus spp, My own observations for Taurotragus. Walther's (1974) comments on T. oryx in square brackets.

Key (as in Walther 1974):

- + = clearly observed or described.
- ++ = especially pronounced and/or frequent.
- + = performance somewhat diminished or aberrant.
- ?? = clearly observed or described but uncertain connection with behaviour under discussion.
- ? = possibly present, but not clearly observed or described.
- exc = exceptionally observed in exceptional circumstances.
- = never observed or reported, probably does not occur.
- = = never observed or reported, but material insufficient.



	<u>Taurotragus</u>		<u>Tragelaphus</u>				
	<u>oryx</u>	<u>derbianus</u>	<u>scriptus</u>	<u>spekai</u>	<u>angasi</u>	<u>imberbis</u>	<u>strep- sicerus</u>
<u>Dominance</u>							
Broadside Arched neck posture	- [?]		-	-	+	-	?
Broadside head low posture	??[-] ⁽⁴⁾	??			?	-	++
Broadside head and neck stretched forward posture			-		?	++	++
Broadside erect posture	? [++] ⁽⁵⁾		-	-	+	++	++
Frontal head turn	(+) ⁽⁶⁾					+	+
Erect frontal posture	+ []	(+)				+	+
Frontal lifted head posture	?? ⁽¹⁾ [-]	?? ⁽¹⁾			?	+	?
Frontal head and neck stretched forward	?? ⁽⁷⁾ [exc]	?? ⁽⁷⁾	?	+		-	-
Broadside lifted head posture	?? ⁽¹⁾ [-]	exc	-		?	++	++
<u>Male Courtship</u>							
Broadside head low posture	[-]				(+)	-	exc
Parallel neck stretched forward posture	++	++	++	+	+	++	++

	<u>Taurotragus</u>		<u>Tragelaphus</u>				
	<u>oryx</u>	<u>derbianus</u> (8)	<u>scriptus</u>	<u>spekei</u>	<u>angasi</u>	<u>imberbis</u>	<u>strep- siceros</u>
Broadside lifted head posture	-	?	-	-	+	++	++
Broadside erected posture	-		-	-		++	++
Following cow, head turn	+ [?]	+	?	?		exc	+
Following cow, erect posture	+ [?]	??	+	?		+	+
Following cow, head lifted	-	+				exc	+
Following cow, head and neck stretched forward posture	++	??	++	++	++	++	++
Mounting posture - neck laid along back	++		++	++	?	+	++

- (1) Possibly seen in an aberrant form in the upright "head toss".
- (2) Defensive threat and submission.
- (3) As a threat when combined with grazing or as an intention-to-feed movements directed towards the other's head; as submission laterally or when passing behind a dominant animal.
- (4) Only seen when combined with grazing.
- (5) Rarely seen in field observations.
- (6) "Aberrant" from the display seen in many ungulates, but very similar to the normal "concentrated alert" posture which probably forms the basis of the ungulate display.
- (7) Seen as a lay fight preliminary from dominants and subordinate animals and is probably an expression of interest rather than a dominance activity.
- (8) The T. derbianus records are partly derived from the activity of the female when apparently in heat. The yearling bull was unresponsive and there seemed to be some reversal in male and female roles, as Fraser 1968 notes for other ungulates. All such records are indicated as ??



Towards the end of the giant eland study period, in March 1975, an almost complete courtship sequence was seen. Before this, the bull had apparently been very unresponsive to the cow, and it was not until he was almost two years of age that he showed any distinct initiative in courtship. Since the sequence is at some points very different to that seen in other tragelaphines, and at others is very similar to common eland courtship, it is illustrated here.

From Figs 49 and 50E, G, there seems to be a neck or dewlap display. In all of these, the bull stood for a minute or more without moving, sometimes, but not always, obviously watching something e.g. people outside the enclosure. In Fig 49E, the cow is licking the dewlap following a (play?) fight and the display shown in Fig 49D. A clearer example of a neck display is seen in Fig 50F. The bull had been following the cow for some time when a male ostritch threatened them: the bull usually yielded to the ostritch, but this time he stood in the nose-up, broadside on position for about half a minute; later he chased the ostritch away.

When the bull was standing chinning or rubbing the cow's anal region, she often gently horned at the fence (Fig 49C) or else stood with her nose to the ground. From her postures in Figs 50A and 50D, it is likely that she was ready to be mounted; but the bull's youth and inexperience was probably prolonging the courtship. In Fig 50B, she reversed roles as he stood in his "alert" position, rubbing and nuzzling his hindquarters and reaching her nose between his forelegs. This latter posture was maintained for some time and was seen in both bull and cow: it resembles "Unterfähren" in lesser kudu (Walther 1964a) except that it is only directed to the forelegs.

Asterisks indicate that similar orientations and postures were seen in common eland courtship, but in all cases in T. oryx they were milder, being closer to the "normal" posture. Giant eland showed much more interest in each other, particularly in the contact phases, and paid more attention to the underside of their partner.

Figure 49. Courtship behaviour in T. derbianus at the National Zoological Gardens, Pretoria (i).

- A. The bull approaches the cow, nose slightly out, as she lies.
- B. He stands over her and she sniffs his nose.
- C. He lowers his horns and attempts to engage hers. She repeatedly turns her head away before finally engaging horns for a minute or more.
- D. The bull disengages his horns and stands over the cow, looking into the distance.
- E. He turns back to the cow and she licks his face and neck region, particularly his dewlap.
- F. He turns away and she muzzles his underside then licks his penis.
- G. He sniffs her vulva.
- H. He rubs his forehead on her hindquarters (c.f. Fig. 33).
- I. He reaches inside her legs and licks her underside.

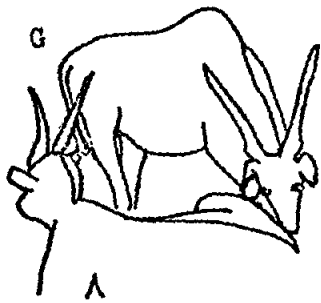
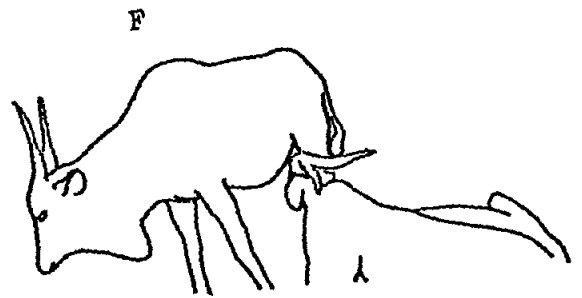
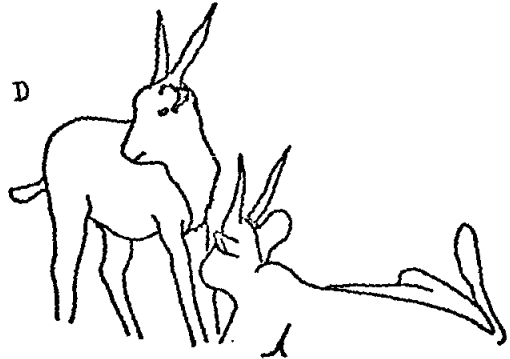
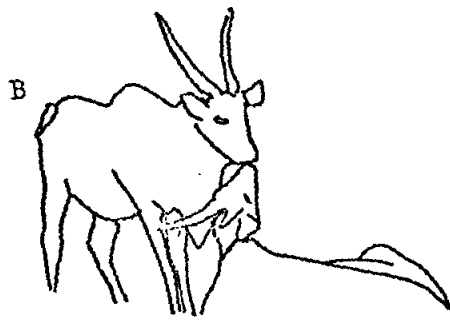
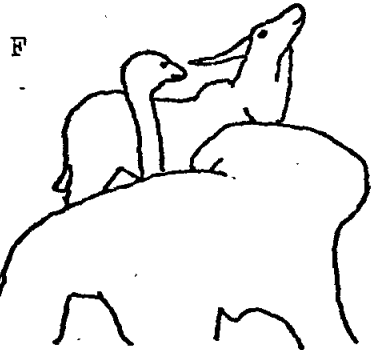
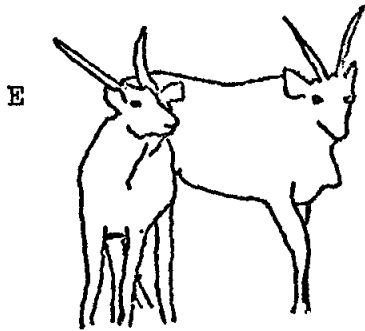
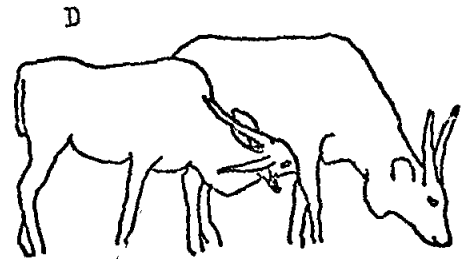
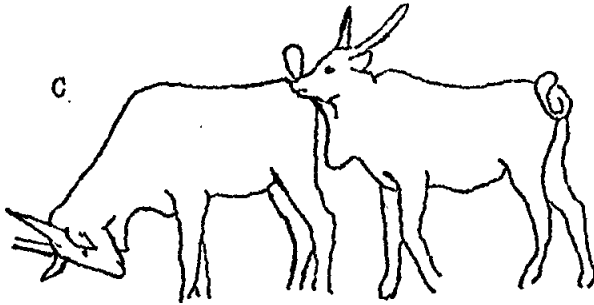
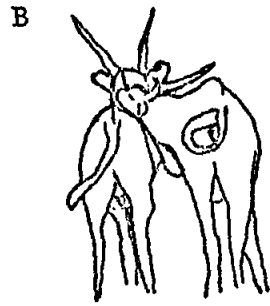
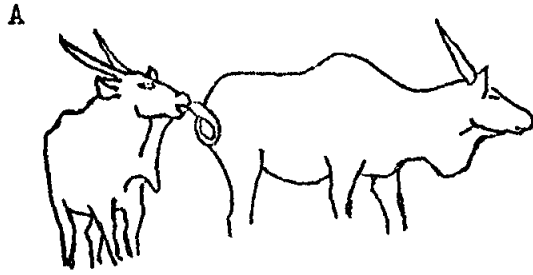


Figure 50. Courtship behaviour in T. derbianus at the National Zoological Gardens, Pretoria (ii).

- A. The bull nuzzles the cow's vulva and flehmens.
- B. As the bull stands looking to one side and into the distance, the cow nuzzles his side and rubs her cheek along his back.
- C. As the cow stands horning at a fence, the bull nezzles and chins her hindquarters.
- D. The bull reaches his nose between the cows forelegs.
- E. The bull stands looking to one side, into the distance while the cow watches him before approaching.
- F. The bull stands before a threatening ostritch with nose lifted.
- G. The cow nuzzles the bulls forequarters and dewlap as he looks into the distance.
- H. Both rub cheeks on the other's shoulder following a head on approach.
- I. The bull grooms the cow's back as she lies.



APPENDIX 6

BIRTH PROCESS IN ELAND

The cow "Sally" was taken into the paddock on 20/8/73. She was obviously near term, having a swollen vulva and hollow-looking flanks, 17/9/73 (Three days prepartum). Vulva turgid and red.

18/9/73 The udder had rapidly enlarged and was the same size as those of nursing cows.

20/9/73 02h00 Sally was pacing along the fence in her normal restless manner.

02h30 Pacing the fence with tail slightly lifted and feet of calf protruding. Contractions probably began at 03h10.

03h31 Lies normally.

03h35 Gets to feet, turns around and stands sniffing ground, ears down, for $\frac{1}{2}$ minute, lies.

03h37 Series of contractions in 1 min. 20 sec. Pause 10 sec. Short, rapid bout of contractions forces calf's head out. Calf already kicking forelegs. Contractions with no visible effect.

03h41 Single, gentle-looking contraction expels all of calf except its hindfeet. Calf lifts head and makes darting movements of nose (undirected). Tries to stand.

03h45 Calf's nose twitching as if sniffing.

03h49 Sally gets to her feet and the calf's hindlegs and the remains of the sac fall free, fluids splash onto the ground. Calf (named Sii) gets onto its knees, weaving its head. Sally licks it and it turns its head towards her and follows her tongue's movement over its body with its nose. Calf's nose touches its own body 5 cm from where Sally is licking. A yearling female investigates, sniffing, and moves away: neither calf nor dam show any response to her.

03h51 The calf lies. Sally licks the remains of the embryonic membrane from its body. Calf again weaving head, with head dropped so that it resembles a play-fighting animal. Sii turns and follows Sally's licking with its nose, turns away head again after a while but immediately turns toward the cow when she stops licking. Sally laps up fluid and chews membrane lying on the ground. Sii tries



to stand, falls, gives its first faint whimper. Sally crosses to calf and licks it, calf lies still. Immediately she stops, Sii turns its head towards her. Sally turns her head away and the calf stretches its neck out towards her, following her movements. Sally licks the calf as it gets to its knees, then turns away. The calf frenziedly struggles to its knees, turning towards Sally. It falls, whimpers, bleats; Sally grooms it.

03h55 Calf gets to knees. Sally looks at it, then away. Calf falls and adopts the sleeping position, licking its side.

04h05 Calf pulls itself onto its four feet. Sally grooms its anus, then stands one metre away, giving choked moos (Chapter 6). Calf staggers forward, away from Sally, gets three metres, falls by me. Sally licks it and it thrusts its nose at my face. Sally resumes drinking birth fluids. Calf remains lying, thrusting its nose at my rucksack.

04h10 Sii stands briefly, then falls. Remains lying but stretches neck forward continually, whimpering.

04h15 Sally lies. There is a brief flow of fluid from her vulva. Calf stands, stretches neck out, stands whimpering for one or more minutes. Staggers forward, away from Sally and myself. Comes to a stop with nose against a tree. Stands thus for about one minute before falling.

04h18 Sally ruminating. Calf gets up, staggers away downhill. Slips but keeps balance. Moves on, whimpering every few seconds. Other calves go to it sniffing its nose. One jumps away with headshakes. Sii moves on and sniffs at a lying heifer, who jumps up and trots away. Sii moves on; other calves follow it, sniffing at it.

04h25 Sii nudging at an Acacia karroo shrub. An adult female goes to Sii, then sniffs and licks rear. It immediately staggers forward towards the female. The female sniffs its nose and it falls to the ground.

04h30 Sii stands and follows another (three week) calf. The calf's dam nudges her own calf aside, sniffs Sii and licks and nudges it towards her udder. Sii nudges her side and she horns her own



calf and walks off. A preparturient cow sniffs Sii hesitantly, then whirls and trots off. Sii follows this female who sniffs it, horns at it, kicks at it and trots off again. Sii staggers away until it gets to a tree, when it weaves its head and nudges the trunk. Lies.

04h48 Calf gets to feet, nudges tree-trunk. Turn aside and moves downhill.

05h00 Calf apparently by chance returns to Sally, who stands and walks towards it with a choked moo. An adult cow leaves the calf as Sally, dominant, approaches. Sally sniffs the calf's nose then its rear. Calf nudges her foreleg briefly, stands and wanders off. Sally gives a choked moo and the calf turns back to her. A heifer has been sniffing the calf and turns away from it. Sii immediately follows her. Sally watches, then follows both of them. All stop and Sally stands by Sii as it lies, licking and nudging its own flank.

05h05 Sally licks the calf then walks ten metres away.

05h25 Sii stands two calves approach it and it sniffs and nudges at the others; they race away. Sii is sexed as a bull, with difficulty since he struggles vigorously when restrained. When he is released, Sally goes straight to him and sniffs his rear, at which he almost immediately goes to the udder and suckles successfully for three minutes.

05h35 Sally changes position to avoid suckling from another calf. Sii loses contact with the udder and nuzzles Sally's dewlap, quickly along her chest, then to the udder to suckle properly immediately. Sally licks the calf's rear as it sucks. She steps forward, he loses contact and nudges between her hindlegs, suckling as Sally walks away. He breaks off and follows her, then switches to following a yearling bull as he passes. Sii nudges the bull's inguinal region while walking. Sally, 20 m away, is calling repeatedly; the calves move to her as a group with Sii. When Sii stands before her, she stretches out her nose to him, he approaches till their noses almost touch, then Sally swings her nose around to the rear at the calf's nose height and the calf follows it, reaches her rear, locates the udder and suckles almost immediately. Sally sniffs the calf's rear briefly, then stands in "normal" position. Suckling for eight minutes. Sally moves away to avoid a domi

nant cow and Sii moves to a nearby heifer, nuzzling the outside of her leg. The heifer moves away and Sii immediately returns to Sally (two metres away). Sally nuzzles the calf's rear, then feeds at food trough. Sii attempts to suckle through her hindlegs, and she steps away. He stands with head and nose low, a passing cow sniffs and nuzzles his rear. He walks to Sally when the cow finishes licking him, and when she lies, lies under her chin.

05h58 Sally delivers the afterbirth after a series of gentle contractions over a ten minute period. Sally at one point gets to her feet and reaches around, attempting without success to pull it out with her teeth. As soon as it is delivered, Sally begins to eat it. Another cow (with a three week old calf) also sniffs at the afterbirth and begins to eat a small piece. The same cow approaches Sii, sniffs him, then chews at the remains of the umbilicus. He steps away and she flehmens. She nuzzles and licks his rear. The cow moves away and a bull calf attempts to mount Sii. Sii moves forward, off balance, towards me and stands, nose out, sniffing, two metres away. He then moves forward and sniffs my face, turns away and approaches several other eland similarly. One, an adult cow, stretches her nose out as he passes and follows him as he goes 15 m to a corner of the paddock and lies. She sniffs and grooms him and then moves away.

06h20 Several calves have separately approached and sniffed Sii, then have lain one to two metres away from him.

06h25 Sii stands and is immediately groomed by a heifer, then moves away to Sally when the latter, three metres away, turns her head to him. Once again he goes to her nose, she swings her nose round to her rear and he moves round to suckle, tail wagging. Sally nuzzles and licks his rear and nudges him between the hindlegs: he immediately splay his hindlegs and she licks his penis.

06h32 Sally lies and he lies in front of her, but immediately stands again and nudges the top of her neck and her dorsal crest. Another bull calf chins and mounts him, he steps forward, the bull calf immediately grooms Sii's neck, crest and ears. Sii lies in the sleeping position with Sally for 40 minutes.

07h20 Sally stands, sniffs Sii in the neck region and he also stands. He sniffs and nudges Sally's side for a few seconds, then

turns away and makes a series of dashes between nearby (up to ten metres away) objects (eland, trees, myself) and Sally.

07h35 Sii lies beside Sally. She stands and goes to the food trough, followed by Sii. All other animals are driven out; one cow remains by the calf, sniffing it, for several minutes before following the others. Sii watches the others leave and dashes down to the gate. Sally gives a moo, the calf stands and she walks down to him, stands by him briefly then walks back to the trough. He follows her but turns away and runs along the fence, whimpering, as the other animals move about outside. They show no response. Sally again moos, the calf freezes but then resumes dashing up and down the fence. He follows the movements of particular animals, stopping and whimpering when he reaches the end of the fence and is prevented from following further. Sally moos and he turns towards her but remains by the fence, calling and looking towards the animals outside. His calls now shade from "whimpers" to "bleats". He resumes following animals outside. Sally comes down to the fence, five metres from Sii, moos, then walks back to the trough and eats. This time the calf follows her and stands by her as she eats, but turns away and goes back down to the fence when another cow looks in and calls. He runs with his nose alongside the base of the fence, whimpering, comes to the end of that side and slowly starts to go uphill. The same cow calls and he turns back to her, but follows another's movements when he gets to the fence. This time when he gets to the end of the fence, he moves uphill until he gets to an enclosed corner formed by two solid sections of fence and several trees, sniffs the ground, calls, looks over to the other animals, and lies with his back to the corner.

08h20 Sally goes to Sii, sniffs and licks him for three minutes, then walks 20 m to the troughs. The calf lies in the sleeping position for the next four or more hours with Sally remaining at the furthest side of the paddock. This corresponds exactly with the lying out behaviour of kudu in captivity as described by Walther (1964a).

From 21/9/73 onwards, the calf moved with the other calves at all times and was kept in a small stall during the day, where it spent more time sleeping. This would presumably correspond to lying out in the wild. After the first week of life, sleeping began to diminish. This management regime obscured the development of lying out, since the calves could do little except stand or lie during the day.