THE ECOLOGY AND BREEDING BIOLOGY OF THE GEMSBOK
ORYX GAZELLA GAZELLA (LINNAEUS, 1758)
IN THE HESTER MALAN NATURE RESERVE

by

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Submitted in partial fulfillment of the requirements for the degree M.Sc. (Zoology) in the Faculty of Science, University of Pretoria, Pretoria.

DECEMBER 1980

TO MY PARENTS

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ABSTRACT

The study investigates certain ecological and behavioral adaptations of the gemsbok in the Hester Malan Nature Reserve. Gemsbok breeding system was found to be aseasonal with a high reproductive potential, being able to produce a calf every nine months. The social organization was characterized by a territorial system with the size of the territories among the largest found in ungulates. Seasonal variations in sizes of mixed herds are related to the availability and nutritional value of food plants, factors which also influenced their feeding pattern. Opportunistic feeders as a result of their restricted existence. Variations in activity patterns are discussed in relation to endogenous and exogenous factors. The management implications of all these factors are examined.

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CHAPTER 1: INTRODUCTION

THE GEMSBOK

The gemsbok, Oryx gazella gazella (Linnaeus) is a bovid artiodactyl belonging to the sub-family Hippotraginae. Although somewhat smaller than the other members of the sub-family i.e. Hippotragus niger and H. equinus it is just as striking an animal with vivid facial- and body-stripe patterns. Possibly more numerous than the latter species, in the past and at present, the gemsbok has re=ceived comparatively less attention in the literature of naturalists, hunters and pioneers and has been neglected by researchers in recent times.

This study set out to investigate the social organization and ecology of the gemsbok to contribute to a better understanding of the species, particularly under semi-na=tural conditions.

STUDY AREA

The Hester Malan Nature Reserve in which this study was undertaken is located some 12km east of Springbok in Namaqualand (29° 34' S, 17° 57' E)(Fig. 6). The geologi=cal composition of the area is represented by the Namaqua=land Basement Complex consisting of granite-gneiss for=mations with numerous strongly metamorphasized relics of metasediments (Martin, 1965; Truswell, 1970). Granite koppies with large rounded boulders rise abruptly from gentle sloping sandy plains (Fig. 1).

The very shallow "desert-soils" are light reddish brown sand to light sandy loam and are covered in some parts by a thin layer of gravel (Van der Merwe, 1940). The large alluvial sandy plain in the southern part of the Reserve lies at an altitude ranging from 880m to 930m. This con=

Fig. 1: General view of the terrain on HMNR, showing rocky koppies seperated by sandy flats.

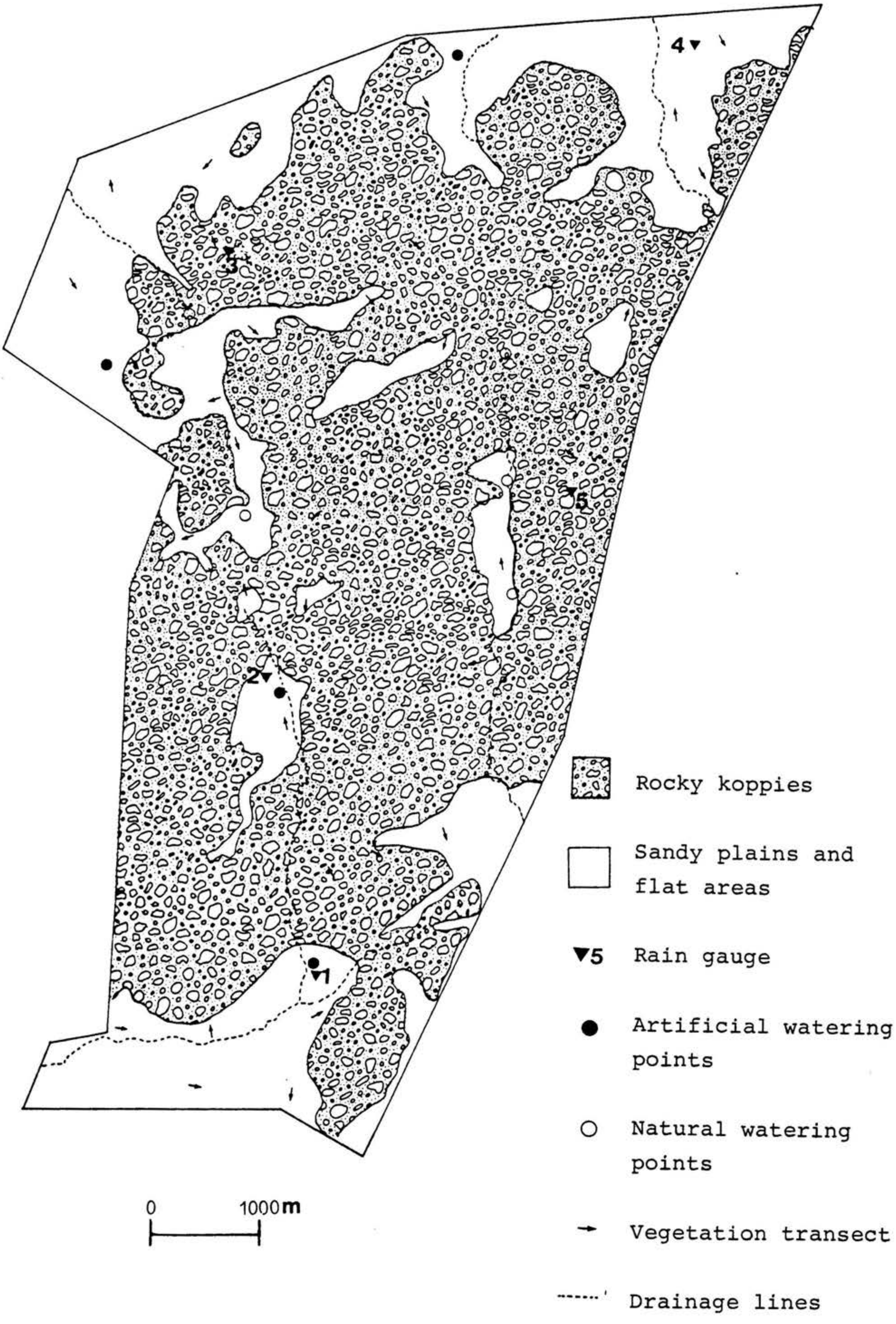

Fig. 2: Map of the Hester Malan Nature Reserve

trasts sharply with the largest part of the Reserve which consists of high koppies gradually descending to a large plain in the north at an altitude of 110m to 1 070m (Fig. 2). Carolusberg, the highest point in the Reserve is 1 346m above sea level.

Climatically the area can be classified broadly as a hot arid region, characterized by sparse and erratic rainfall with great daily and monthly temperature fluctuations. Longterm rainfall figures obtained from the permanent weather station at Okiep (29° 36' S 17° 52' O; H = 918m) show a mean annual rainfall of about 160mm of which approximately 75% falls within the winter season from April to September (Fig. 3). Isolated thunderstorms in summer result in considerable local variation, even within a relatively small area such as the Reserve (Table 1). Yearly rainfall figures also show great fluctuations.

Other forms of precipitation are mist that comes up from the Atlantic as well as dew, which is a regular occurrence in Namaqualand, on the ground and plants where it can serve as an important source of moisture for animals.

Ground frost and sleet was recorded during the winter when temperatures can drop to freezing point in the early morning while the highest temperature can rise to 40°C in the summer (Fig. 4).

Variation in wind conditions, associated with changes in season are obvious in Namaqualand (Rösch, 1978). Summer winds (September to March) blow mostly from the southern sector while north easterly winds, also the strongest, are more common in the winter (April to August). Easterly winds were recorded at a similar frequency in winter and summer (Rösch, 1978).

Mists or fine rains often accompany the south westerly wind coming from the coast and is associated with a sudden de=

Table 1: Monthly rainfall figures obtained from five rain gauges in the HMNR (Fig. 2) for the period June 1976 to June 1977

Month	R1	R2	R3	R4	R5	Mean
June 76	23,8	33,5	30,9	22,5	29,5	28,0
July 76	30,2	49,3	43,7	28,8	33,5	37,1
Aug. 76	10,0	11,5	11,8	11,8	13,0	11,6
Sept. 76	-	2,8	1,5	1,3	1,0	1,3
Oct. 76	7,5	18,7	16,0	12,8	13,8	13,7
Nov. 76	20,0	24,0	21,0	16,0	18,0	19,8
Dec. 76	14,2	21,3	16,0	11,0	11,0	14,7
Jan. 77	-	-	-	-	-	-
Feb. 77	8,0	11,0	10,5	12,5	10,0	10,4
March 77	20,0	5,7	1,7	22,6	10,3	12,0
April 77	9,0	12,0	7,3	22,3	11,8	12,4
May 77	24,2	36,8	27,0	20,8	28,8	27,5
June 77	14,7	34,0	27,2	24,2	25,0	25,0
Total (June 76- May 77)	166,9	226,6	187,4	182,4	180,7	188,5

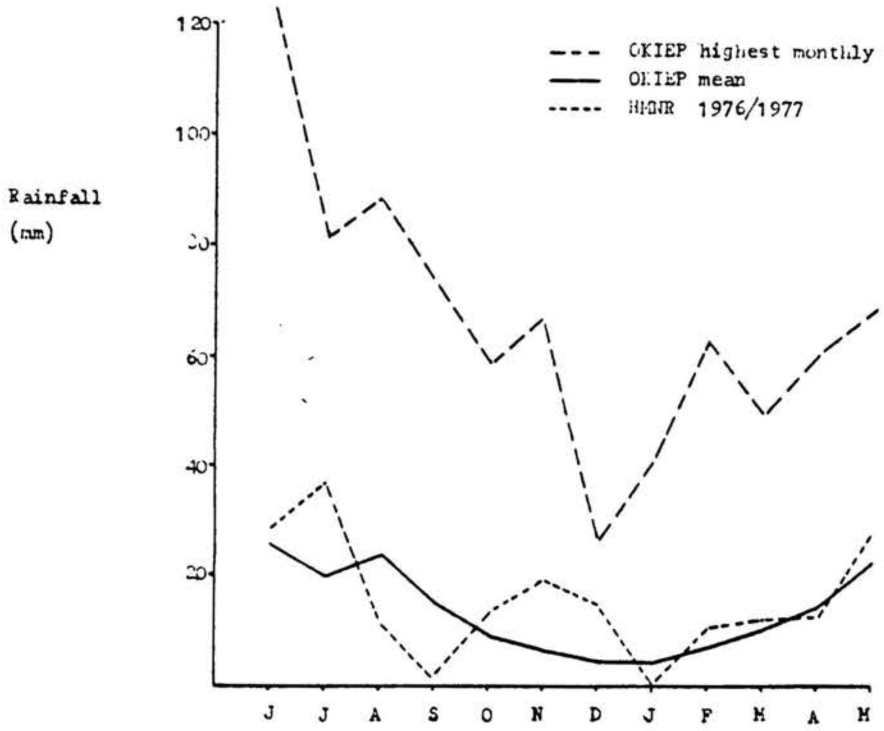

Fig. 3: The monthly rainfall at the Hester Malan Nature Reserve for the period June 1976 to May 1977 shown in relation to the mean and highest month=ly rainfall at Okiep for the years 1881-1950 (Dept. Transport, 1954).

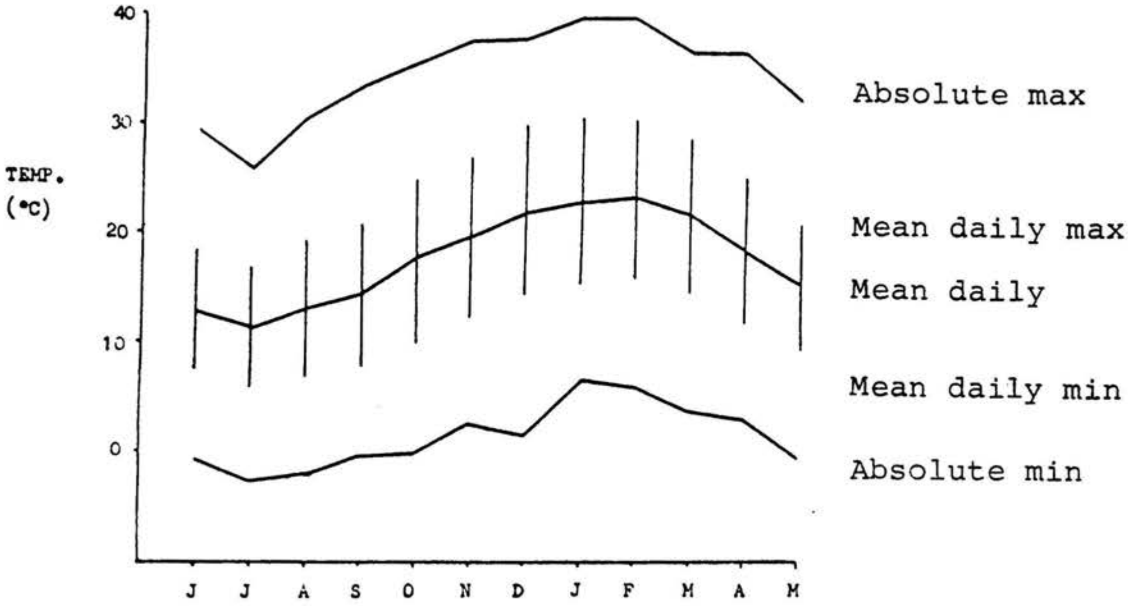

Fig. 4: Monthly variation in temperature at Okiep for the years 1881-1950 (Dept. Transport, 1954).

crease in temperature.

The vegetation of the Reserve has been discussed in great detail by Rösch (1978) and Le Roux (in prep). Two of Acocks's (1953) veld types are represented in the Reserve, with the Namaqualand Broken veld (No 33) occurring in the greater part of the Reserve, on the rocky areas with a transition to False succulent Karoo (No 39) on the northern plain. The most striking feature of the vegetation in Namaqualand is the seasonal variations in ephemeral plant population composition and density.

CHAPTER 2: STATUS OF THE GEMSBOK

INTRODUCTION

Formerly distributed throughout the arid regions of southern Africa the gemsbok has shown a steadily decreasing range of distribution and declining numbers since the eighteenth century. This general tendency applies also to the other members of the genus Oryx, formerly distributed throughout the arid regions of the African continent and on the Arabian peninsula. The Saharan and Arabian species had reached the level of extinction but populations have since been increased artificially by a worldwide conservation effort.

In this chapter an attempt is made to review the literature on the taxonomic status of the gemsbok and its relation to the other Oryx species. Information on the past and present distribution of the gemsbok has also been assembled from available literature.

TAXONOMIC STATUS

The bovid sub-family Hippotraginae, of which the genus Hippotragus is a typical representative, also includes two genera which are adapted to live in arid areas, the Oryx and the Addax. The Oryx which are the second largest hippotragines, are distinguishable from the other genera by the straight or curved cylindrical horns which arise behind the orbits and grow back more or less in line with the facial plane.

At the turn of the century Sclater (1900) and Bryden (1909) recognized five species within the genus. These were O. gazella Linnaeus, 1758; O. leucoryx Pallas, 1777; O. dammah Cretzchmar, 1826; O. beisa Rüppell, 1835 and O. callotis Thomas, 1892.

O. beisa and *O. callotis* were lowered to sub-species of *O. gazella* by Ellerman, Morrison-Scott and Hayman (1953) while Haltenorth (1963) recognized them all as conspecifics of *gazella*. However, in the most recent reappraisal of taxonomic literature, Ansell (1971) retains the three species recognized by Ellerman and Morrison-Scott (1951) on the grounds of their morphological differences, although acknowledging that they are allopatric. The three oryx species are listed by Ansell (1971) as follows:

i) *O. dammah* (= *algazel*; *tao*), the scimitar horned oryx. Horns very long and parallel with a backward curvature. Body white with neck and chest reddish brown. A faint longitudinal stripe of the same colour on the lower flank (Schomber, 1963; Dorst and Dandelot, 1970; Ansell, 1971).

This species has a small, but probably primitive pre-orbital gland which is not found in the other species (Ansell, 1971). It also has a reduced rhinarium and curved horns, and it was on the basis of these three morphological characteristics that Pocock (1918 in Ellerman and Morrison-Scott, 1951) considered this species generically separate, (*Aegoryx*), from the remaining species. This was however not accepted by other taxonomists.

ii) *O. leucoryx* (=*beatrix*), the Arabian or white oryx. Smallest member of the genus with horns nearly straight. Body colour white with strongly contrasting dark brown markings on the head, neck, legs and tail. In some specimens there is also a faint flank stripe (Stewart, 1963; Harrison, 1968; Ansell, 1971).

iii) *O. gazella*, the gemsbok and beisa. Largest oryx with long straight diverging horns. Body colour greyish fawn with a striking and conspicuous stripe pattern on the head and body. A broad black band separates the lower flank from the white belly. The gemsbok has a black stripe uniting the stripe extending from the base of the horns across the eye to the corner of the mouth with the nasal patch, and a conspicuous flank and rump patch. In addition to other morphological differences, these obvious characteristics distinguish the two sub-species (Dorst and Dandelot, 1970; Ansell, 1971).

O. gazella and *O. dammah* represent the genus in the Ethiopian zoogeographic region (Fig. 5). The former species occurs in the Somali and Southwest arid zones while *O. dammah* ranges through the Sudanese arid zone and to a limited extent into the Sahara (Schomber, 1963; Dorst and Dandelot, 1970; Ansell, 1971). *O. leucoryx* occurs on the Arabian peninsula, an area traditionally included in the Ethiopian region (Bigalke, 1968; Harrison, 1968; Ansell, 1971).

Ansell (1971) following Ellerman *et al*. (1953) and Haltenorth (1963) lists five sub-species of the species *gazella*. These are *gazella*, *beisa*, *callotis*, *gallarum* Neuman, 1902 and *annectens* Hollister, 1910, of which the latter two are probably inseparable from *beisa*, while *callotis* is distinct (Stewart and Stewart, 1963).

Gazella and *beisa* are two populations of oryx, occurring in the Southwest arid and the Somali arid zones respectively. They were probably one population with a continuous distribution within comparatively recent times.

Geological and palaeobotanic evidence, the latter mainly from the analysis of fossil pollen, indicates that the climate and with it, the extent of various vegetation types, fluctuated considerably during the Pleistocene and at one time during this epoch the two arid zones were connected by a belt of less arid region (Brain in Balinsky, 1962; van

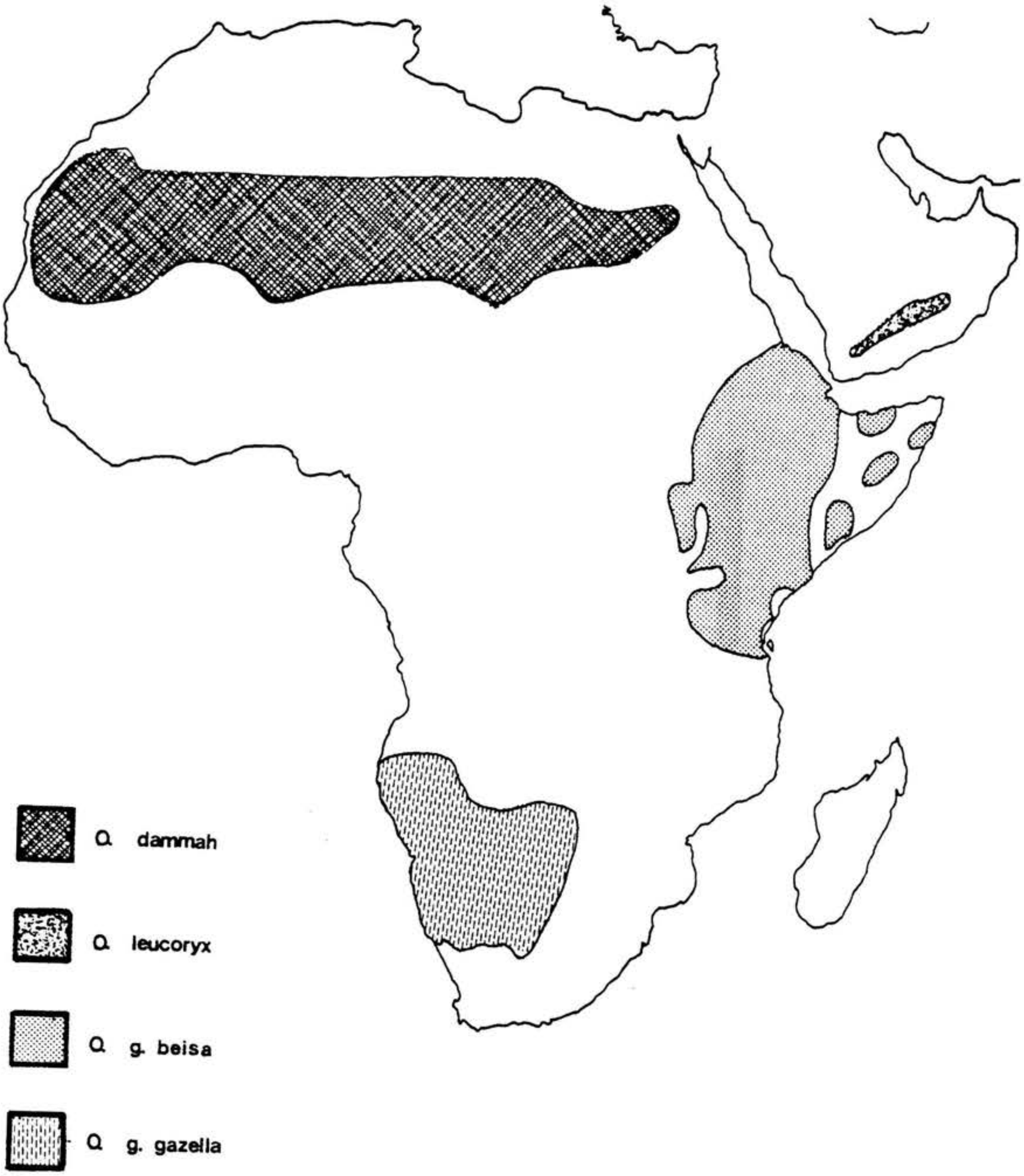

Fig. 5: The present distribution of four Oryx species.

Zinderen Bakker, 1962; Van Zinderen Bakker and Coetzee, 1972). Numerous examples of disjunct distribution of both plants and animals also provide indirect evidence of these past events (Roberts, 1973; Ansell, 1960; Balinsky, 1962; Meester, 1965; Van Zinderen Bakker, 1966; Tinley, 1969; Verdcourt, 1969).

The two oryx populations are now geographically separated by the intervening moist savanna biomes. Isolation is relatively recent and phylogenetic divergence is probably still at an early stage. Ansell (1960) postulates that "*gazella* and *beisa* seem to be one of those borderline cases where in the absence of data on interbreeding potential, it is a matter of opinion whether to rank them as conspecific or not".

The classification of *beisa* and *callotis* as sub-species of *gazella* as advocated by Ansell (1971) is accepted in the present study although the following classification, used by numerous workers, is equally justifiable. Allen (1939), Swynnerton and Hayman (1951), Roberts (1951), Stewart and Stewart (1963), Meester (1965) and Dorst and Dandelot (1970) recognize *beisa* as a distinct species within which *callotis* is a sub-species. *Beisa* is the northern and *callotis* the southern Kenyan race with no apparent overlap between them (Stewart and Stewart, 1963).

Shortridge (1934) divided the Southwest arid population of *gazella* into further sub-species, *O.g. aschenbornei* Strand, 1924, from southern South West Africa and *O.g. blainei* Rothschild, 1921, from Angola. He believed *O.g. aschenbornei* to be synonymous with *O.g. gazella* while Roberts (1951), Ellerman *et al*. (1953) and Halternoth (1963) agree that both sub-species are synonymous with *gazella*.

DISTRIBUTION

No attempt has been made in this section to give a detailed literature review of the past and present distribution of the gemsbok as this has been done by Du Plessis (1969) for southern Africa and in more detail by Skead (1977) for the Cape Province and the southern South West Africa. The intention is rather, to discuss briefly the change in distribution after the arrival of the European in the Cape.

Being the "ecological counterpart in arid and sub-arid desert regions" of the mesic savanna inhabiting sable and roan antelope (Pienaar, 1974), gemsbok occurred principally in the central, northwestern and the northern Cape Province, throughout South West Africa with the exception of Caprivi, southern Angola, as well as throughout Botswana and the extreme western parts of Rhodesia (Bryden, 1899; in Sclater 1900; Shortridge 1934; Roberts 1951; Du Plessis 1969). There is no evidence of its occurrence in the Transvaal in historic times while it did not penetrate far into the Orange Free State and was recorded only near the confluence of the Vaal and the Orange rivers (Du Plessis, 1969; Pienaar, 1974; Skead, 1977)(Fig. 6).

The impression gained from the writings of the pioneer travellers and hunters reviewed in Skead (1977) is that the gemsbok population began declining from the southern Cape northward, soon after it was first described, during the latter half of the seventeenth century.

Namaqualand and Bushmanland, the latter regarded as one of the "strongholds of gemsbok before man interfered" (Skead, 1977), experienced a steady decline in gemsbok numbers during the first quarter of the twentieth century. In the 1930's gemsbok still survived in the Richtersveld near the mouth of the Orange river (Shortridge, 1942). Small herds which cross the Orange river from South West Africa are occassionally seen there to the present day and formed the stock from which the nucleus herd in the Hester Malan Nature Reserve was established. In Bushmanland,

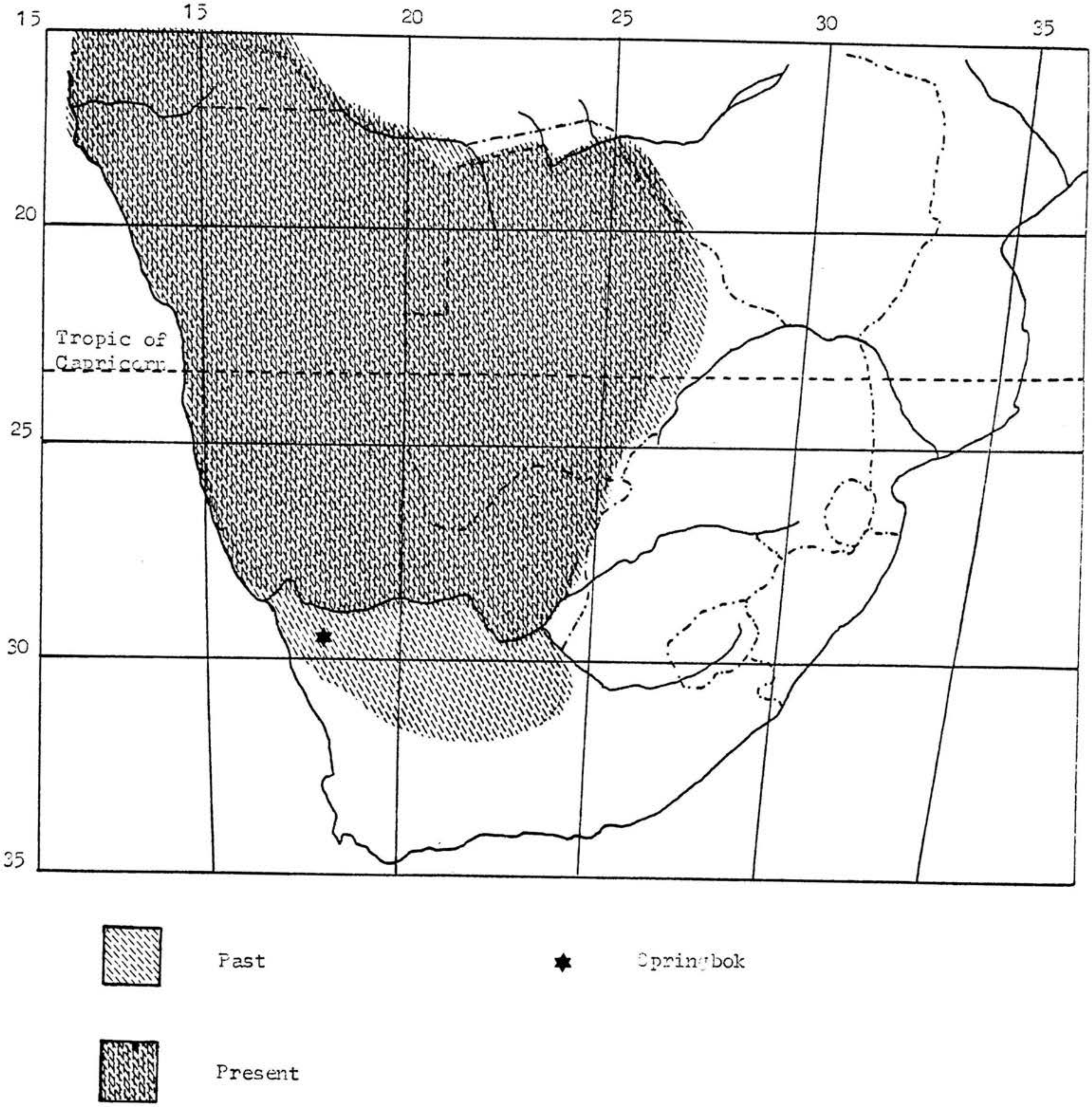

Fig. 6: The past and present distribution of the gemsbok, after Du Plessis (1969), and showing the locality of the study area.

natural populations have become extinct. The largest populations of gemsbok in the Cape Province at present occur in the Kalahari, particularly the Kalahari Gemsbok Park.

Their distribution in South West Africa and Botswana is largely unchanged although numbers have decreased consi=derably (Du Plessis, 1969), while in Zimbabwe, gemsbok are restricted mostly to the Wankie National Park and im=mediate surroundings (Booth* pers. comm).

In South Africa gemsbok have been reintroduced into the greater part of their former distribution range as well as into areas where they were not recorded in the past e.g. Mountain Zebra National Park (Du Plessis, 1969), the Willem Pretorius Nature Reserve in the Orange Free State and Langjan Nature Reserve in the Transvaal where viable herds have been established.

CONCLUSIONS

Although reference is made in the literature reviewed by Skead (1977) to gemsbok occurring in Namaqualand (Alexan=der, 1838), they were recorded only in western Namaqua=land (Sandveld) which is ecologically similar to Bushman=land (although a predominantly winter rainfall area) and the eastern margin of Namaqualand which consists of "tongues" of Bushmanland penetrating between the kopjies of the broken-veld. Localized migrations may have occurr=ed from the numerous herds in Bushmanland along these san=dy valleys at certain times of the year, e.g. after the winter rainfall, but the broken-veld was probably never a permanent refuge for gemsbok, particularly not for large herds.

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* Mr V. Booth, National Parks, Zimbabwe

The Hester Malan Nature Reserve does therefore not fall within the typical former distribution range of the gemsbok, a postulation supported by the lack of "typical" habitat in the Reserve. More suitable habitat occurs however, as close as 2km to the east of the Reserve.

CHAPTER 3: AGE DETERMINATION

INTRODUCTION

The determination of the precise age of an animal is often unimportant but the recognition of some age classes may be essential with respect to certain biological phases in the animal's life (Walther 1972). In the present study it was necessary to recognize age classes of gemsbok in the field. Studies on the ageing criteria for African ungulates have been based largely on tooth and skull characteristics of specimens collected during culling programmes or from natural mortalities. As it was impossible to collect specimens during this study, ageing had to be based on characteristic morphological features easily recognizable in the field.

Horn development, as an index of age, has been used in previous studies for the following antelope: duiker (*Sylvicapra grimmia*) (Riney & Child 1964); springbok (*Antidorcas marsupialis*) (Rautenbach 1970); nyala (*Tragelaphus angasi*) (Rowe-Rowe and Mentis 1972); kudu and bushbuck (*T. strepsiceros* and *T. scriptus*) (Simpson 1972); topi (*Damaliscus korrigum*) (Jewel 1972); tsessebe (*D. lunatus*) (Huntley 1972), and Simpson (1971) who discussed the horn growth in a number of southern African species. In most cases the general horn comformation and twisting offered criteria for field ageing.

Due to the lack of well defined breeding peaks in this species, age class criteria had to be determined by using individual animals at different times. The growth and development of known age animals was monitored with the aid of photographs and ageing criteria were formulated from these. They were based on the changes in pelage colour, horn length and body development.

METHODS

Because of the straight growth of the gemsbok horns, horn development as an index of growth could not be used. Growth checks were also found to be impractical as they could not be seen very well in the field even with a 16 x 40 telescope. A comparison of horn length with ear length for young animals was therefore used in the present study. When possible, horn length was estimated in centimetres using 7 x 50 binoculars and a 16 x 40 daylight telescope. Joubert (1976) found that estimates of horn length in roan antelope were lower than the true lengths but these errors were constant. In his opinion, this validates estimation of horn length as a rough but readily applicable field method for determining the age of immature animals. In addition Ansell (1966) employed a method of field classification for several species including Oryx spp. based on height classes relative to the adult female. He used the following categories: infant, juvenile, subadult and adult (Fig. 7). The height of the withers of younger gemsbok is compared with the dam's "elbow"(level A) and withers (level C) levels. The withers of an infant are level with or below the "elbow" of the dam.

A juvenile was classified as such from the time its height at the withers was above the dam's "elbow" until reaching halfway between her "elbow" and withers (level B). After this the individual was classed as a subadult as long as its height at withers was clearly less than that of the adult female. The height classes were used in the present study to recognize the broad age categories while horn growth and pelage colour were used to assist ageing and made it possible to distinguish smaller classes within the above mentioned broad categories.

RESULTS

Males were found to grow more rapidly than females but

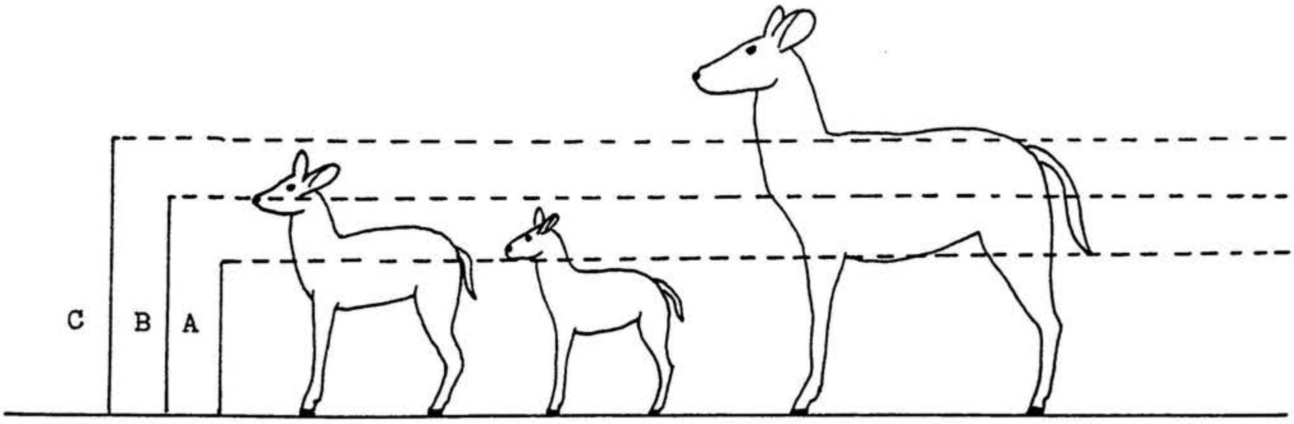


Fig. 7: Height classes of gemsbok after Ansell (1966) see text for explanation

a) 0 - 1 weeks

b) 0 - 1 weeks

Fig. 8: Horn growth and development as an indication of age of gemsbok in the Hester Malan Nature Reserve

could not be distinguished from them in the field on the basis of morphological characters until they were about ten months of age. The ageing criteria were therefore not determined separately for both sexes.

Seasonal variations in growth and development were also evident to a degree. The gemsbok born at the beginning of the wet season appeared to increase in size more ra=pidly than those born at the end. These differences were however not believed to be large enough to affect age recognition.

Pelage and stripe pattern

At birth gemsbok neonates have a fawn or reddish brown coloured pelage which is replaced between the fourth and the sixth month by the pale fawn-grey adult pelage colour. The adult stripe pattern is absent in the neonates and de=velopes gradually, also becoming distinct at four to six months of age.

Horn development

Of the seven calves found within a week after birth only two had horns which were about 2cm long and curved poste=riorly against the head (Fig. 8b). In one individual the horns were visible as small buds partly concealed by twist=ed hair while in the remainder the horn cores were visible only in cleaned skulls.

Horn growth was found to be rapid. At the age of two weeks they were clearly protruding through the hair and were visible in the field with the aid of binoculars. In an eighteen month old female the horns had attained adult length but not thickness. The horns of males showed grea=ter variations in length than those of females, being mostly shorter. Differences in horn length and thickness between males and females first became evident at about ten months of age.

Horn annulations or ridges appeared in six month old individuals and the rate of annulation varied considerably between individuals.

Body size

Adult body size was attained at about 24 months of age.

AGE CLASS RECOGNITION

1. Infant - height class A

0 - 1 week (Neonate) Fig. 8a & b.

At the age of one to seven days the pelage is a uniform fawn or light reddish brown colour.

The tail is the same colour as the pelage and the only evidence of the striking adult stripe pattern is a dark brown stripe, 2cm wide, beginning about 2cm above the eye and extending downwards through the eye to about 4cm below it. In some individuals a darker patch on the muzzle and the side of the legs may be visible. Horn buds may have appeared at this age or short flat curved horns may just be visible.

2 - 4 weeks Fig. 8c.

Pelage colour unchanged but tail beginning to darken. Stripe pattern on face appearing. The horns are visible above the twisted hair about 2,0cm long and less than half the length of the ears.

Fig. 8
c) 2 - 4 weeks

d) 1 - 2 moths

e) 2 - 4 months

2. Juvenile - height class B

1 - 2 months Fig. 8d.

The pelage colour is still unchanged but the facial stripe pattern is becoming more distinct as light and dark brown markings. The rump patch is also distinguishable. The horns are 5 to 12cm long but still shorter than the ears.

2 - 4 months Fig. 8e.

Pelage is lighter fawn than in the previous age groups. The facial pattern consists of dark brown and off-white markings. The body stripe pattern beginning to appear. Horn length is 15 to 20cm and thus longer than the ears.

4 - 6 months Fig. 8f.

The adult pelage colour and the complete adult stripe pattern are attained at this age but markings are not as dark as in the adults. The horns are 20 to 40cm long which is approximately two and a half times the length of the ears or half the length of the horns of an adult female. The first horn annulations are apparent in this age group, in which the animals look like dwarf gemsbok as the body size and horn length are more or less in proportion.

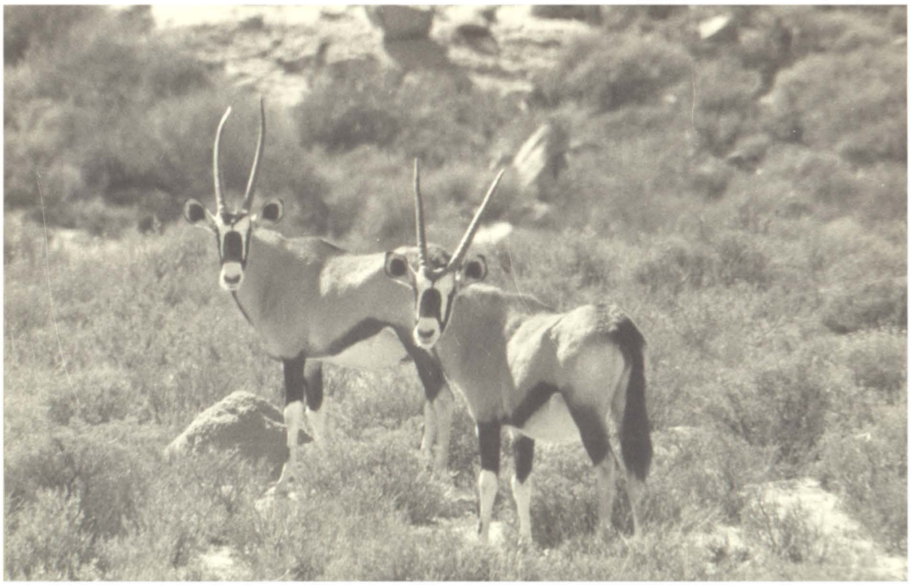
3. Sub-adult - height class C

6 - 10 months Fig. 8g

Horn length is approximately two thirds that of an adult female's and in the males horns are usually thicker than in the females. From this stage onward the females have longer horns than the males.

Fig. 8

f) 4 - 6 months



g). 6 - 10 months

h) 10 - 18 months

10 - 18 months Fig. 8h.

Toward the end of this age the horns attain full adult length but not the adult thickness. Height at the withers is still less than that of an adult female's.

4. Adult Fig. 8h.

In this age class the younger animals can be distinguished from the older ones by virtue of thickness of horn bases.

DISCUSSION

Gemsbok horns grow rapidly after birth and attain adult length in about eighteen months. As a result of the straight conformation of the horns, horn length as an index of age had to be used with care. For example when compared with the ear length, horn length could only be used as an ageing index to the age of four to six months. After this age the horn length had to be estimated and therefore age determination using only this criterion became more subjective. Riney and Child (1964) found similar limitations when they used the horn height as an ageing index in the common duiker male.

The only other report on gemsbok development is that of Thomas (1962) who described the post-natal development of a gemsbok in the Lincoln Park Zoo, Oklahoma City. The juvenile was weaned at about three and a half months and had attained its adult pelage colour when it was five months old. He estimated the body size at four months to be roughly half the size of the adults and he suggested that the body bulk increased proportionately with horn length which reached over 45cm by six months of age. The more rapid development of this captive individual can probably be attributed to a higher and more constant plane of nutrition than that found at HMNR. The age at which the captive gemsbok was weaned was also much younger than that found in the present study although adult pelage colour was attained at a similar age in both cases. This comparison suggests that field ageing from different localities varies.

CONCLUSION

Ansell's (1966) height classes were applicable for the gemsbok in the HMNR and the categories used by him could be recognized in the field without much difficulty. However it was possible, with the aid of additional criteria such as changes in pelage colour and horn growth to age gemsbok more accurately in the field up to the age of 18 months.

CHAPTER 4: POPULATION ATTRIBUTES

INTRODUCTION

In this chapter the reproductive potential and mortality factors, i.e. recruitment rate will be investigated. They form the basic biological characteristics of a population and knowledge thereof is a prerequisite for wildlife manage= ment. This is particularly true where populations are con= fined to relatively small areas and manipulation of numbers has been enforced upon man.

REPRODUCTION

METHODS

Data collected on reproduction were limited to field ob= servations as no systematic culling could be undertaken for this purpose. Parturition dates were estimated to the nearest month using the formulated ageing criteria if the actual birth dates were not obtained. Conception dates were extrapolated back assuming a gestation period of 264 days (Brand, 1963). The reproductive status could be de= termined directly from observations in the case of preg= nant and lactating females while in the case of oestrous females the behaviour of associated males was found to be a fairly good indication of their status.

RESULTS

AGE AT SEXUAL MATURITY

As a result of the small sample size and the lack of phy= siological information it was impossible to determine re= liably at what age gemsbok females become sexually active. Twenty to twenty-four month-old females were seen to sex= ually attract adult males as they were intensively follow= ed and mounted although copulation was not observed. It is therefore possible that the females first became receptive toward the end of their second year giving birth for the first time at an age of twenty-nine to thirty-three months.

PARTURITION INTERVALS

From behavioural observations it was established that gemsbok females experience no post-partum anoestrus and that they came into oestrus three to six weeks following parturition. If they conceive during this oestrus they could then give birth every nine to ten months. Table 2 shows 12 parturition dates of five females. AF02 whose age has been estimated as eight years plus, had four consecutive calves with the time intervals between births of 9, 10 and 9 months respectively. For the four other females the parturition interval between two consecutive calves was 10, 10, 9 and 9 months respectively. This gives a mean parturition interval of 9,4 months, or approximately 289 days with a range of 274 to 304 days. Conception may have occurred after the last birth of each female but this could not be established reliably as the fieldwork had already been completed at that stage, however it will be noted that a conception rate of 100 per cent was maintained by the five females throughout the period of observation.

Taking a gestation period of 264 days, conception in the above related births therefore took place within 40 days after parturition which is probably the duration of two oestrus cycles as was determined from the following observations. From 23 to 27 June 1976, F18 was intensively followed and mounted by different territorial males, a sign that she was in oestrus. Eighteen days later on 15 July she again attracted a number of adult males and this behaviour was again observed on 31 July 1976. The three consecutive oestrus periods thus followed each other at intervals of 16 to 18 days. Conception had however not occurred during the last oestrous cycle as the female was

Table 2: Parturition dates for five gemsbok females

Female	Parturition	
	Date	Interval (months)
02	2/76 20/11/76 9/77 6/6/78	9 10 9
04	25/6/76 26/4/77	10
12	6/76 4/77	10
24	7/76 3/77	9
28	20/10/76 8/7/77	9
Mean parturition interval (months)		9,4

again followed and mounted by TM s 10 and 13 on 26 Sep=tember 1976. She gave birth during July 1977 (exact day not known), approximately nine months later.

The reproductive lifespan of the gemsbok females could not be determined as a result of the relatively young age of the population in the reserve. AF02, the oldest female in the population had attained an estimated age of ten years when she gave birth to the last of her four calves. Flower (1931) and Jones (1958) in Crandall (1964) give a longevity of 10,5 and 18 years respectively for captive gemsbok while Labuschagne and Van der Merwe (1963) give a potential longevity of 18 - 19 years. The longe=vity of wild gemsbok could however be expected to be less than the last two figures given. Breeding activity is probably sustained into old age as occurs in other ungu=lates e.g. roan antelope (Joubert, 1976) impala (Skinner, 1969).

ANNUAL DISTRIBUTION OF PARTURITION AND CONCEPTION

Since gemsbok females experienced no post-partum anoestrus, which resulted in a mean parturition interval of 9,4 months, the distribution of birth could be expected to be aseasonal with parturitions occurring throughout the year. This is shown in Fig. 9, which gives the parturition dates and extrapolated conception dates from April 1975 to August 1977 of 33 calves. The figure clearly shows that no obvious major peaks occurred but that three minor par=turition peaks were recorded in January, June and October/November 1976 and March, June/July 1977. However, when the monthly parturition counts were averaged for twenty-one months Fig. 10, parturition peaks occurred in June/July which corresponds with the middle of the normal win=ter wet season, rainfall ($r = 0{,}74$, $P < 0{,}001$) and tempe=rature ($r = 0{,}46$, $P < 0{,}01$). A subsequent visit to the Reserve in January 1978 revealed that the low percentage of parturitions recorded for the period of October to December 1977 would not have altered the histogram shown

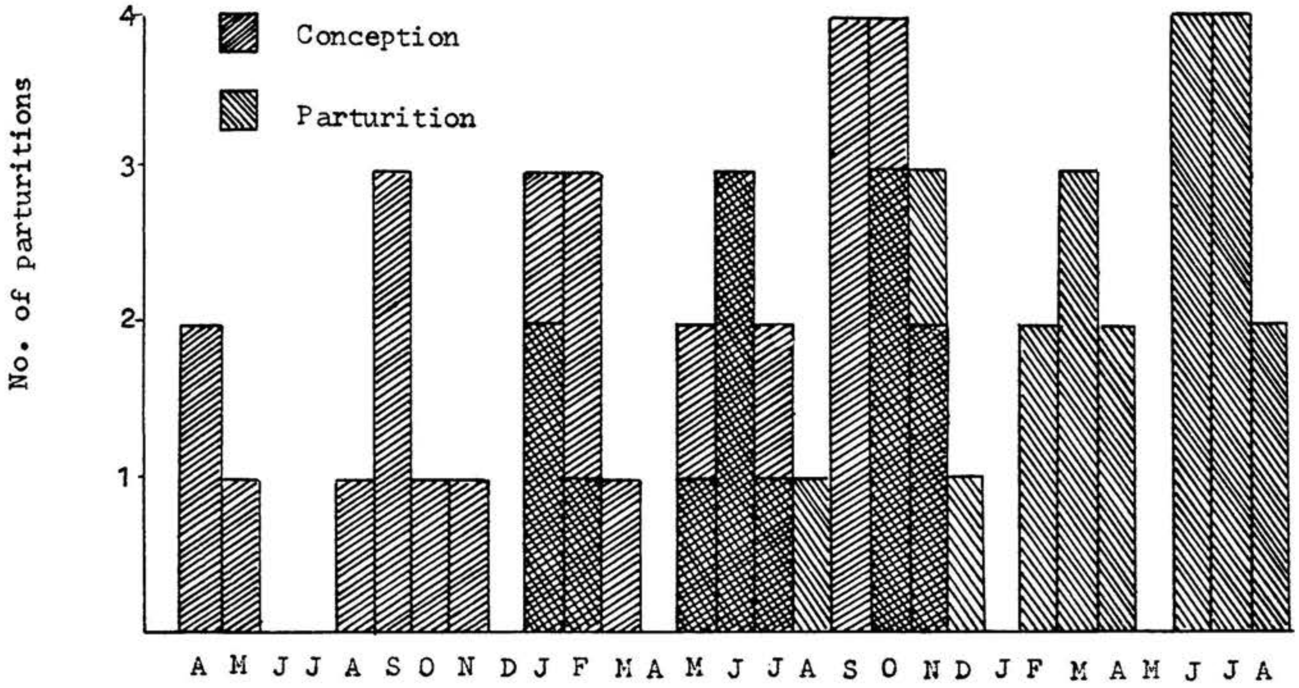


Fig. 9: Parturition dates and extrapolated conception dates from April 1975 to August 1977 of 33 calves

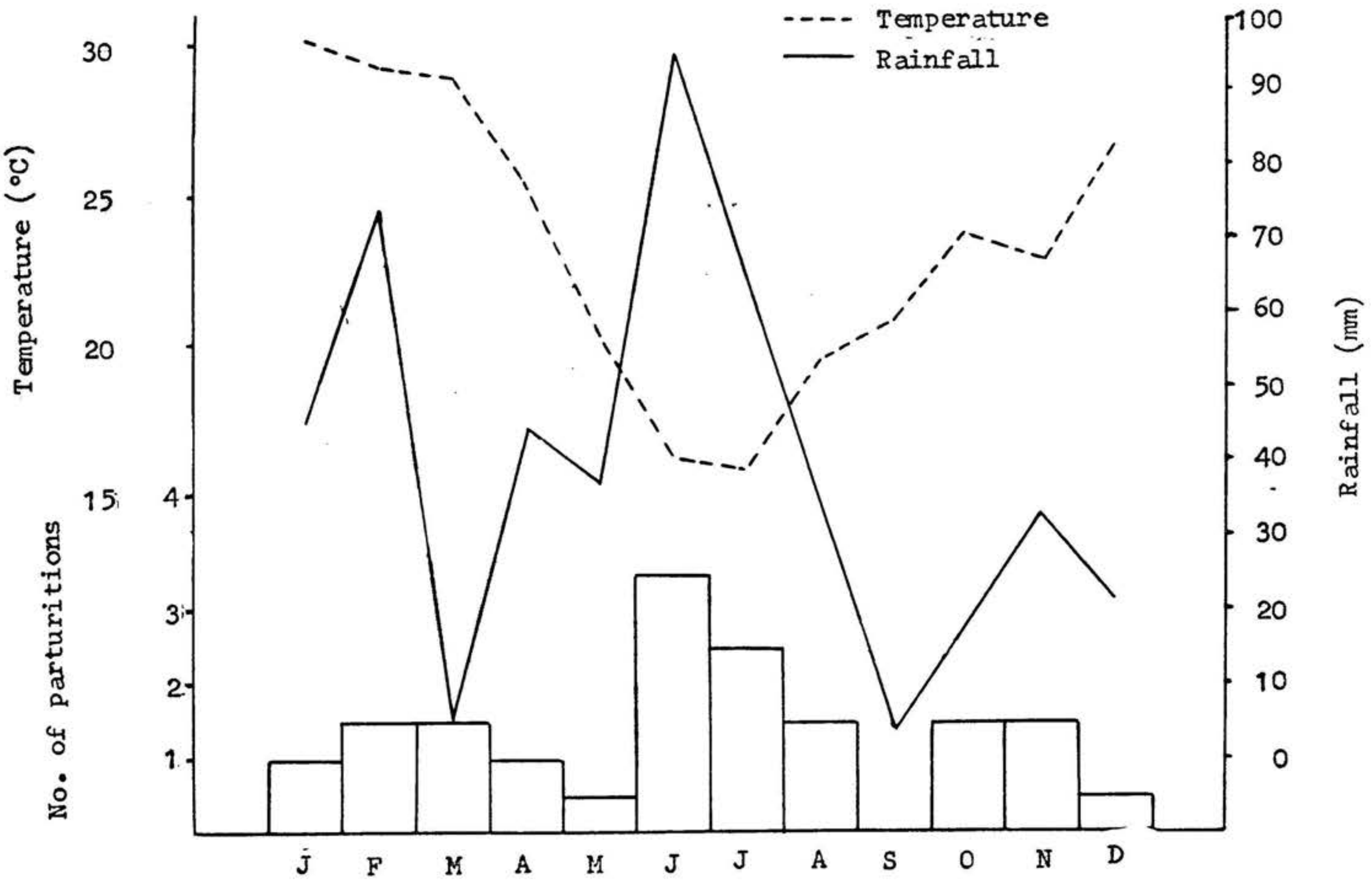


Fig. 10: Mean monthly parturition counts compared with the monthly average rainfall and temperature for January 1976 to August 1977

in Fig. 10 (nevertheless these results should be treated with caution because of the small sample size (n = 33) and relatively short duration of the study).

It will be noted in Fig. 9 that parturition and conception peaks, which correspond with one-another in 1976, occurr= ed in cycles of nine to ten months, the length of the in= ter-calving interval substantiating the occurrence of a post-partum oestrus. The five conception/parturition cycles recorded, ranged from April/May 1975 to January/ February 1976, September 1975 to June 1976, January/February to September-November 1976, June 1976 to March 1977 and September-November 1976 to June/July 1977, respectively.

DISCUSSION

The age at which gemsbok females attained sexual maturity was found to be of the same order as that of the closely related roan antelope which conceived for the first time between 23 and 25 months of age (gestation period nine months)(Joubert, 1976). Joubert also found a parturition interval of 9,5 to 11 months for the roan, and found they breed throughout the year. Skinner, Van Zyl and Oates (1974) showed that gemsbok births were recorded throughout the year on the western Transvaal highveld with a peak in parturition for August and September. However, they con= clude that their sample size (n = 22) was too small to draw any conclusions. Eloff (1961) found a parturition peak in September for gemsbok in the Kalahari Gemsbok Park but continuous data collecting will be required to determine the annual distribution of births there. Never= theless if the results from the study are compared with the averaged monthly birth counts for the Reserve, it will be noted that the parturition peak in the HMNR also oc= curred in the middle of the normal wet season, the corre= lation between parturition and rainfall being significant. This peak occurred two to three months prior to those found in other areas where they also took place at the be=

ginning of the wet season.

The distribution of births in the National Zoological Gardens, Pretoria, (n = 33) shows a similar pattern to that found in the present study, the difference being in the timing of the small peaks (Brand, 1963). In the latter study it could probably be shown statistically that the number of births do not differ significantly from month to month and the differences recorded are probably due to the small sample size.

The adaptational values of a breeding system as found in the gemsbok can only be speculated upon as more information on the subject is required. By spreading the parturition throughout the year in a habitat characterized by a sparse and erratic rainfall, the probability of parturition corresponding with rainfall and therefore a favourable food supply are high. Although long term rainfall data from Okiep and Springbok show a seasonal peak for the period May to August (Rösch, 1978), yearly data show greater fluctuations. The gemsbok were reintroduced into the Reserve relatively recently (1971 and 1972) and may yet adapt to the long term seasonal rainfall pattern because of their restriction to one locality.

The disadvantage of having a post-partum oestrus however, is an increased physiological strain on the females which lactate for approximately six months during the gestation period. The strain on the females became particularly evident if parturition occurred at the beginning of the dry spell or period of scarce food supply. If the physical condition of a female deteriorates drastically the inter-calving interval probably increases and the conception parturition cycles will be disrupted. This became evident in the Reserve during the exceptionally dry period which began in October 1977 and continued into 1978. Six calves that were born from April to June 1978 were abandoned by their dams soon after birth. The dams possibly could not produce sufficient milk due to diminished food resources and one infant appeared to have been killed by its mother when it attempted to suckle (as was seen from a depression on the cranium caused by a horn tip). It remains to be seen whether conception was also delayed in these females and is related to physical condition and therefore indirectly to food supply and ultimately to rainfall.

REPRODUCTIVE BEHAVIOUR

RESULTS

MATING BEHAVIOUR

The basic behaviour pattern consisted of the pre-mating behaviour and copulation. "Flehmen" or urine testing which has been described in many mammals (see Estes, 1972) as an olfactory testing of the oestrous status of a female, was observed frequently in the gemsbok. It was performed by adults and juveniles of both sex classes and was not only associated with oestrous females. It was however observed more frequently during mating behaviour. The term oestrus (which is used rather loosely here) refers to the period during which a male is sexually attracted to a female and includes pro-oestrus. Urethral smelling and the nudging of the female's perineum which was usually associated with the intensive following of the female by an adult male was taken to be a good indication of the reproductive status of a female. A gemsbok male would approach a urinating female and insert his nose into the stream of urine. The male then lifted his head high with the mouth held slightly open and the lips retracted, sometimes moving the head slowly from side to side. (Females and juveniles performed flehmen in the same way).

After the urine test, courtship continued if the female was in oestrus, but seldom progressed further than this stage if she was not. Courtship continued when the male beat up either one of his forelegs between or alongside the hindlegs of the female. Walther (1958) referred to this action as "Laufeinschlag". It is regarded as the most advanced sequence in the courting ritual preceding copulation. "Laufeinschlag" is a means by which the male tests the receptiveness of the female and was found to stimulate the receptive female to stand and copulate. Non-receptive females walked away or began to circle with the male if the latter was persistent.

Copulation was observed on two occasions only, though precopulatory behaviour and mounting with unsuccessful intromission was frequently seen. Copulation was very brief, lasting only 2 - 4 seconds. In the following observation, recorded on 2 November 1976 at 07h00, TM16 which had been following a young female when first sighted a few moments before, approached her at a run from 10m away with his tail held semi-erect. He performed "Laufeinschlag" and mounted. Intromission lasted approximately two seconds and copulation was terminated when the female walked forward. During copulation the male had clasped the female with his forelegs around her haunches (see Walther, 1965) holding his head high while the female adopted a head-low posture. No post-coital behaviour was observed as the male chased away other males which had approached too closely during copulation. During the second recorded observation of copulation the male was seen to mount six times in close succession but it was impossible to see whether intromission had occurred every time.

When a female was in pro-oestrus she would not allow the male to mount, usually initiating a following response in the male. This behaviour sometimes continued throughout the day with interruptions during feeding and resting bouts. To prevent the male from gaining a position behind her from which he could mount, the female would turn in towards the male or circle, beginning the characteristic "mating-whirl" in a reverse parallel position, called

"Paarungskreisen" by Walther (1958). This behaviour was found not to form an obligatory part of the courtship ri=tual (see abovementioned observation and was regarded purely as a means by which unreceptive females prevented the males from mounting as was shown by the following observation: On 5 November 1976 two weeks before she gave birth to a dead full-term foetus (approximately nine months after previous calf - Table 2) AF02 was followed intensively by TM 10 within a mixed herd. After bouts of feeding or resting TM10 would approach the female with his tail held semi-erect, perform "Laufeinschlag" and at=tempt to mount. When the female walked away, the male followed close behind her attempting to mount again seve=ral times. The female then turned in towards the flank of the male and the animals began the "Paarungskreisen" which lasted for approximately five minutes. During the circling the male held his tail semi-erect and beat up his foreleg behind the hindquarters of the female. The circling was interrupted when the female threatened the male with sweeping horns and when she lay down, from which position she was soon chased up again. In another observation of mating behaviour, TM16 approached a female with a neonate, at a run and performed "Laufeinschlag" and mounted without previously having performed any of the other precopulatory behaviour. No mating took place however.

PARTURITION AND THE MOTHER/YOUNG RELATIONSHIPS

Towards the end of the gestation period some preparturient gemsbok females were observed to isolate themselves from a mixed herd. This behaviour was however not observed for all births. (Only 0,9 percent of all sightings of gems=bok were of solitary females). This low figure may be attributable to the fact that solitary individuals were difficult to see because of the terrain of the Reserve and because solitary females were more wary than when with a herd, remaining mostly in the koppies. Isolation be=

haviour was also interfered with by conspecifics, particularly territorial males which would herd the female back or follow her when she had left the herd. During a parturition witnessed by Myburg* (pers. comm.) three adult males which had followed the female were seen approx. 50m from the parturition site.

Parturient behaviour of a gemsbok female can be described by means of the following observations. A day-old placenta found on 25 June 1976 with many fresh spoor near it and in the immediate vicinity suggested that parturition had occurred while the female was in the herd or that she had joined the herd soon after parturition had occurred (Placenta usually detaches a little while after birth in ruminants, Skinner* (pers. comm.)). The calf CM19 was seen on the following day, 3km from the parturition site and approximately 100m from a large mixed herd. Mother and calf appeared therefore to have remained with the herd after parturition. Three days later the female left the herd and was joined by TM13.

Isolative behaviour was observed in AF 02. On 15 November 1976, five days before parturition she was seen alone in the central region of the reserve, (where she had been seen three days earlier with two other gemsbok). On the next day she was still alone but on 18 November she was seen with TM5 on the southern plain, to which she may have been herded by the male. Three days later she was again seen alone, standing near her dead calf about 2km from the previous sighting. The female remained in the vicinity of the parturition site for four days and then rejoined the territorial male.

The parturition, observed by Myburg (pers. comm.) was the only one witnessed in the reserve. When first sighted at 10h00 the female was in recumbency with part of the foetus

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* Prof. J.D. Skinner. Dept. Zoology, Univ. Pretoria.

projecting. At the approach of the observer the female stood up, with the result that the observation had to be discontinued. The duration of the birth could therefore not be recorded. At 11h00 the female was seen about 50m from the cleaned neonate, in the company of three adult males which appeared to be sexually attracted to her. The placenta had not yet been expelled. The next day the neonate was still near the parturition site and four days later was found dead there.

The three located parturition sites mentioned varied in features from an open sandy area with low and sparse vegetation cover, at a koppie base to a site on a koppie plateau with a dense cover of low shrubs.

POST-PARTUM BEHAVIOUR, CONCEALMENT PHASE

After parturition females with neonates either remained with a mixed herd or established nursery herds with other females with calves which were usually of different ages, varying from a week-old to three months-old. Nursery herds often contained non-lactating females while 29,8 percent of all the nursery herds sighted were accompanied by a territorial male (Table 14).

During the first three to six weeks following parturition, gemsbok calves concealed themselves (lying-out phase) and were ignored by the dams for most of the day with the exception of a few nursing bouts. While the calves were concealed the dams would feed with the herd as far as 2 000m from the concealment sites. Concealment was performed solely by the calves although females were seen to prompt their calves into staying behind when they followed at the end of the nursing bout. This was achieved by threatening with a head low posture or by hitting the calves with their horns. The choice of the concealment site was then left up to the calves. They usually lay down next to an upright object such as a shrub or large rock and on one occasion next to a fence.

Gemsbok calves lay with their heads facing the rear in a curled-up fashion similar to the resting posture of the adults. When they were disturbed the calves lay with their heads and necks stretched out in front of them with the ears extended backwards or forward in an alert position (Fig. 8a).

During the early stages of concealment the calves could be approached to within 2m before they stood up and could thus be captured and handled without much difficulty. Flight distance increased with age and varied from one individual to the next. When CM19 was two weeks old he jumped up when approached to within 10m and ran in a large circle for approximately 2km returning to the vicinity of the concealment site. During this time the mother AF04 was not seen.

The duration of the concealment period varied in different individuals and was influenced by the association of the dam with other gemsbok. If the dams rejoined a mixed herd after parturition their calves had a longer lying out phase than those in a nursery herd. This may be as a result of the influence and stimulation from the older calves in the nursery herd. Playful bouts of running and frolicking were observed more frequently in a nursery herd and the females tended to remain with the young for longer periods during the day than did the females which were with a mixed herd. Calves in a nursery herd lay out near each other.

Towards the end of the lying out phase the calves gradually spent less time concealed and more time resting together and playing. They eventually followed the dam in the nursery herd or joined a mixed herd with her. This period has been called the attachment period and contrasts sharply with the behaviour found in the follower type where the calves remain in contact with their dams in the herd. During this period the relationship between mother and calf remained as loose as during the concealment period. The attachment period lasted until the calf was gradually weaned at approximately six months, which varied among individuals. Juveniles and calves in a mixed herd like the calves in a nursery herd showed a preference for peers forming a "creche" subgroup within the herd, (also observed by Eloff (1961) in the Kalahari Gemsbok Park) which often showed a different and partially independent activity pattern. Members of "creche" groups spent more time resting during the day than other members of the herd.

NURSING

Contact between the dam and her calf occurred only during nursing bouts which varied in frequency from three times per day in the young calves to one or less in the juveniles prior to weaning. Figure 11 shows the times of day nursing (suckling) was recorded for calves of different ages. The nursing times were found to correspond with the end of resting or ruminating periods of the adults.

Nocturnal nursing periods and nocturnal activity of the calves could not be determined. However, from the spoor and the fact that concealment sites in the morning were sometimes as far as 3km from the last one on the previous day, it could be established that concealed calves were more active and spent more time with their dams at night. The calves may therefore also have suckled more at night than during the day. Thomas (1962) made similar observa=tions in captive gemsbok in which early morning nursing bout was a continuation of the last nocturnal nursing pe=riod in the same way as the late afternoon nursing bout extended into the night.

When the time came for a dam in a mixed herd to nurse her concealed calf, she would leave the herd, usually followed by the territorial male and approach the area where she had left the calf at the end of the previous nursing bout.

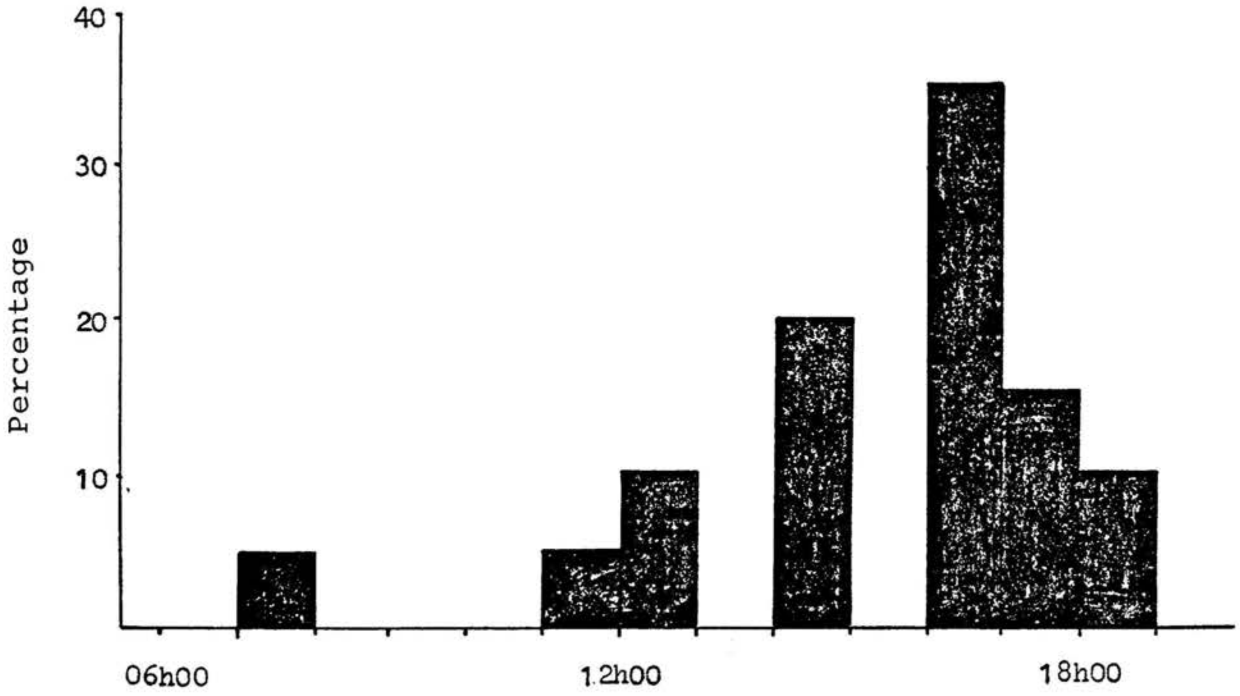

Fig. 11: Diurnal suckling times of gemsbok calves in the HMNR

In a nursery herd all the dams returned to the conceal=ment area at the same time. When she neared the conceal=ment site, the dam called her calf by means of a nasal whirr-like call. This vocalization was also heard when dams called their calves in a mixed herd. The concealed calf would then soon make its appearance and run towards its dam. Calves and juveniles in a herd were seen to approach rapidly from approximately 50m when called. Nursing then took place after naso-nasal contact between the dam and calf. Older calves would often begin to suckle without previous naso-nasal contact and the dam sniffed at the infant only after suckling had commenced. Eating of the calve's faeces by the mother was not observed in either concealed or older calves. A thorough search of concealment sites and surrounding area however revealed no faeces.

Vocalization by the calves was heard only when the indivi=duals were being handled or when concealed calves had been abandoned by their dams as was observed by Van der West=huizen* (pers. comm.). The dam had not returned to the neonate after parturition which had occurred during the night. On the second day the neonate was seen walking around near the parturition site, bleating. This vocali=zation could best be described as sounding like a repeti=tion of short "ehs".

Females with concealed calves were very wary of humans and seldom returned to their calves when they were aware of an observer, even when watched from a distance of 1,0km. The following observation was made when CM19 was two days old. When first sighted at 07h00 the dam AF04 and a territorial male TM13 were with the calf while a mixed herd was feed=ing 500m away. The dam and the male left the calf soon afterwards and rejoined the herd at 08h30. At 12h55 AF04 and TM13 left the herd and approached the concealment site

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*Mr P. van der Westhuizen, HMNR. P/Bag X1, Springbok, 8240.

of the calf. This time they were followed by three adult females and three juveniles. When AF04 located the calf it attempted to suckle between her forelegs at first, but soon found the teats and suckled for approximately thirty seconds. Suckling was interrupted when the dam chased away the curious juveniles. Suckling bouts lasted from thirty to sixty seconds and were interrupted by bouts of playful behaviour and running by the calf. Nursing was terminated after ten minutes when the dam walked towards the herd. The calf followed for approximately 20m but was prompted to remain behind by the dam. It wandered around for a few seconds and then lay down next to a low mesembreanthemum shrub with very little cover. At 16h30 AF04 and TM13 left the herd again and walked toward the area in which the calf lay concealed. The calf remained with the dam for the remainder of the diurnal hours (sun= set 17h00). On the following day the concealment site was approximately 1km from the previous one.

During the observation recorded above, TM13 showed no in= terest in the calf and did not interfere with the nursing. However interference by territorial males was observed on other occasions. This occurred mostly when the males at= tempted to mount the nursing female and active chasing of the calf by the male was then also observed.

Nursing of calves within a herd was synchronized and all individuals suckled within a period of five to ten minutes. This was attributed to the fact that nursing usually oc= curred after bouts of ruminating and resting, activities which were synchronized among animals in a herd. The fe= males would get up after resting and call their young or wander through the herd looking for their young. A dam with obviously distended teats was seen to approach her juvenile which was lying down and nuzzle it. The calf got up, sniffed at her perineum and then suckled vigorously. Nursing bouts gradually decreased as the calves were weaned.

CM19 was however once observed to suckle when he was 10 months old. This occurred during a synchronized nursing bout in a mixed herd. The female had probably been stimulated to nurse when she saw the other juveniles suckling, while the 10 month old CM19 was being opportunistic.

Suckling in gemsbok was of the normal bovid type, standing in the infants and kneeling as they grew larger. No vigorous tail wagging was observed during suckling. Nursing was usually terminated by the dams when they walked away and chased off persistent young with a head-low posture or with sweeping horns.

DISCUSSION

The mating behaviour of the gemsbok resembled that of the Beisa oryx, as described in detail by Walther (1958, 1961, 1965 and 1974). The main difference being that "Paarungskreisen" in gemsbok is thought not to form an obligatory part of the courtship display as it did in the Beisa oryx and is regarded rather, as a means by which an unreceptive female prevents a male from mounting. The gemsbok mating and the post-partum behaviour also shared features with the behaviour of the closely related roan and sable antelope (Joubert, 1970 and Grobler, 1973). This was in particular the courtship ritual and the concealment behaviour of the young.

Isolative behaviour of preparturient females did not occur for all births as it was greatly influenced by conspecifics, particularly by adult males. This may be as a result of scents emanating from preparturient female which resemble those of an oestrous female and therefore tend to arouse sexual interest in the males (Leuthold, 1977). Isolation and subsequent concealment were thought to be essential for the development of the mother/young bond during the critical period immediately after birth (Leuthold, 1977). Concealment of the calf also made it possible for the dam to remain in social contact with fellow herd members without endangering the mother/young bond.

The obvious advantages of concealment behaviour in relation to predators in ungulates have been discussed by Walther (1968 in Leuthold, 1977), Joubert (1970), Lent (1974) and Leuthold (1977). No large predators were found in the re=serve but calves were often chased by Hartmann zebra mares (Equus zebra hartmannae), who attempted to bite and kick them. Once the calf had joined the herd it could escape from the zebra by running in among the other members of the herd. Maternal defence, i.e. chasing of the zebra by the mother with lowered horns was only observed once. Walther (1965) made similar observations with Beisa oryx and "Damara-zebras" (Equus guagga antiquorum) in the Münch=ner Tierpark, Hellabrunn. He concluded that this aggres=sive behaviour in the zebra is stimulated by the size and colour of the infant which resembles that of a canid or feline predator. This could not be verified in the present study but it was interesting to note that only the small brown calves were chased even when there were older calves in the herd.

Gemsbok calves probably have non-functional interdigital glands as was found in Coke's hartebeest calves (Gosling, 1969). Gemsbok dams were never seen to walk directly to their concealed calves but would walk around near the pre=vious concealment site and call their calf which suggested that location of the calf was not done by smell. The scent of the calf is also reduced by the removal of the urine and the faeces by the mother and as the calf chooses the actual concealment site itself the possibility of the site being marked by the adult's scent is minimized. By lying very still and having no flight distance concealed neonates are difficult to detect. Thomas (1962) described concealed neonates as going into a "semi-catalyptic" state. Kruuk (1972) found that hyaenas passed within 2 - 3m of Thomson's gazelle lambs if these lay still. The longer flight dis=tance of older and therefore stronger infants enable it to have a head start on a predator which would increase its chances of escape.

Concealment behaviour in the gemsbok seems to contradict the assumption by Lent (1974) that the "follower" type of infant behaviour was more typical of migratory or nomadic species and that it also appeared to be a better strategy for open habitat species.

POPULATION STRUCTURE

INTRODUCTION

Ecologically, a population is a group of organisms of the same species occupying a particular space, albeit artificially restricted, as in this instance. This section deals with the sex ratio of the various age categories, the age structure and variations in group size of the population during the period May 1976 to June 1977.

Many ungulate species show seasonal variations in typical group size which can be correlated to the species' reproductive behaviour (Rodgers, 1977) or can be associated with the differences in either the amount of available food or the dispersion of food (Jarman, 1974). Food supply is directly affected by rainfall which would then have an indirect effect on the variations in group size (Leuthold, 1977).

METHODS

The network of roads in the Reserve was travelled at least once a week by vehicle and areas that were inaccessible to a vehicle were covered by foot. Whenever possible, with a bias for small herds, the sex and age composition of the whole herd was determined. Large herds could be accurately counted and sexed during activity studies. On 25 January 1977 the entire gemsbok population which consisted of 54 individuals could be classed into age and sex classes. The individuals occurred in six groups and included four solitary territorial males.

Ageing was based on the ageing criteria formulated with only three age categories being used. These were calves, sub-adults and adults. Sub-adult and adult males could be distinguished from the females in the field by means of their penile sheath. Young calves could only be sexed when they were observed urinating. Game censusses were conducted on a monthly basis. These took the form of drive counts during which observers walked within sight of each other along unmarked but regular routes. This technique was found to have deficiencies however, as a result of the terrain, where observers soon lost sight of each other and individual gemsbok were often double-counted. Nevertheless a general trend in population changes could be determined from these censusses.

All groups were placed into one of five size classes and the percentage frequency of occurrence of gemsbok per group size was determined on a monthly basis. The frequency of sightings of solitary males was determined in a similar way. The sightings of solitary females which made up an insignificant percentage of all gemsbok sightings were not taken into consideration.

To examine the physical factors influencing changes in group size, the mean monthly percentage moisture content of plant species eaten was determined (See Chapter 5).

RESULTS

SEX RATIOS

Table 3 shows the sex ratios of the gemsbok population as censussed on 25 January 1977.

Table 3: Sex and age categories of gemsbok as censussed on 25 January 1977.

Age Group	Number sexed		Ratio		Percentage		Chi-squares values	f-value
Adults	15	23	1,0	1,53	39,5	60,5	1,68	N.S.
S/Adults	3	3	1,0	1,0	50,0	50,0	-	-
Calves	5	5	1,0	1,0	50,0	50,0	-	-
All age groups	23	31	1,0	1,35	41,5	58,5	1,53	N.S.

Table 4: Seasonal variations in the occurrence of gems=bok herds in different herd classes

Group Size	"Wet"				"Dry"			
	n	$\bar{x}$	SD	%	n	$\bar{x}$	SD	%
1- 5	23	3,45	1,06	2,54	63	3,44	1,14	7,6
6-10	30	8,33	1,44	7,67	49	7,51	1,38	12,92
11-20	39	14,58	3,08	17,45	22	16,45	2,97	12,7
21-35	28	26,92	4,69	23,13	32	30,25	3,97	33,98
36-50	39	41,07	3,84	49,16	22	42,40	4,07	32,75
Seasonal total	157	20,36			188	15,48		

Calves

The sex ratio of the ten calves was 1:1.

Sub adults

This group also showed a sex ratio of 1:1.

Adults

The ratio of males to females was 1:1,53 which indicated a decline on male numbers of 26,8 percent when compared with the sub-adults and calves. The decline may possibly be attributed to a slight sex differentiated mortality affecting bachelor or potential territorial males. It is also exaggerated by the presence of old females originally introduced into the reserve.

HERD POPULATION STRUCTURE AND COMPOSITION

In the gemsbok population censussed on 25 January calves made up 18,5 percent of the population and the juveniles 11,1 percent. These two age classes, which together con=tributed toward the young of the year, give an indication of the recruitment rate for the period January 1976 to January 1977.

The ratio of adult females to young of the year was 1,44:1. However as approximately five of the females had not yet achieved full reproductive status during this period, the ratio of reproducing females to young would be reduced to 1,31:1.

With the short inter-calving interval and the high repro=ductive potential of a continuously breeding population of gemsbok, 20 percent of the adult females could be ex=pected to give birth twice per year. That is if the re=

productive potential of each adult female was realized. If there was no infant mortality, a theoretical ratio of 0,83 females per young would be achieved. However under natural conditions, the full reproductive potential of the female cannot always be realized. This can be attributed mainly to the erratic rainfall and therefore unpredictable seasons, which will interrupt the breeding cycles. Neonate mortality, as experienced during the serious drought in 1978 also contributes to a lower reproductive potential being realized (See Parturition intervals).

GROUP SIZE

Group size data were obtained from mixed herd records and are expressed as monthly frequency distributions of different herd size classes (Fig. 12).

Large herds of 36 - 50 individuals were recorded only during the months from June to November 1976. (The higher percentage in October). This period corresponded with the period of vegetative growth of the food plants (see Rösch, 1978). Correspondingly few records were obtained of gemsbok in the smaller herd classes during this period, and as could be expected, solitary territorial males were sighted more frequently then than during the following "dry" period (Table 4).

Records of gemsbok in the smaller herd class were obtained throughout the year with the exception of July and September. The highest percentage sightings of small herds was recorded in December 1976 and March 1977. A delayed correlation, by one month, was evident between the frequency of occurrence of gemsbok in the 36-50 herd category (r = 0.79) the 2-5 herd category (r = -0,71), and the monthly mean percentage moisture content of food plants. The monthly group size (Fig. 13) also showed a correlation with the plant moisture of the previous month (r = 0,72), which in turn showed a delayed correlation with rainfall (r = 0,66).

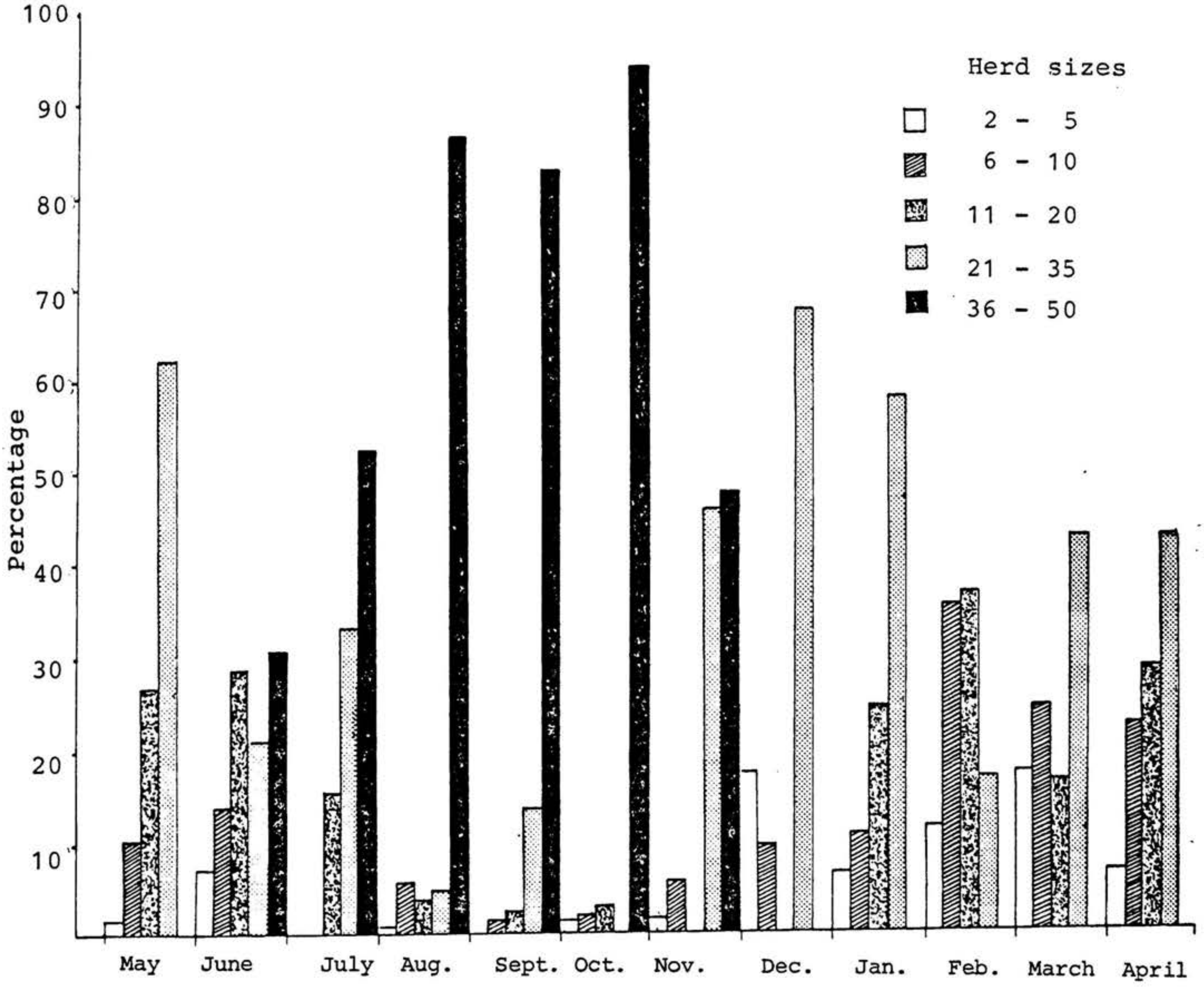

Fig. 12: Monthly variation in occurence of gemsbok in five herd classes, May 1976 to April 1977.

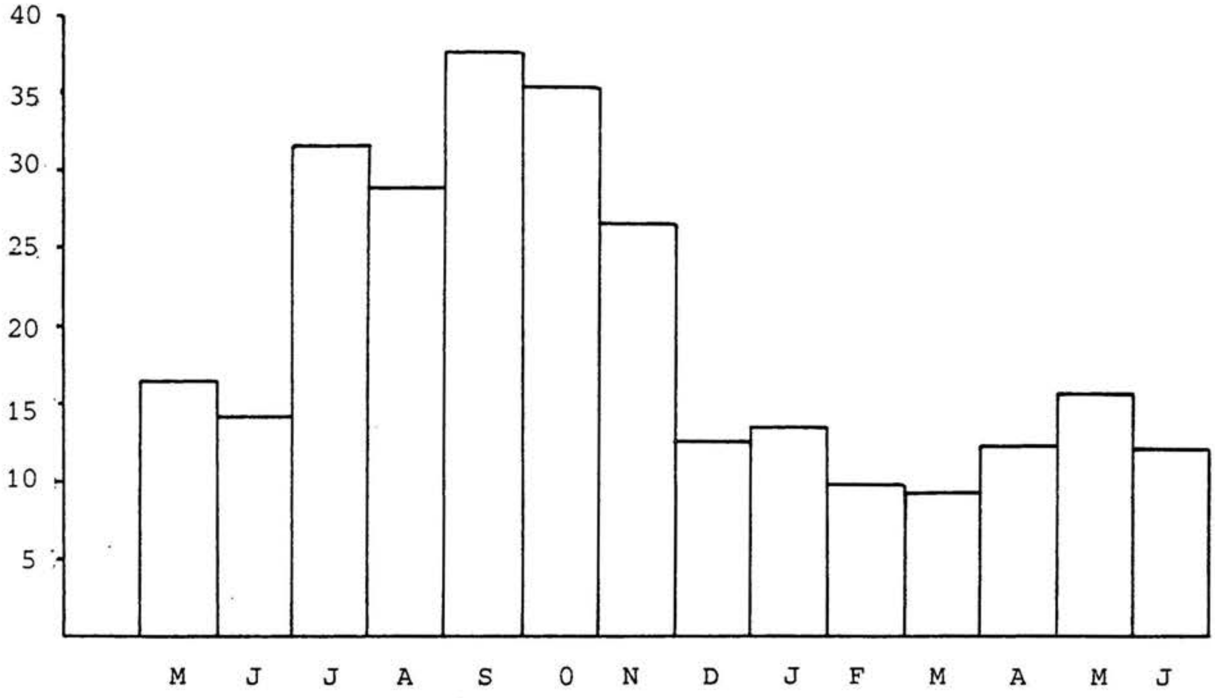

Fig. 13: Mean monthly herd sizes of mixed gemsbok herds in the HMNR May 1976 - June 1977.

DISCUSSION

During the wet season, when large quantities of flowering ephemerals were available, the food supply was dispersed uniformly and the gemsbok could feed in large herds with a close inter-individual distance, without competing for food. In the dry season, perennial plant species, which formed a major part of their diet at that time, were widely and unevenly dispersed and gemsbok therefore had to move greater distances between feeding stations. This resulted in a greater inter-individual distance being established, which ultimately led to the break-up of large herds into smaller groups. Variations in group size in gemsbok as in other species (Underwood, 1975, Rodger, 1977) was therefore also found to be influenced by rainfall, through the food plants.

CHAPTER 5: FEEDING ECOLOGY

INTRODUCTION

A knowledge of the food plant s utilized by particular species is essential for management purposes. It enables the evaluation of the suitability of a particular habitat.

Gemsbok are known to be essentially grazers but they also utilize dicotyledons and are classed as bulk and roughage eaters or mixed "rough" feeders (Van Zyl, 1965; Leistner, 1967; Dorst & Dandelot, 1970; Bigalke, 1971; Estes, 9171; Smithers, 1971; Pienaar, 1974; Leuthold 1977). In the Hester Malan Nature Reserve however, grasses constituted only a fractional percentage of the plant biomass and it was therefore possible to see how the gemsbok had adapted to a different habitat making use of the available food plants.

METHODS

Feeding records were obtained by carefully inspecting an area in which individual gemsbok or a herd had recently been feeding. All plants and plant parts that had been utilized were recorded. Some food records were also obtained from direct observations with the aid of a Wetzlar 40 x 60 dialyte scope. These records were however verified later by closer inspection.

Various techniques to determine food preference used by other workers (e.g. Goddard, 1968; Leuthold, 1971) could not be applied in this study as the gemsbok could not be approached close enough to identify all plant species eaten. Short ephemerals and grasses would have been underrepresented. Faecal analysis, which is commonly used for grazers was impractical because of the low percentage of grass in the Reserve and in the daily food intake.

Records were collected on a monthly basis, from as many areas in the reserve as possible. Samples of all species recorded during the month, were collected (before 10h00) weighed, ovendried to a constant mass and the percentage moisture content was determined. (Moisture content is thought to be related to mineral concentrations in plants which will possibly effect their palatability).

The importance value of the utilized perennial plant spe=cies in the vegetation was calculated for thirty-six 100m transects scattered through-out the Reserve subjectively, in areas most frequented by the gemsbok (see Fig. 2 of stu=dy area). The transects were sampled at 1m intervals and the importance value (i.v.) was calculated as follows: the mean of the relative % frequency + relative % density + relative % dominance.

RESULTS

The 145 food plants recorded for the gemsbok in HMNR are listed in the appendix according to Phillips (1951). Plant parts eaten as well as the months in which the re=cords were obtained, are also given. Table 5 gives the importance value of some of the utilized species.

The plant species are further categorized into four clas=ses (A - D), based on the number of months, they were re=corded as food plants. Class A contains species that were eaten throughout the year, during the wet and the dry season. Interruptions of 1 to 2 months were not taken as significant, as these may have resulted from a lack of re=cords rather than non-utilization. Class B contains the species utilized primarily during the wet season while Class C includes species utilized during the dry months. Class D contains plants that were only recorded sporadi=cally.

Class A contains only one grass species, Stipagrostis brevifolia which had the lowest importance value in the transects. This perennial species grows as a dense and prickly tussock in the reserve as a result of the heavy feeding pressure. Young shoots are eaten as soon as they grow beyond the prickly mass with the result that this species actually contributes minimally to the daily biomass consumed by the gemsbok. Nevertheless it is possibly the most preferred food plant in the reserve.

Of the shrubs in Class A Hermannia trifurca is one of the few adeciduous shrubs in the reserve and was therefore heavily utilized. It had an importance value of 2,1 and cannot be regarded as an economically important plant to the herbivores in the reserve. As with the former species, the majority of the plants were stunted, with a hedge-like appearance because of the high feeding pressure. In the north-eastern section of the reserve, in an area most frequented by springbok during the study, this species appeared to be underutilized and grew into metre high shrubs. When feeding on the stunted plants the gemsbok could only take in small quantities of leaves although pencil-thick twigs were often consumed during the dry season.

Osteospernum sinuatum, another shrub, was not recorded as a food plant during October and November when the leaves were drying. It was however recorded again in December and subsequent months when the leaves were completely dry and 1cm thick twigs were then also eaten. As the leaves were drying out the plant possibly became less palatable than other available species. During December however, it was again utilized as the gemsbok became less selective out of necessity and other available species had attained a similar level of palatability. Because of its high importance value, 5,2, the second highest of the utilized plants in Table 5 and its relative popularity, this species

Table 5: Importance values of some plant species in the Hester Malan Nature Reserve

Plant Species	Rel. % freq.	Rel. % density	Rel. % dominance	Importance value	Number months eaten
Ruschia robusta	2,98	12,97	17,3	11,08	not eaten
Leipoldtia pauciflora	3,52	9,42	7,38	6,77	8
Osteospermum sinuatum	3,52	5,36	6,74	5,21	12
Ruschia brevibracteata	2,56	4,86	7,48	4,97	8
Eriocephalus ericoides	3,11	4,80	5,64	4,52	not eaten
Galenia africana	3,93	4,25	6,47	4,88	not eaten
Tetragonia reduplicata	3,11	2,33	2,46	2,63	12
Hirpicum alienatum	2,56	2,72	2,03	2,44	7
Galenia sarcophylla	1,62	3,64	1,71	2,33	12
Hermannia trifurca	1,76	2,64	2,09	2,16	12
Hermannia dissermifolia	2,02	1,25	1,75	1,68	11
Wiborgia monoptera	1,35	0,47	0,52	0,78	9
Peliostomum virgatum	1,35	0,53	0,09	0,66	11
Aptosimum indivisum	0,94	0,75	0,07	0,59	11
Stipagrostis brevifolia	0,81	0,33	0,25	0,46	10
Ehrharta barbinodis	0,41	0,38	0,075	0,29	8
Stipagrostis namaquensis	0,13	0,027	0	0,05	9

is regarded as economically significant in the reserve.

Other shrub species such as *Monochlamys albicans*, *Tetragonia* cf. *reduplicata* and *Wiborgia monoptera* (I.V. 0,78) were also eaten when they contained no leaves, an indication of a high preference rating.

The forbs *Lineum aethiopicum*, *Aptosimum indivisum* (I.V. 0,59) and *Peliostomun virgatum* (I.V. 0,66) contained vegetative growth throughout the year although the normally succulent leaves of *L. aethiopicum* were quite dry in December and January. These species contributed minimally to the daily bulk consumed by the gemsbok.

The most important plants in this class in terms of biomass consumed, and preference rating were two ephemeral species, *Osteospernum amplectens* and *O. hyoceroides* which were plentiful during the wet season and were available throughout the dry season as well. During July and August these species contributed toward the largest percentage of daily plant biomass (bulk) consumed, their flowers giving the gemsbok dung an orange hue. The entire plant with the exception of the roots was utilized. In the dry season when their mean monthly percentage moisture content had decreased from 90,7% (July) to 3,9% (March) the two species still formed a large percentage of the gemsbok diet, although they existed only as dry stalks. A regurgitated bolus found in January consisted entirely of dry twigs of these species. The dry plants were still eaten at the beginning of the following wet season when young plants were already available.

As a result of the unpredictable and erratic rainfall in this region however, ephemeral plants cannot be considered in any management policy for the reserve.

Class B contains a sedge, *Scripus dioecus*, which occurs along some drainage lines and emphemeral rivers. Although it remained green in the dry season it was never utilized extensively and only small mouthfuls were taken of it.

Of the shrubs in this class the legume, _Lebeckia sericea_, was first recorded as a food plant when it was in flower in August. The flowers and fruiting bodies were eaten then while the leaves were utilized during the driest time of the year. The leaves of _Hermannia gariepina_ which occurs only on the southern plain of the reserve were extensively utilized by the gemsbok, even when the leaves were dry and powdery. (In this state they are harmful to domestic stock causing eye irritation (G. Cloete* pers. comm.).) This species and _Tribulus zeyheri_ were the most abundant plants on the plain and constituted the largest percentage of the diet of gemsbok when they remained in this area for months, in some instances. The whole _Tribulus_ plant was eaten, as it was broken off with a bit of the root by means of a short forward jab of the hoof.

The remaining species falling within this class were recorded as food plants mainly in the early wet season when young shoots were present, and again in the late dry season when the gemsbok ate what was available.

Class C, the largest of the four classes, contains eight grass species. These species were recorded only during the wet season after which they were completely grazed down and were therefore not available in the dry season.

The mesembreanthemums, which form the largest percentage of the plant biomass on the reserve, are also represented in this class. _Leipoltia pauciflora_ and _Ruschia brevibracteata_, had the highest and third highest importance values respectively of the utilized shrubs in the vegeta=

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* G. Cloete Hester Malan Nature Reserve, P/Bag X1
Springbok 8240.

tion transects (Table 5). *Ruschia robusta*, possibly the most abundant shrub in the reserve, with an importance value almost twice as high as any other shrub (11,08) (Table 5), was never recorded as a food plant. Mesembreanthemums generally did not contribute largely to the daily plant biomass consumed, (leaves, twigs and flowers were eaten), although they are adeciduous and still succulent during the dry season. A higher concentration of minerals in the leaves during this period probably made them unpalatable.

Only young shoots of *Galenia africana* were eaten but these records appeared to have been mostly experimenting by young gemsbok. *Grielum humifusum* was the only plant recorded in which the roots were deliberately dug up with the hooves (Fig. 14). The whole plant was consumed in the wet season and only the roots were available in the dry season. At this time, no sign of the plant was evident above ground while the remains of the succulent roots were approximately 5cm below the surface. These could be located by the gemsbok and were dug up.

The hooves were also used when gemsbok were feeding on *Lotononis brachyloba*, a small prostrate legume growing in disturbed sandy areas particularly on the old lands. In this case the plant was "kicked" out while the animals were feeding (forward jab of hoof as for *T. zeyheri*) rather than definite pawing action as was recorded for the previous species.

The remaining class, *Class D* contains species that were recorded as food plants once or twice only and includes the economically important shrub (for domestic stock) *Salsola tuberculosa*. This shrub was also eaten during the drought in 1978 when the gemsbok had resorted to eating accumulated litter around the entrance of termite burrows and small *Leipoltia pauciflora* plants.

Fig. 14: *Grielum humifusum* plants dug up by gemsbok

Two Curcubitaceae species fall into this class, Citrullus lanatus and Cucumis africanus. Only the fruits were eaten and as a result of competion from porcupines, Hystrix africaustralis, they were available for only a short time.

DISCUSSION

The seasonal but irregular rainfall regime in Namaqualand produces pronounced temporal changes in the quantity and quality of plant species which is reflected in the oppor= tunistic feeding habits of the gemsbok in the reserve, with availability playing the major role in selection. Of the 582 species listed by Rösch (1978) 24,9% (145) were record= ed as food plants for the gemsbok while Van Zyl (1965) found that the gemsbok in S.A. Lombard Nature Reserve uti= lized only 12,5% (33) of the available species. The higher percentage plants utilized by the HMNR gemsbok may be ex= plained by the virtual lack of grasses, their preferred food plants and the seasonal fluctuations of species diver= sity and biomass.

This situation is aggravated by their restricted or non= migratory existence. Migrating ungulates feed upon a nar= row range of forage components, i.e. on only few forage species (Talbot and Talbot, 1963) or on a specific growth stage or stratum of vegetation (Vesey-Fitzgerald 1960, Bell 1971).

Faced with seasonally fluctuating conditions - variations in the nutritional quality of many forage species related to the variations in the plant moisture content, gemsbok in HMNR have out of necessity become less selective than animals in a more suitable habitat.

For example the gemsbok feed on a particular species du= ring the wet season when the plant moisture content is high. When the moisture content reaches a certain level at the end of the dry season, the gemsbok stop feeding on this plant and continue eating other species. At the end of the dry season they may again feed on the former species although the plant moisture content is much lower than what it was at the end of the wet season. This switch back can be attributed to the gemsbok eating what is available i.e. plants that are still green or have a higher moisture content than the majority of species. Exceptions to this rule are some of the ephemerals which are eaten even when their moisture level is as low as three percent, which does not appear to influence their palatability. Dry emphemerals were still eaten when young plants were already available in the following season. The variation in percentage moisture content of perrenial plant species eaten throughout the year appeared not to have effected their palatability e.g. Hermannia trifurca, an indication of a high preference rating.

DRINKING

No drinking records were obtained during the period May to September indicated by the lack of tracks at the watering points during this period. The frequency of drinking could not be ascertained in the dry period as the animals drank at night, in some instances only after 22h00. At the end of the dry season the animals drank at sunset. They remained in the vicinity of the water throughout the night and could be found there early the next morning before they moved to their diurnal feeding and resting sites.

CHAPTER 6: SPATIAL DISTRIBUTION AND MOVEMENT PATTERN

INTRODUCTION

The salient feature of the perennial vegetation throughout the reserve is its homogenity, both floristically and structurally with the result that variations in habitat are related primarily to the topography. Exceptions are the disturbed old lands in which the vegetation structure and composition has been artificially modified to a retrogres=sive successional state. Habitat selection studies were therefore not undertaken although daily and seasonal move=ment patterns were determined.

METHODS

Diurnal movement patterns of gemsbok herds were recorded during activity studies. The general path of movement of the entire herd was plotted directly onto an aerial photo=graph. Nocturnal herd movements were recorded only as the distance travelled between two consecutive diurnal sight=ings. A straight line between the two sightings was taken as the minimum distance travelled. All sightings of indivi=dual gemsbok and of herds were recorded on a gridded aerial photograph where the grid sizes in the field were approx=imately 350m x 350m. An accuracy of ±50cm could be obtain=ed and in the case of large herds scattered over a number of grids, all grids were plotted. Records were grouped in=to three classes; i.e. one sighting per block, 2 - 5 sight=ings and more than five sightings, based on the technique used by Mason (1976).

Five rain gauges were distributed in the reserve (Fig. 2) with the aim of determining the effect of isolated or loca=lized showers of rainfall and seasonal variations in rain=fall on gemsbok movement patterns.

RESULTS AND DISCUSSION

The diurnal movement patterns of gemsbok herds on four dif= ferent days are shown in Figs. 15.

On 3 July 1976 a herd of 20 individuals was first sighted at 07h40. They were feeding on ephemeral plants amongst the shrubs while slowly walking in a south-easterly direc= tion toward the old land. The land contained few shrubs and was covered at the time by the prostrate ephemeral Lotononis brachyloba. The herd remained on the old land from approximately 08h20 until 14h50 resting and ruminating and intermittently feeding, never moving out of an area of approximately 1ha. At 14h50 the gemsbok then walked, while feeding, in the direction from which they had come in the morning. The total area in which the gemsbok had moved during that day was approximately 50ha covering a dis= tance of not more than 2km.

During the diurnal movement pattern plotted on 31 May 1977 (Fig. 15) a herd of fourteen individuals was seen at 08h00 in a dry stream bed, feeding and walking in an easter= ly direction into a strong wind. At 11h40 the gemsbok lay down in the leeward side of the koppie to rest and ruminate. Between 15h00 and 17h15 they fed in the vicinity of their resting site and then walked while feeding to the dry stream bed. Area covered, approximately 115ha.

Two dry season diurnal movement patterns were plotted on 17 November 1976 and 18 March 1977 (Fig. 15). On 17 No= vember a mixed herd of 37 animals was sighted at 06h00 at an artificial watering point where they had been drinking. From here they moved to the old land (as in 3 July plotting) while feeding. They remained on the old land from 08h40 until 16h30 when they moved back toward the water point where they were again seen on the following morning. Area covered, approximately 100ha.

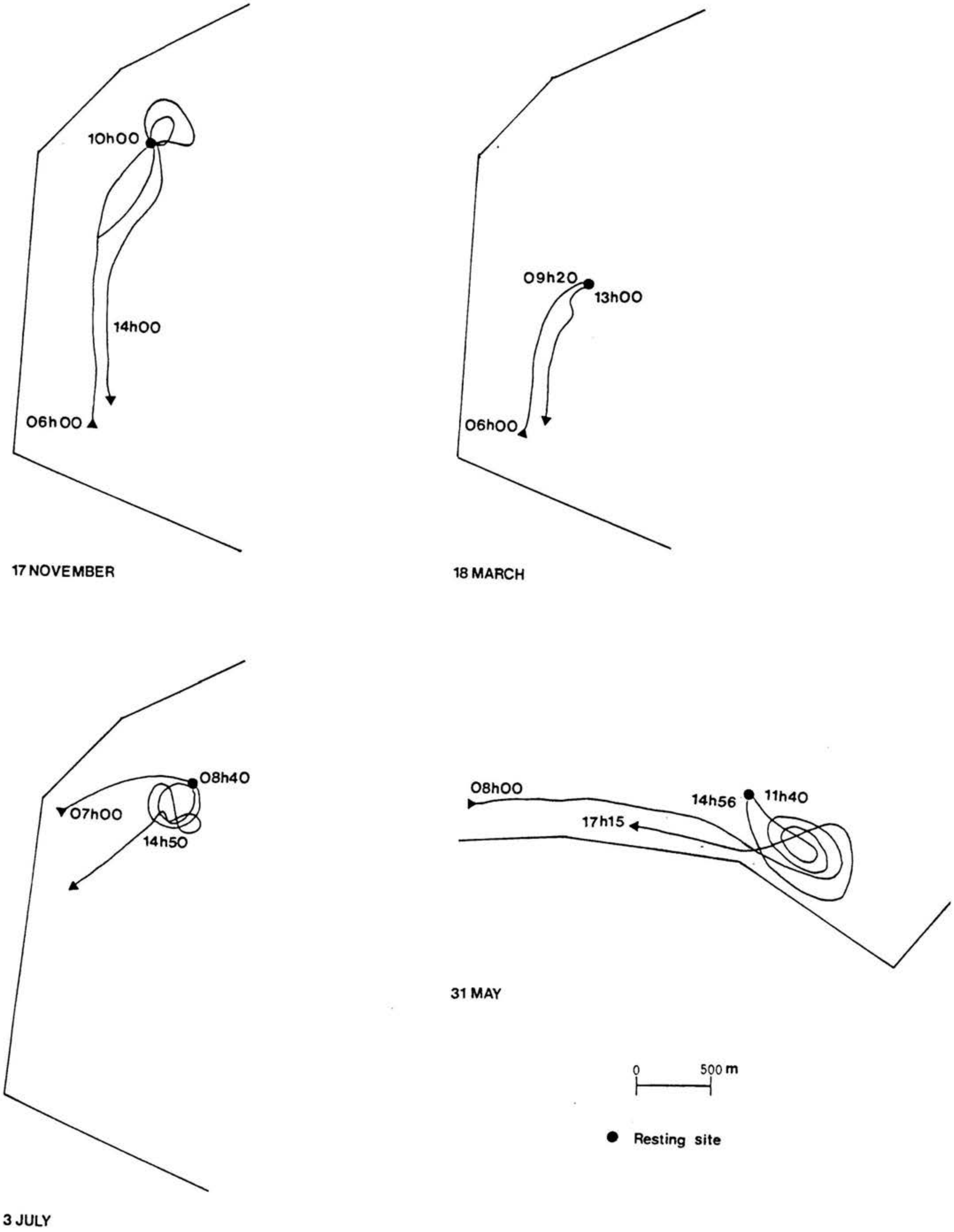

Fig. 15: Diurnal movement pattern of gemsbok herds on four different days (See text for explanation, p.65)

On 18 March a herd of 11 individuals moved from the same watering point approximately 1km to the koppie where they rested in the shade of large boulders from 09h00 until 13h00 and then walked back to the water. Area covered approximately 50ha.

In the wet season diurnal movement occurred between a nocturnal feeding site and the daily resting site. The resting site on the old land which was also used during the dry season was an open sparsely vegetated sandy area with few wind barriers. On the sandy plain in the south the gemsbok lay in the open or on the leeward side of the koppies or in the shade of large boulders.

Dry season patterns were determined by the movement between a drinking site and the lying site and depending on how far these were apart, were usually longer than the wet season pattern.

NOCTURNAL MOVEMENT PATTERN

The wet season nocturnal movement pattern of adult female 02 and associated herds is shown in Fig. 16, while the approximate distances covered between sightings are shown in Table 6. The longest distance covered during one night was 4,17km.

In the dry season the mean distance walked by individual gemsbok or herds at night did not differ significantly from that walked in the wet season (Fig. 17 & Table 7). There was however a greater fluctuation in herd sizes in the dry season and when the herds split up only some of the individuals left the diurnal feeding site compared with the movement of the entire herd in the wet season. Movement of individuals rather than the herd - in the dry season.

At night the gemsbok covered greater distances than during

Fig. 16: Nocturnal movement pattern of AF02 and associat= ed herds in the "wet" season

Table 6: The nocturnal movement pattern of AF02 and associated herds during the "wet" season

	"WET" SEASON		
Sighting	Date	Size of associated herd	Shortest distance between sightings (km)
	1976		
1	4 May	24	
2	6 May	24	
3	9 May	24	
4	20 May	1	
5	24 May-12 June	14-29	
6	13 June	5	2,93
7	23-26 June	25-37	
8	28 June	40	
9	3 July	20	
10	5 July	22	
11	6 July	17	0,37
12	10-16 July	34-40	
13	19 July	40	
14	31 July	38	
15	2-3 August	38	
16	4 August	40	2,07
17	5-6 August	39-40	
18	7 August	40	3,17
19	12 August	39	1,24
20	13 August	40	2,09
21	14 August	2	0,86
22	17 August	40	
23	18 August	40	2,34
24	19 August	40	4,17
25	20-21 August	38	0,96
26	22 August	38	2,07
27	23 August	40	1,65
28	24 August	40	0,51
29	28 August	39	
30	29 August	35	0,93
31	2 September	33	
32	3 September	36	2,93
33	11-12 September	40-49	
34	14 September	49	1,13
35	15 September	49	1,13
36	16 September	35	
37	17 September	37	1,13
38	20-21 September	25-48	
39	23 September	49	
40	25 September	2	
41	26 September	49	1,03
42	29 September	39	
	1977		
91	13 April	4	
92	18 April-12 May	10-30	

Mean distance walked
at night : 1,72km
Range : 0,37-4,17km
SD : 1,02
n : 19

Most days
spent at one
location
= 24

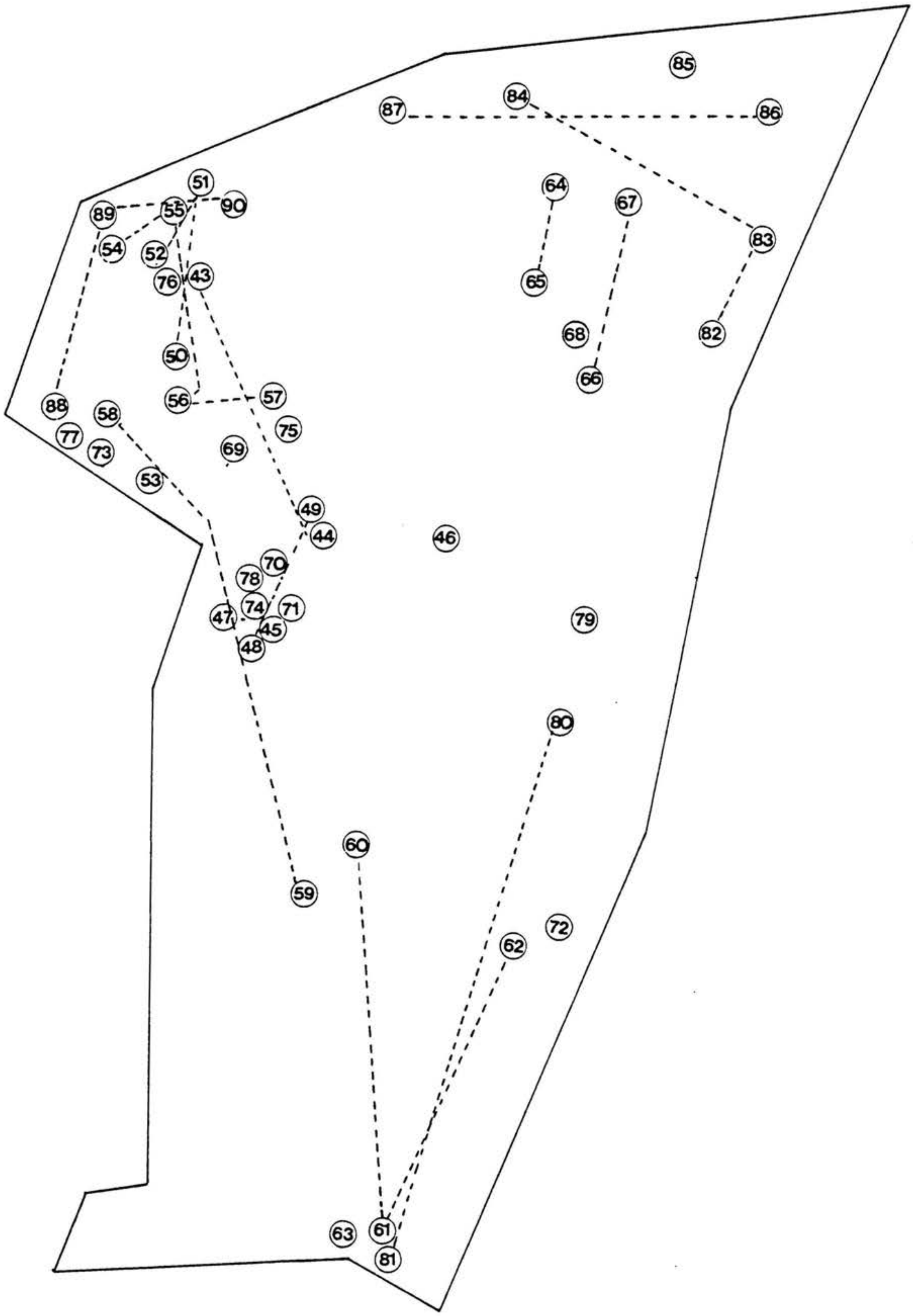

Fig. 17: Nocturnal movement pattern of AF02 and associated herds in the "dry" season

Table 7: The nocturnal movement pattern of AF02 and associated herds during the "dry" season

Sighting No	Date	Size of associated herd	Shortest distance between sightings (km)
	"DRY" SEASON		
	1976		
43	2 October	48	2,34
44	3 October	2	
45	5 October	48	
46	8 October	48	
47	11 October	5	
48	13-16 October	4-43	1,10
49	17-18 October	44	1,48
50	24 October	44	0,79
51	25 October	44	
52	26 October	8	
53	31 October	4	
54	5 November	10	0,58
55	6-7 November	10	1,51
56	8 November	6	0,79
57	9 November	40	
58	11 November	38	4,34
59	12 November	3	
60	15-17 November	1	3,03
61	18 November	2	2,48
62	19 November	1	
63	24 November	2	
64	11 December	3	0,79
65	12 December	6	
66	15 December	5	1,48
67	16 December	5	
68	19 December	6	
	1977		
69	12 January	27	1,00
70	13 January	16	0,41
71	24 January	3	
72	17 January	7	
73	23 January	2	
74	25 January	3	
75	27 January	4	
76	29 January	33	
77	30 January	33	
78	16 February	6	
79	19-20 February	19	
80	21 February	3	4,48
81	22 February-14 March	8-10	
82	16 March	5	0,86
83	17 March	31	2,24
84	18 March	31	
85	20 March	2	
86	22 March	27	3,03
87	23 March	2	
88	25 March	31	1,55
89	26 March	31	1,13
90	27 March	31	

Mean distance walked
at night : 1,77km
Range : 0,41-4,48km
SD : 1,18
n : 20

Most days spent
at one location
= 20

the day in which movements were confined mainly to feeding bouts or walking between resting, drinking and feeding sites. Nocturnal walking resulted in the change of feeding sites. At night the gemsbok also made more use of the koppie slopes and plateaux, where they were seldom seen during the day.

When the herd was on the move as in the early morning, the individuals were mostly engaged in feeding. No gemsbok were conspicuous because of any distinctive behaviour and a territorial male if present was usually not readily distinguishable. However if the herd was heading toward a neighbouring territory when the incumbent was near the boundary, the first territorial male became conspicuous through his efforts to interfere with the movement of the herd (see chapter on territoriality). Bachelor males were scattered within the herd, forming no specific aggregation. The calves were the only members of a herd that remained in close proximity with each other, but not near their dams during herd movements.

During directional movements which were also initiated and lead by an adult female, the majority of the herd members were not engaged in feeding. This type of movement usually occurred along game paths with the gemsbok walking in a line.

A more restless movement pattern in the dry season may be related to their natural migratory instincts. Although the mean distances covered per night do not differ significantly between wet and dry season, the largest distance between two sight records was recorded at the end of the dry season (Table 7).

Gemsbok movement patterns could not be related directly to the rainfall pattern in the Reserve. A large herd (31) congregated in the north eastern section of the Reserve only 12 days after 22mm of rain was recorded there on 4 March 1977 while 1,7 - 9mm were recorded at the other gauges. The springbok and zebra also congregated in this area at that time.

The animals remained in the area because of the green flush but it would appear that they were not attracted to the area by the higher rainfall. The relatively small area of the Reserve restricted this type of study but if the rain=fall had been more isolated than was the case it could be speculated that a correlation between movement and rainfall would be obtained. It is assumed (Leuthold, 1977) that animals possess the ability to perceive even very local rainstorms over considerable distances.

SEASONAL DISTRIBUTION

The change in observed diurnal distribution of gemsbok in the Reserve between the wet and dry season is shown in Figs. 18 and 19. For both seasons there was a markedly higher frequency of sightings on the plains and koppie pla=teaux than on the slopes. During the wet season in 1976 the gemsbok were frequently sighted on the southern sandy plain and in the flat north western section of the Reserve which included the old land. This distribution pattern is related to the good ephemeral growth in both these areas during that season. In the dry season the gemsbok appear to have a more spread out distribution with a high frequen=cy of sightings scattered throughout the reserve. The occurrence of the gemsbok in smaller herds during this sea=son, and the decrease in available food, requiring a larger searching area appear to have contributed to this distribu=tion pattern. During this season the gemsbok were frequent=ly sighted along the ephemeral streams and drainage lines, particularly along the eastern streambed which contained a permanent natural waterhole. Green plants were available here for a longer time than in surrounding areas.

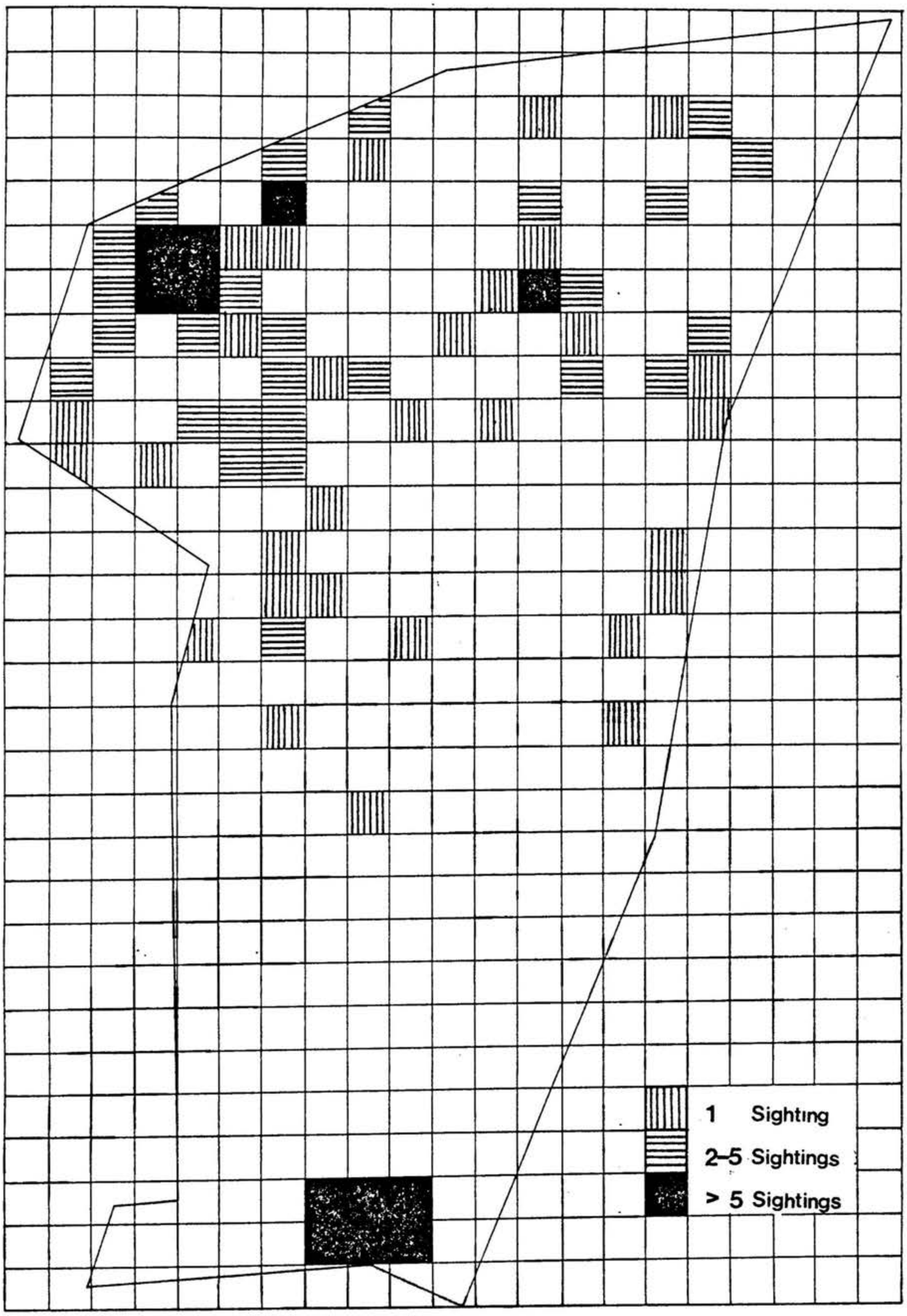

Fig. 18: Distribution pattern of gemsbok in the "wet" season

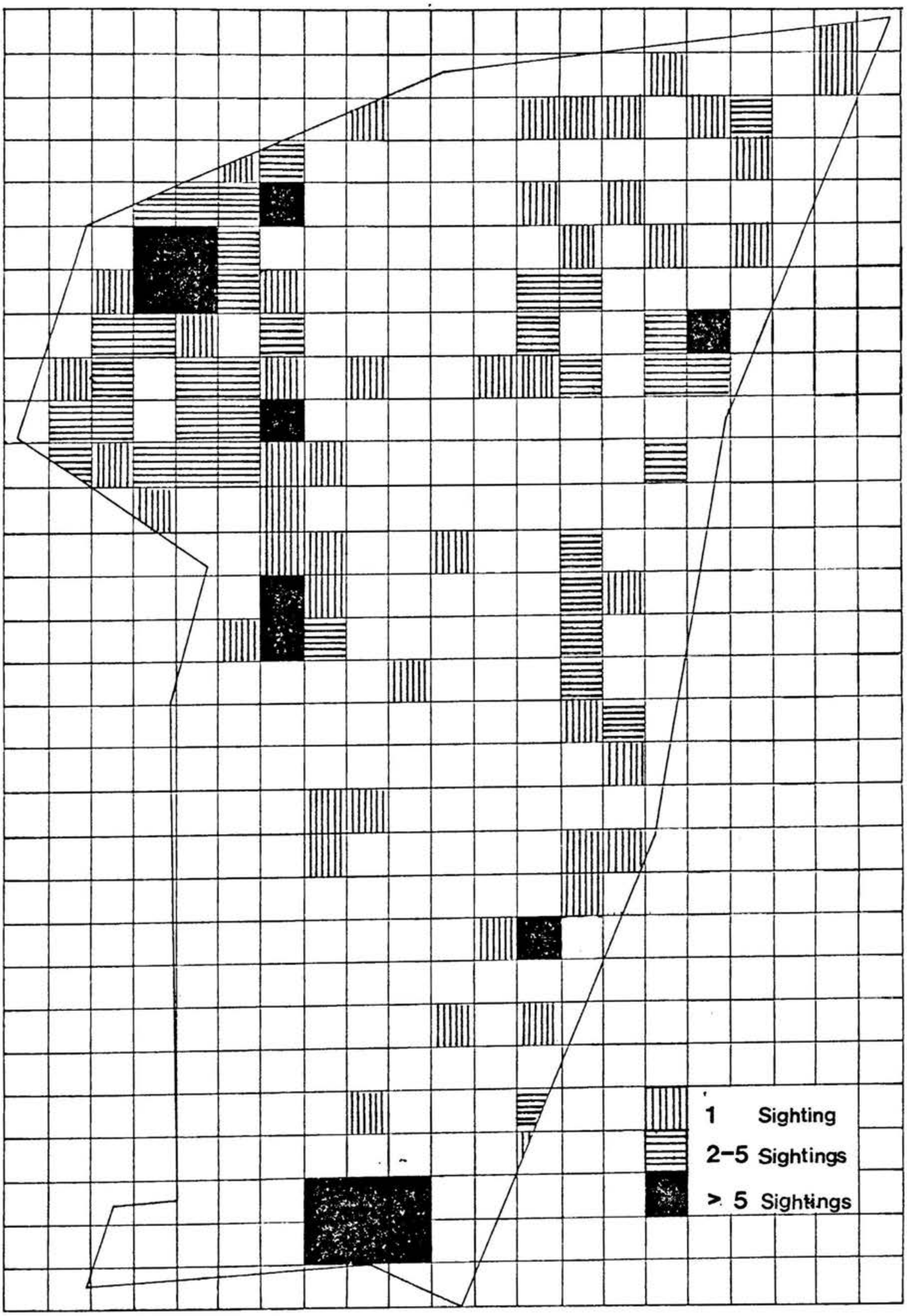

Fig. 19: Distribution pattern of gemsbok in the "dry" season

CHAPTER 7: DIURNAL ACTIVITY PATTERNS

INTRODUCTION

A knowledge of the activity pattern of the gemsbok was required to provide background information for the wider behavioural and ecological study. The basic activity patterns are described, as well as changes in the activity in relation to changes in environmental factors. Standardized procedures were used to allow for direct comparison with other species.

The collection of data was based on the 4-minute recording interval method, devised by Harker, Taylor and Rollinson (1954) to study the activity of zebu cattle in Uganda. This method has since been used for a number of wild herbivores in eastern and southern Africa (Spinage, 1968; Clough and Hassan, 1970; Jarman and Jarman, 1973; Wyatt and Eltingham, 1974; Lewis, 1975, 1977; Grimsdell and Field, 1976) while similar techniques were used in studies elsewhere (Owen, 1970; Joubert, 1972; Walther, 1973, 1978; Kok, 1975; Waser, 1975).

METHODS

Diurnal activity was recorded between 06h00 and 19h00 on one day per week. The procedure normally followed, consisted of locating a group of gemsbok as shortly as possible after first light and observing them from a stationary vehicle at distances varying from approximately 50 to 200m, until twilight. For most observations it was possible to remain on one vantage point throughout the entire observation, while occasionally it was required to follow the herd. This was done without disturbing their activity pattern as the gemsbok became accustomed to the vehicle.

Selected individuals (17 in all) which were easily recognizable, were used for recurrent activity studies, for as many as 27, while the activities of individuals which were recognizable only when in a particular herd, were recorded only once.

The following activity categories were recorded:

feeding, resting-standing, resting-lying, ruminating-standing, ruminating-lying and other, which included directional movement (walking without feeding), sexual activity (circling, mounting, copulation), comfort behaviour and social interactions i.e. dominance displays. Ruminating was identified by the lateral jaw movement which could be seen with the aid of a 40 x 60 telescope. If the head of the animal was obscured in some way, the activity was recorded as undetermined-standing or lying.

The activity of individual animals (2 - 8) as well as that of the herd was recorded at 4-minute intervals. Herd activity was taken to be the activity performed by the majority of herd members at that particular time.

Meteorological data were obtained during the activity study at 20 min. intervals and consisted of the following variables: ambient temperature and relative humidity (which were obtained from a wet and dry bulb thermometer placed 1,5m above the ground in the shade of the vehicle), four categories of wind direction (NE, NW, SE and SW) wind strength (determined subjectively - no wind, mild, moderate and strong) and climatic conditions (rain, overcast, scattered clouds and clear).

Field data were transferred to a computer tape and cards and activity was summarized for individuals, age and sex classes and different herd sizes into: hourly, daily, monthly and seasonal patterns as well as under meteorological variables.

Nocturnal activity studies were attempted during all phases of the moon with the aid of an image - intensifier star=light telescope. The gemsbok as well as many of the activi=ties could not be recognized without major disturbance to the activity pattern. This study was therefore disconti=nued.

RESULTS

A sample of 495h of diurnal activity studies was obtained on 56 days covering a period of 14 months.

A. GENERAL DAILY ACTIVITY

1. Feeding

This was the most time consuming activity taking up 47,3% to 62,0% of the day. Feeding activity was al=ways recorded at first light and was the last activi=ty recorded before dark. Feeding was recorded during all hours of the day, usually with two major peaks, at dawn and at dusk, and a minor peak around midday. In the herd activity, some members of the herd were continuously feeding even during the resting periods.

The gemsbok fed in a slow but almost continuous for=ward movement, when feeding on ephemeral plants. This movement was however interrupted when they fed on the prostrate plants such as *Lotononis brachyloba* and *Tribulus zeyheri.* Feeding on large ephemerals or browse also interrupted the continuous movement. During intensive feeding bouts such as at dawn and dusk the gemsbok walked toward specific areas - rest=ing site or watering point, with all members of the herd facing in the same direction. During the midday feeding bouts in the vicinity of the rest site, indi=viduals moved around in a zig-zag pattern but remained in a relatively small area in the vicinity of the herd.

2. Drinking

This activity was not recorded during the activity studies. From April - September 1976 the gemsbok did not drink at any of the watering points in the reserve. (Watering points were checked on a weekly basis for tracks).

In the dry season the gemsbok were recorded drinking at dawn (07h00) and late afternoon (17h00). At the watering point near the houses gemsbok were seen drinking at 22h00 (at which time there was no more disturbance from the houses, therefore possibly unnatural).

3. Ruminating

Ruminating activity is divided into ruminating-lying and ruminating-standing and was the third most time-consuming activity during the day and usually followed a feeding bout but was also recorded at the end of a resting bout.

Ruminating-lying was recorded during all months of the year while the gemsbok only ruminated while standing during the dry months in this instance from September 1976 to April 1977. This was related to the higher diurnal temperatures when the gemsbok only lay down if large enough patches of shade were available, i.e. next to a large rock or under a large shrub or *Aloe dichotoma*. If shade was limited its availability became dominance dependent. When there was no shade the gemsbok stood facing away from the sun during the hottest time of the day.

4. Resting

This activity also consisted of resting-lying and rest=

ing-standing and as with ruminating it also showed seasonal variations. Lying, as with feeding, is contagious among members of a herd. If one individual lies down others soon follow. When the herd arrived at a particular lying site at the end of a feeding bout the majority of individuals would lie down within a few minutes while others still fed or groomed. At low temperatures, with a wind, gemsbok would lie behind a shrub, while at higher temperatures they would lie in the open, facing into the wind. This was particularly evident in August and September when they were pestered by insects more than during other months. By facing into the wind the head was kept relatively free of insects. During this time the gemsbok were also more restless than in the other months, standing up frequently (not detectable in the histograms of individuals). The tail cannot be swished to chase the flies when the animal is lying down, therefore when their irritation becomes too intense the animal stands up. Hence the long standing bouts in herd activity for September (Fig. 22a).

Lying gemsbok usually adopt a posture with the head held erect. Short bouts of deep sleep were recorded when the gemsbok tucked their heads onto their flanks. When resting while standing the gemsbok never lowered their heads below the height of the shoulder.

5. Grooming

This activity was under-represented in the procedure used as casual grooming while the animal was engaged in another activity i.e. feeding, resting or ruminating was not recorded. Continuous bouts of grooming (longer than four minutes) were however recorded occasionally, particularly during increased insect disturbance (ob=

vious from the intensified swishing of the tail). Grooming was recorded with more regularity for juveniles than for adult animals.

Allogrooming was not recorded.

6. Directional movement

Walking without feeding was not recorded frequently, either at the end of the major morning feeding bout when the herd was near a lying site, or mostly when the herd was moving toward a nocturnal feeding site or watering point at dusk. A long "evening move" was also observed for fringed eared oryx (*O. beisa callotis*) by Walther (1978).

Young calves, which were not yet weaned, spent some of the time during which the herd was feeding, just walking, keeping up with the herd, a form of directional movement.

7. Sexual activity

This activity, which included intensive following of a female by a male, circling and mounting, was recorded mainly while the gemsbok were feeding with the result that it had a similar temporal distribution pattern as feeding activity. Sexual activity was the privilege of the territorial males and occasionaly of dominant males in a mixed herd. It was recorded at all temperatures and climatic conditions, in one instance at 2°C, in the sleet.

8. Playing

Recorded for calves and juveniles and peaks coincided with the end of the dawn and the beginning of the dusk feeding bouts.

9. Other social interactions

a. Territorial and Dominance displays. These are dependent on the presence of oestrus females in the herd and the proximity of the herd to a territorial boundary and therefore also a change in territorial male's ownership. Occasional dominance displays by females were seen when the availability of shade became critical.

b. Low and High intensity fighting. The former activity was recorded more frequently while the latter could be related to aspects of territorial display and was rarely seen and not recorded during an activity study.

Low intensity fighting was the step after playing for juvenile, sub-adult as well as adult gemsbok. It was rarely recorded for territorial males as their proof of dominance was achieved by means of displays. This activity was recorded mainly at the beginning of the dusk feeding bout.

B. INTER-INDIVIDUAL VARIATIONS IN THE ACTIVITY PATTERN DURING ONE DAY

The percentage of the day spent at different activities by eight individuals and a herd of 25 on 20 September 1976 is shown in Table 8 while Figure 20a and b shows their activity pattern hour by hour.

The basic activity patterns of the individual animals and the herd showed little variation in the temporal distribution, in which a certain sequence of activity occurs, while variations are more obvious in the overall proportion of the different activity. The mean activity patterns for males and females show no significant differences. The alternations of feeding and

Table 8: Percentage of the day spent at different activities by individual gemsbok and the herd on a particular day

Gemsbok Refe= rence No.	Sex	Age	Feeding	Rumi= nating Stand= ing	Rumi= nating lying	Rumi= nating Total	Resting Standing	Resting Lying	Resting Total	Lying Total	Standing Total	Other
09	♂	Adult	50,0	-	18,9	18,9	2,2	28,9	31,1	47,8	2,2	
10	♂	Adult	48,3	-	14,4	14,4	5,0	26,7	31,7	41,1	5,0	5,6
13	♂	Adult Territorial	42,2	-	15,0	15,0	0,6	36,1	36,7	51,1	0,6	6,1
23	♂	Juvenile	48,6	-	15,4	16,4	1,7	32,2	33,9	48,6	1,7	1,1
02	♀	Adult	36,1	-	21,7	21,7	1,1	40,6	41,7	62,3	1,1	0,6
14	♀	Adult	55,5	-	18,3	18,3	3,9	22,2	26,1	40,5	3,9	
07	♀	Juvenile	56,7	-	8,9	8,9	1,7	32,2	33,9	41,1	1,7	0,6
22	♀	Calf	46,7	-	8,9	8,9	2,8	40,6	43,4	49,5	2,8	1,1
Mean	♂♂		47,3	-	16,2	16,2	2,4	31,0	33,4	47,2	2,4	3,2
Mean	♀♀		48,7	-	14,5	14,5	2,4	33,9	36,3	48,4	2,4	0,6
Herd			48,7	-	22,2	22,2	2,2	26,7	28,9	48,9	2,2	

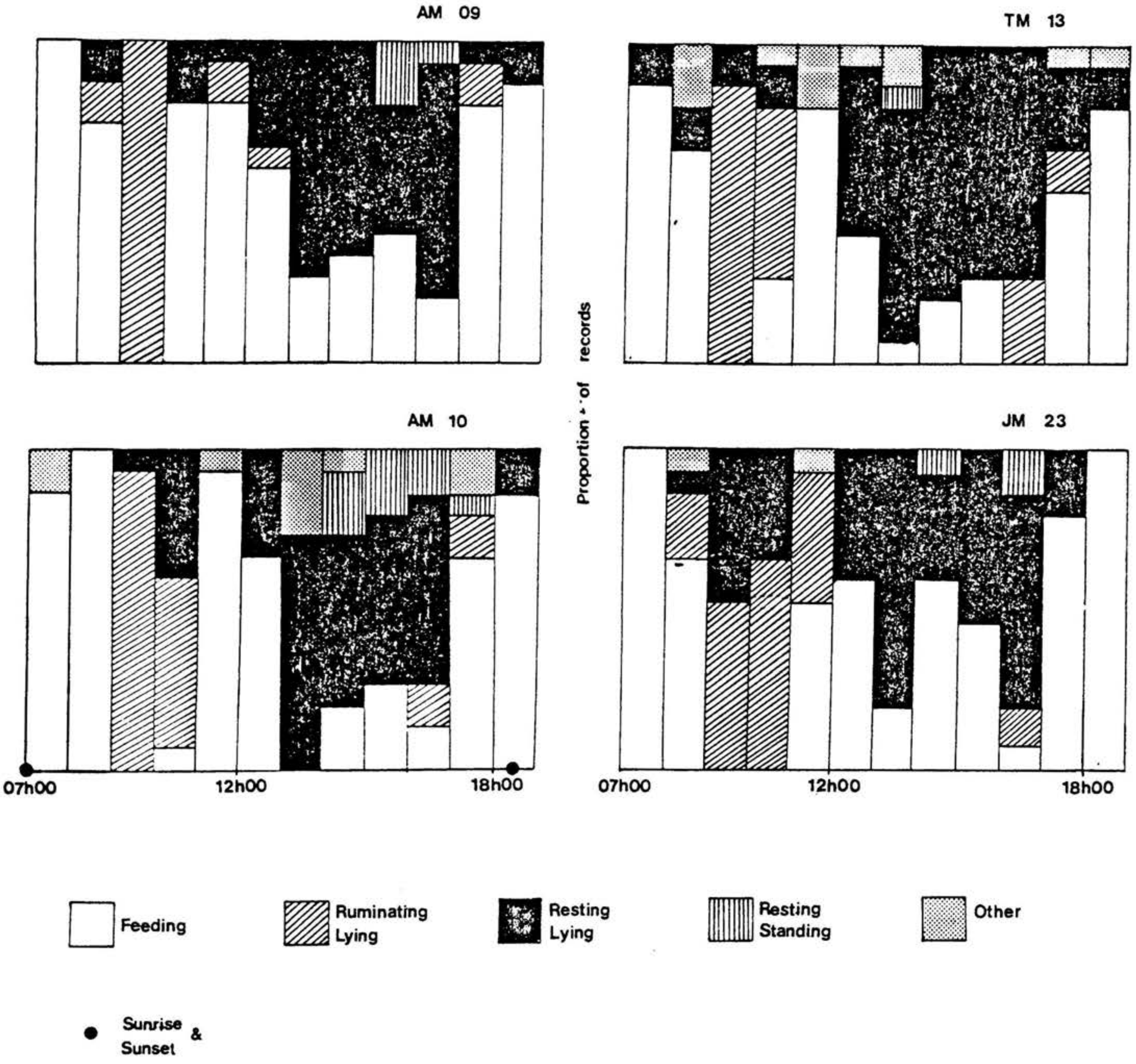

Fig. 20a: Diurnal activity pattern of four gemsbok males on 20/9/76. (Terrirotiral male 13, adult males 09 and 10, and juvenile male 23)

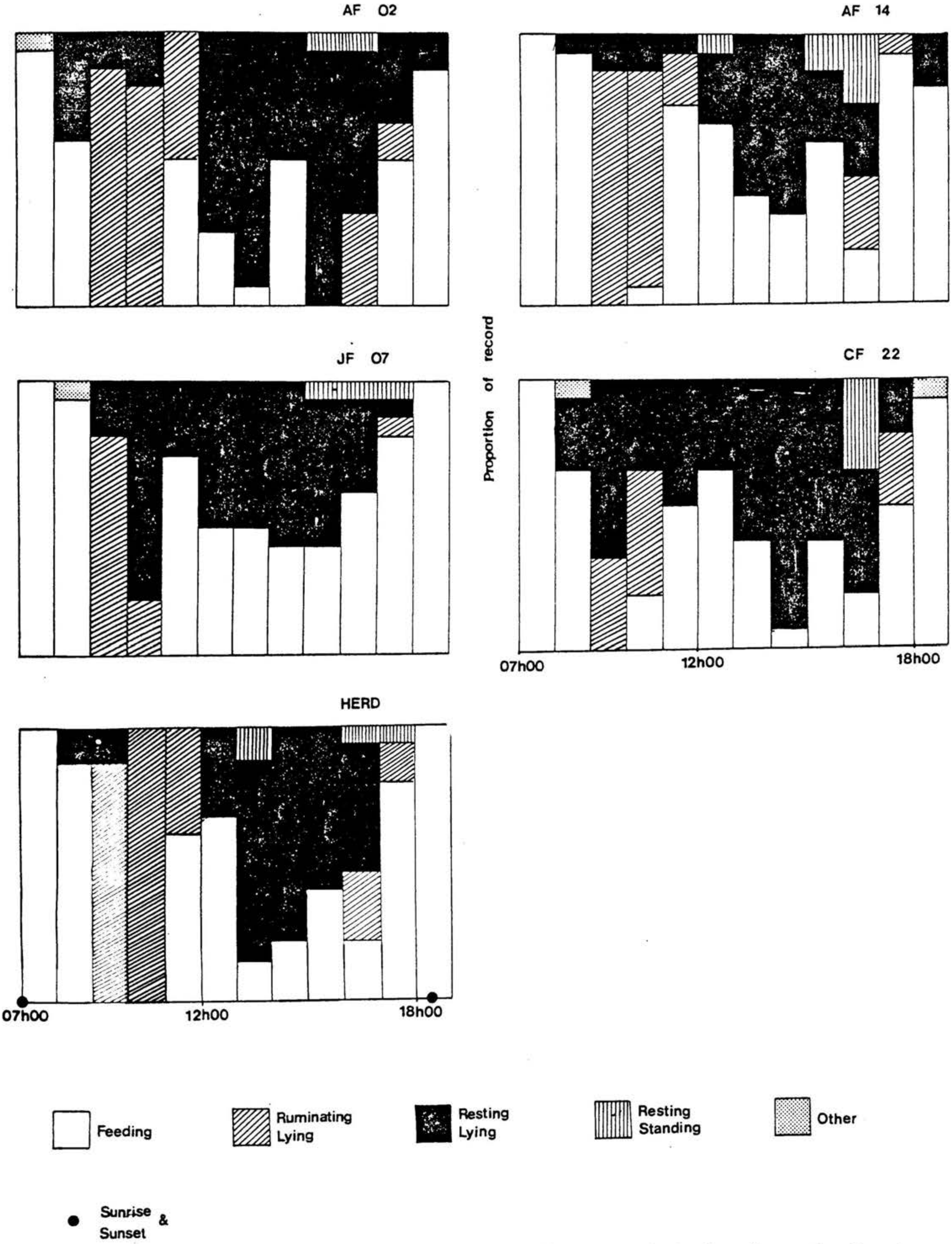

Fig. 20b: Diurnal activity pattern of four gemsbok females, the herd, on 20/9/76. (Adult females 02 and 14, juvenile female 07 and female calf 22)

ruminating or feeding and resting are synchronized for all individuals and therefore also for the herd. This phenonemon is the result of the following factors (Walther, 1973):

a. The biological clock and time givers are almost similar for all individuals.

b. Certain activities are contagious among members of a herd. For example, if an animal which is inclined toward lying down due to the endogenous rhythms and/or external time givers, and then actually lies down, others will soon follow.

c. The males often co-ordinate the activity of a herd. For example, by threatening and fighting they may cause members of a herd to arise from lying resulting in a shift from one activity to another.

The gemsbok showed major feeding peaks at dawn and dusk. The former was a continuation of the feeding bout which probably began before light while the latter peak continued into the early part of the night.

Female AF02, which was seven months pregnant at the time, spent less time feeding (36%) but more time ruminating-lying (21,7%) and resting-lying (40,6%), (a total of 62,3% of the day spent lying down) than any of the other gemsbok.

The other adult female AF14 and the juvenile female JF07 spent more than half the time under observation feeding, at the expense of lying down. JF07 however spent less time ruminating (8,9%) than the adult female (18,3%) and more time resting (33,9% compared with 26,1%).

The 5-month-old calf CF22 spent a total of 49,5% of the day lying down, although it was recorded feeding during every hour under observation (Fig. 20b) with the exception of one (09h00-10h00). During this time no other gemsbok in the herd were feeding (More restless than older animals and easily disturbed).

The patterns of the males show a similar temporal dis= tribution as the females but vary in the overall proportion. The males spent less time feeding than the females (with the exception of the pregnant fe= male) while the mean lying time for males was fraction= ally more than for females. The averaged ruminating time for males and females is similar. TM13 the ter= ritorial and therefore dominant male in the herd, spent less time feeding and more time lying-resting than the other males and fractionally less time on sexual activity (5,6%) than the sub-dominant male AM10 which took the opportunity to show interest in females while the dominant male was resting. (Sexual activity entailed just sniffing and checking females.)

C. VARIATION IN THE ACTIVITY PATTERN ON FIFTEEN DIFFERENT DAYS BY ONE INDIVIDUAL

The percentage of the time between 08h00 and 18h00 spent at different activities by AF02 on fifteen days from 29 May 1976 to 26 April 1977 is depicted in Table 9.

The temporal as well as overall proportion of the diur= nal activities on the 15 days showed great variations (also on different days in the same month, see July and September). The greater variation of the activity pattern shown by the same individual on different days compared with the smaller difference between individuals on the same day suggest the influence of exogenous fac= tors.

Table 9: Percentage of the day spent at different activities by an adult gemsbok female on fifteen days

	Lactating + Pregnant	Pregnant										Pregnant (not lactating)			
Activities	25/9/76	3/7	11/7	16/7	31/7	7/8	28/8	3/9	11/9	20/9	17/10	22/7/77	26/3	18/4	26/4
Feeding	84,7	74,0	69,3	79,3	48,7	26,7	36,7	28,0	10,7	25,3	64,0	32,0	59,3	50,7	56,0
Ruminating - standing	-	-	-	-	0,7	-	-	-	-	-	0,7	0,7	14,7	0,7	-
Ruminating - lying	14,7	14,7	11,3	-	13,3	13,3	9,3	0,7	5,3	26,0	14,7	14,0	-	32,0	20,0
Total Ruminating	14,7	14,7	11,3	-	14,0	13,3	9,3	0,7	5,3	26,0	15,4	14,7	14,7	32,7	20,0
Resting - standing	0,7	0,7	-	-	-	2,7	3,3	3,3	26,0	1,3	-	36,7	15,3	-	-
Resting - lying	10,0	10,7	19,3	20,0	37,3	55,3	50,7	67,3	58,0	47,3	20,7	16,7	10,0	16,7	24,0
Total resting	10,7	11,4	19,3	20,0	37,3	58,0	54,0	70,6	84,0	48,6	20,7	53,4	25,3	16,7	24,0
Total lying	24,7	25,4	30,6	20,0	50,6	68,6	60,0	68,0	63,3	73,3	35,4	30,7	10,0	48,7	44,0
Total standing	0,7	0,7	-	-	0,7	2,7	3,3	3,3	26,0	1,3	0,7	37,4	30,0	0,7	-
Other	-	-	-	0,7	-	2,0	-	0,7	-	-	-	-	0,7	-	-

D. MONTHLY AND SEASONAL VARIATIONS IN ACTIVITY PATTERN

The monthly data for the time between 07h00 and 18h00 are shown in Table 10 while Fig. 21 depicts the month=ly variations in feeding, resting and ruminating pat=tern. The gemsbok spent more time feeding and less ruminating, and resting in the "wet" season than in the dry season. If however the longer daylength in the "dry" season is considered, the percentage time spent feeding by gemsbok herds increases considerably although it still remain lower than for the wet sea=son. Adult males however spent more time feeding and also ruminating in the dry season while adult females showed a similar pattern as the herd with a greater variation in the overall proportion of activities. No significant correlation was shown between feeding and ruminating. The shortest feeding period was recorded in September which corresponded with the end of the flowering season, while the shortest ruminating period was recorded in August.

The temporal distribution of activity patterns also varied from month to month (Fig. 22a and b) with an obvious shift in feeding peaks through the year. The dawn peak which commenced earlier in the "dry" season also ended one to two hours earlier than the wet sea=son peak, while the dusk peak began later. Minor mid=day or early afternoon feeding periods occurred during both seasons.

The seasonal shift in feeding bouts resulted in an ex=pected variation in the inactivity period, - ruminating and resting. More time was spent ruminating and rest=ing in the dry season which was the only time ruminat=ing while standing was recorded. The gemsbok also spent more time resting-standing in the dry season, at the expense of lying.

Table 10: Monthly variations in the activity pattern of gemsbok herds between the times 07h00 and 18h00

	1976								1977							
Activity	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	Wet	Dry
Feeding	59,1	67,3	69,7	45,8	29,4	47,3	36,1	52,1	44,5	42,4	49,4	64,8	77,0	86,4	56,0	45,3
Ruminating - standing	-	-	-	-	-	-	1,2	3,0	8,5	4,5	7,3	-	-	-	-	4,1
Ruminating - lying	20,9	16,4	7,3	1,8	12,7	15,8	25,2	22,7	9,4	14,5	8,5	26,4	13,3	0,3	14,3	16,0
Ruminating	20,9	16,4	7,3	1,8	12,7	15,8	26,4	25,7	17,9	19,0	15,8	26,4	13,3	0,3	14,3	20,1
Resting - standing	2,4	1,2	-	3,3	22,7	9,1	10,3	10,0	28,8	29,4	20,9	-	-	-	4,9	18,1
Resting - lying	17,6	15,1	23,0	47,9	35,2	27,9	27,3	10,9	8,8	9,1	13,9	8,8	9,6	13,3	24,6	16,3
Resting Total	20,0	16,3	23,0	51,2	57,9	37,0	37,6	20,9	37,6	38,5	34,8	8,8	9,6	13,3	29,5	34,4
Standing Total	2,4	1,2	-	3,3	22,7	9,1	11,5	13,0	37,3	33,9	28,2	-	-	-	4,9	22,2
Lying Total	38,5	31,4	30,3	49,7	47,9	52,8	52,5	33,6	18,2	23,6	22,4	35,2	22,9	13,6	38,9	33,8
Other	-	-	-	1,2	-	-	-	1,2	-	-	-	-	-	-		

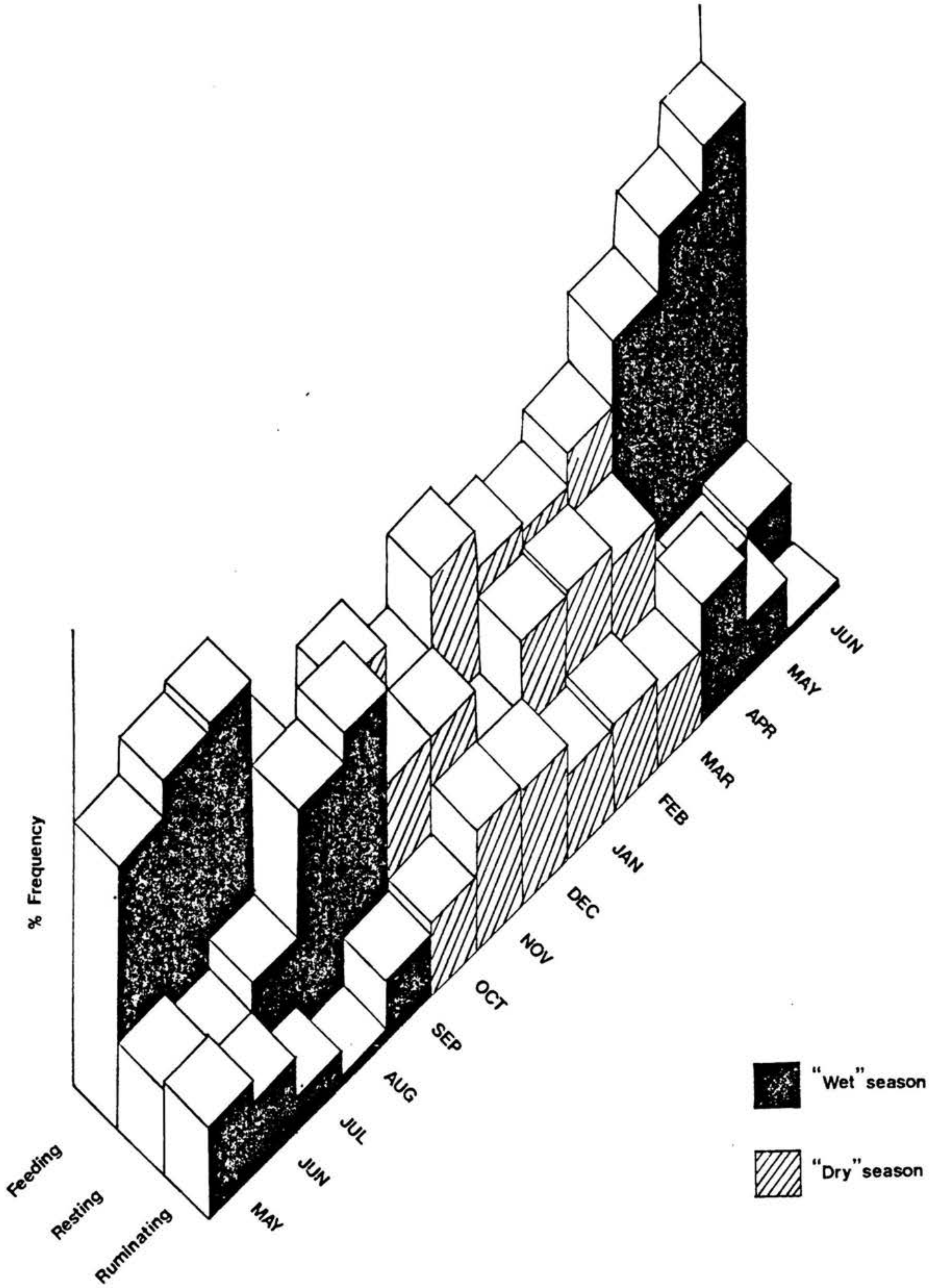

Fig. 21: Monthly variations in the feeding, resting and ruminating pattern of gemsbok herds

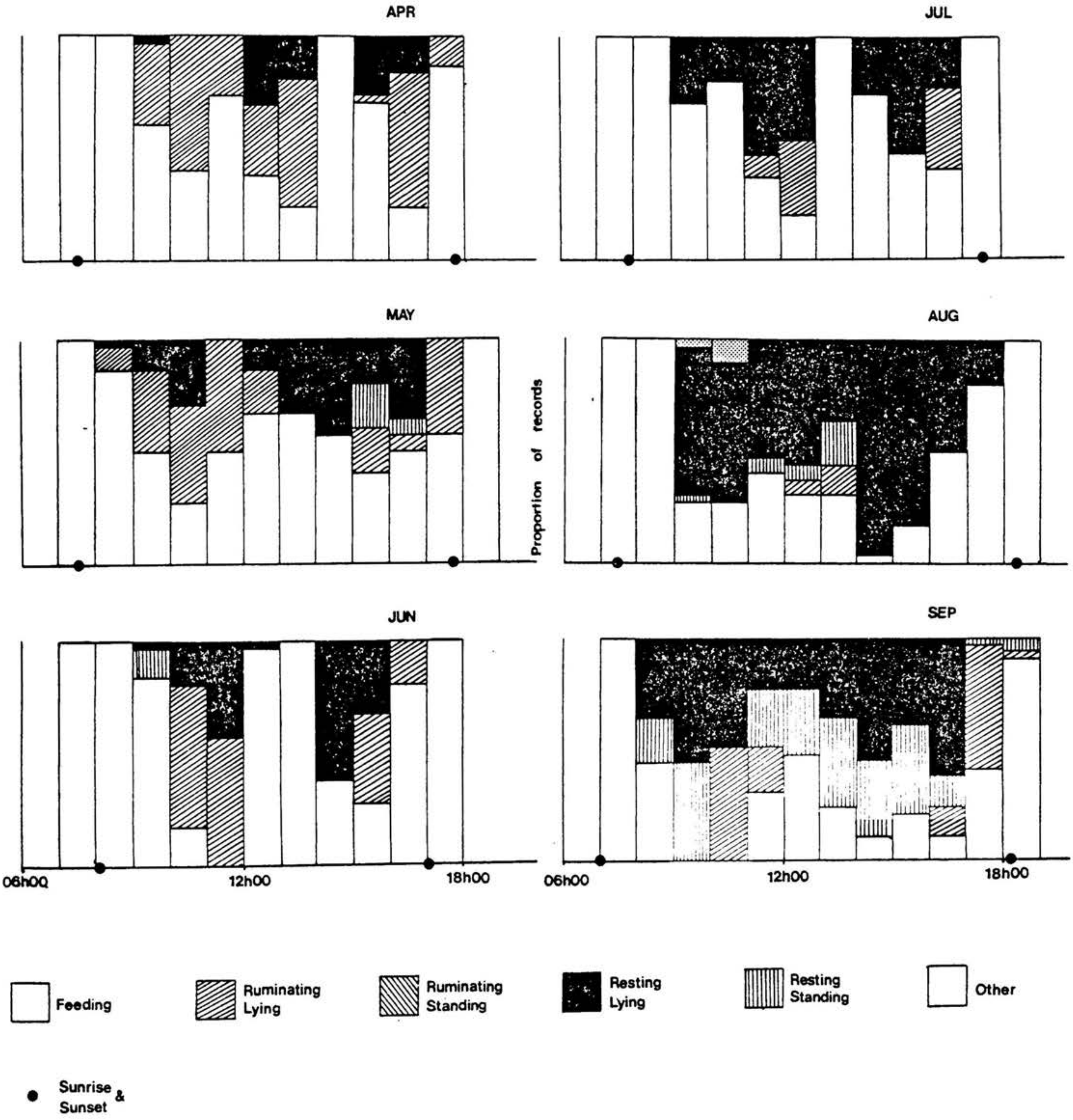

Fig. 22a: Monthly activity pattern of gemsbok herds in the "wet" season

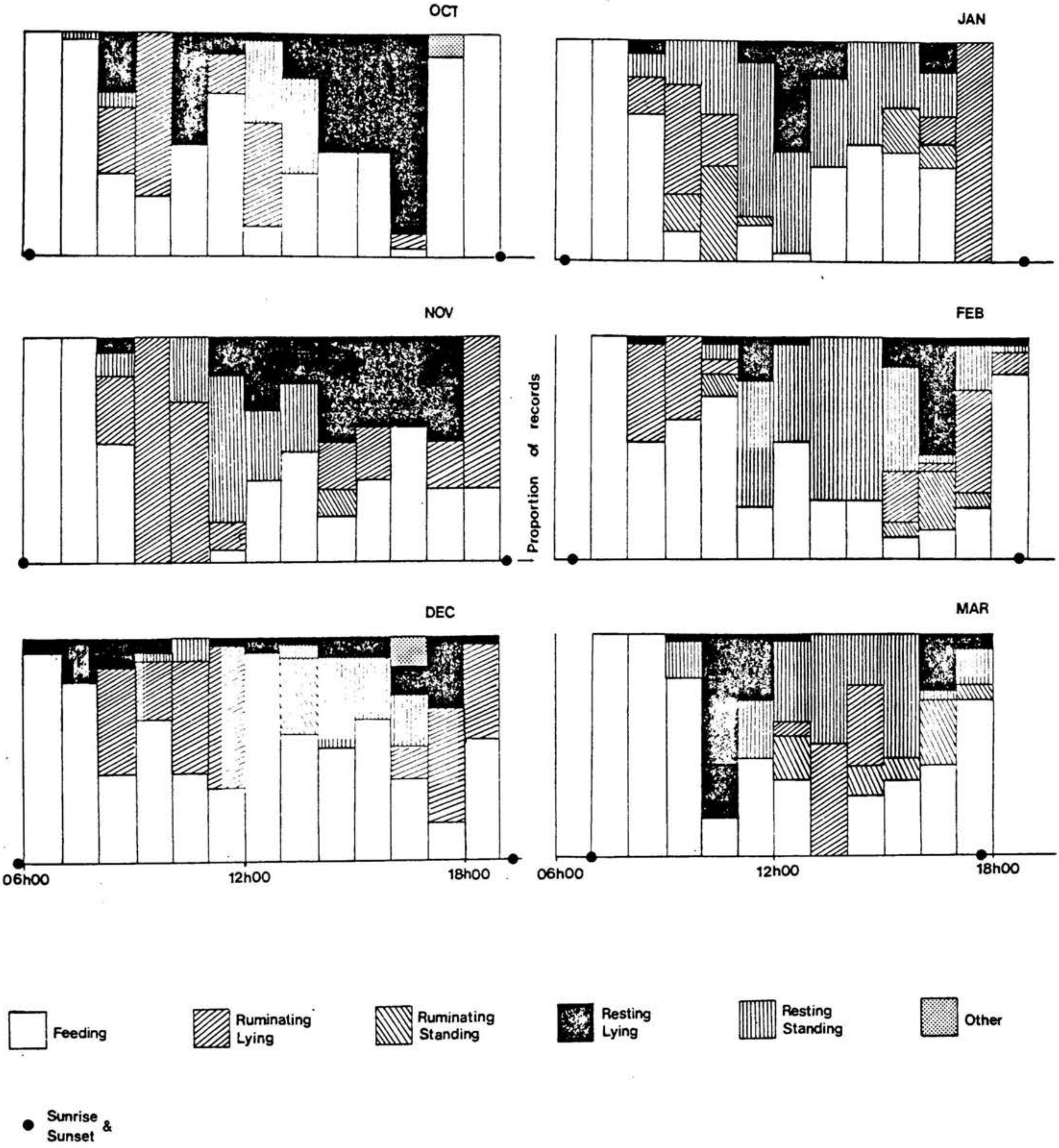

Fig. 22b: Monthly activity pattern of gemsbok herds in the "dry" season

Adult females showed a fractionally higher mean feeding and ruminating time than males (Table 11) but their wet season feeding time varied to a greater extent (58,2% and 50,7% respectively). (No significant correlation could be found between feeding and ruminating time and percen=tage moisture contents of food plants.

RELATIONSHIPS OF ACTIVITY TO METEROLOGICAL VARIABLES

All the data for adult males, adult females and gemsbok herds were combined so that the over-all relation with meterological factors could be investigated.

The correlations in Table 12 show that the gemsbok spent significantly less time feeding during periods of high ambient temperatures and low relative humidities and more time resting. Standing (-resting and -ruminating) sig=nificantly increased when ambient temperatures were high. The high percentage for standing in September is probably related to insect activity rather than high ambient tempe=rature. If no shade was available the gemsbok stood during the hottest time of the day, normally by orientating their bodies with the posterior end toward the sun (no signifi=cant correlation could be obtained). If a mild wind was blowing they stood facing into the wind sometimes with their forelegs on a mound or boulder, to make use of in=creased airflow. At high wind speeds, particularly in combination with low ambient temperatures, standing de=creased and gemsbok lay down usually in the shelter of a shrub or boulder. Ruminating-lying increased with an in=crease in wind speed.

Ruminating ceased during ambient temperatures above 36°C although feeding was then still recorded. The gemsbok also panted at this stage although for short periods only (difficult to detect as mouth was not opened much).

Table 11: Overall monthly and seasonal variation in the feeding and ruminating activity patterns of gemsbok males, females and mixed herds

	Activity	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	Wet	Dry	Mean
Adult ♂♂	Feeding	54,8	59,4	64,5	43,0	31,2	52,1	37,9	44,6	56,3	44,9	76,3	51,4	50,7	52,0	51,4
	Ruminating	1,99	16,8	5,0	0,5	10,8	11,7	12,7	23,6	17,6	20,4	3,3	23,2	12,7	14,9	13,8
Adult ♀♀	Feeding	53,9	74,1	71,4	50,4	37,6	61,5	41,9	42,9	55,5	46,7	57,8	61,7	58,2	51,1	54,6
	Ruminating	19,0	7,0	8,8	4,9	11,7	10,9	12,5	34,2	16,4	19,8	17,3	19,0	11,7	18,5	15,1
All herds	Feeding	54,1	68,4	67,0	53,4	35,7	57,8	43,8	54,9	61,7	47,5	62,1	62,3	56,8	54,6	55,7
	Ruminating	22,0	13,5	12,1	3,7	15,5	18,2	19,8	30,4	18,5	23,0	11,3	24,1	15,2	20,2	17,7

Table 12: Relationship between gemsbok activities and meteorological variables

Activity	Ambient temperatures n = 21	Relative humidity n = 12	Wind speed n = 12
Feeding	-0,90	+0,89	-0,46
Ruminating-standing	+0,70	-0,46	+0,64
Ruminating-lying	-0,08	+0,50	+0,84
Ruminating	+0,29	+0,44	+0,62
Resting-standing	+0,83	-0,74	-0,91
Resting-lying	+0,52	-0,95	+0,25
Resting-total	+0,96	-0,92	-0,41
Lying-total	+0,27	-0,70	+0,70
Standing-total	+0,83	-0,85	-0,72

(r = correlation coefficient)

The influence of wind direction on the activity pattern was related to wind speed and ambient temperatures. Changes in the pattern from lying to standing were evident during sudden changes in wind direction from prevailing warm north easterly (in the dry season) to the cooler south westerly wind from the coast. A sudden change in wind direction from NE to SW, usually around midday, resulted in a drop in temperature of 2 - 4°C. This change in temperature was reflected by an abrupt change in gemsbok activity usually from lying to standing often resulting in a short feeding bout, as though the animals had been disturbed.

Wind direction and wind speed also influenced the direction in which a herd was moving while feeding, usually they walked into the wind while feeding.

Weather conditions had a indirect effect on the gemsbok activity pattern through the other meterological factors. Rainfall did not disrupt the activity pattern unless it occurred in combination with a strong wind which caused the animals to lie down behind shelter.

DISCUSSION

Feeding was the most time consuming activity during both seasons for both male and female adult sex classes and the herds. The monthly pattern showed greater variations, with resting taking up most of the day, for some months, particularly for individual animals. The time spent feeding can be related to the phenology of the foodplants, with the greatest effect evident during July, August and September, (Fig. 21) the flower and fruit formation time for the majority of the utilized ephemerals.

The almost complete diet of ephemeral flowers in July and August is reflected by the low values for ruminating for these months. These soft plant parts require little rumination whereas the more nutritious fruiting bodies avail=

able during September probably had a higher fibre content requiring more rumination. Their expected high nutritive value allowed for a shorter feeding time.

The lower value for ruminating in March (Fig. 21) may possibly be explained by the switch from dry plants to the first of the wet season's green flush and seedlings with a comparatively lower fibre content. The generally shorter feeding time during the dry season, where a longer feeding time is expected because of the lower food availability, therefore longer searching time and lower nutritive level of food plants, is the result of high diurnal temperatures and is possibly compensated for by feeding at night. Ruminating time in the dry season is probably related to the higher fibre content of food plants rather than the increased resting and ruminating time available.

The monthly variations for lying and standing activities appear to be related to solar radiation and therefore ambient temperatures. The high soil temperatures probably prevented the animals from lying down and the limited shade resulted in the longer standing bouts during the dry season. Ruminating ceased during high diurnal temperatures (36°C+) possibly to minimize heat production. During critically high ambient temperatures, heat is lost by short bouts of panting - when water is in unlimited supply.
Where water is not readily available gemsbok probably build up a heat load during the day, which is dissipated at night. Taylor (1969) found that Beisa oryx adapted to waterless environment and high temperatures by accommodating to an extreme body temperature and by decreasing the amount of metabolic heat they produce. The body temperature of a dehydrated oryx exceeded the experimental ambient temperature of 45°C for as long as eight hours without apparent ill affect. It began to pant but not sweat when its body temperature exceeded 41°C. During such high body temperatures the temperature sensitive brain is kept cooler than the rest of the body by means of a countercurrent cooling

system in their cavernous sinus. When water was in unli=mited supply the oryx maintained a body temperature a few degrees below ambient temperature by dissipating heat through evaporation by means of panting and sweating.

As was found for several other species gemsbok females tend to feed longer than males during daylight hours. This may be explained by the higher energy requirement by the female in a species that can theoretically calve every nine months. Under optimal conditions a gemsbok female lactates for ap=proximately six months during her pregnancy. At an advanced stage of pregnancy the female spends more time resting, du=ring the warm time of the day, at the expense of feeding, thereby minimizing extra heat buildup and possibly compen=sating for the loss in diurnal feeding time by feeding more at night.

The cost of territorial status in terms of energy expended in return for exclusive mating rights is more evident when an oestrus female is present in the herd. The increased frequency in dominant displays and sexual activity is re=flected usually by a lower feeding rate, and has a similar temporal distribution in the diurnal patterns. The lower feeding time in the presence of an oestrus female is prob=ably compensated for during periods when the male is soli=tary. Territorial displays take up a small percentage of the territorial male's time because of the well establish=ed social hierarchy, large size of the territories and therefore the low frequency of encounters between territo=rial males (see chapter 8).

The lower percentage feeding of the territorial male than other adult males recorded on 25 September 1976 may have been attributable to a high energy expenditure in the days before. The lack of an oestrus female in the herd gave the territorial male an opportunity to spend more time resting although again at the expense of feeding. At the same time the sub-dominant male in the herd, without the interference of the territorial male, spent more time inspecting the reproductive status of the females, than the latter male.

In addition to the variations in the activity pattern between sexes and between social and reproductive status, the pattern for an individual varies from day to day - even on consecutive days indicating the important role played by interrelated exogenous factors which are all invariably governed by climatic conditions. For this reason the morning activity pattern for example, of one day cannot be coupled with the afternoon pattern of the next or previous day in order to give the impression of a whole day's activity pattern.

CHAPTER 8: TERRITORIAL BEHAVIOUR

INTRODUCTION

Gemsbok social organization is characterized by the unusual occurrence of mixed herds and it has therefore become a moot point as to whether gemsbok are strictly territorial (Estes, 1974). Estes found, however, that a certain percentage of solitary males in sedentary gemsbok populations in the Etosha and Iona National Parks, were spaced out in what appeared to be a typical territorial network. Furthermore he observed that these solitary males dominated all other males in a mixed herd. The latter were supposedly not in reproductive condition. Hamilton, Buskirk and Buskirk (1977) reported the establishment of temporary feeding territories by gemsbok males under the canopy of *Acacia erioloba* trees in the Kuiseb canyon. These territories were established during poor environmental conditions and were defended against all conspecifics regardless of sex and social status.

METHODS

Evidence for territoriality in the gemsbok in the Hester Malan Nature Reserve was provided by the use of criteria formulated by Leuthold (1970 & 1977) which correspond with the features discussed by Owen-Smith (1977). They include the following:

1. Fixation in space - i.e. the repeated observations of a known single adult male in the same location, with - and more important - without females.

2. Dominance of the occupants over conspecifics of comparable social status (exception: direct challenge over "ownership" of the territory).

3. As a consequence of (2) exclusive use of the resources in question present in the area involved.

4. Observations of a new adult male in an area where a known adult male had been seen repeatedly; while at the same time, the original male should be seen elsewhere.

Sightings of adult males, when solitary or with a herd, were plotted on aerial photographs with an accuracy plotting of ±50m. Sightings of two adult females were plotted in a similar way. Individuals could be recognized from natural characteristics such as horn structure and facial markings. Photographs taken with a Canon 35mm reflex camera and a 300mm telephoto lens, were used to facilitate identification of individuals. Associations of the recognized animal with other gemsbok as well as all relevant behaviour, were noted.

RESULTS

The observations suggested that five adult males were each attached to a definite locality where they were seen alone or with a mixed or nursery herd (Fig. 23). Furthermore it was found that females and nonsedentary adult males (Fig. 24 and 25), in mixed herds, moved around over a larger area than the sedentary males and that mixed herd composition changed quite frequently. Further behavioural observations revealed that these discrete areas, satisfied the requirements of a territory as set out in the above criteria and the following modified definition: "A territory is a spatially fixed area within which a given animal consistently prevents certain other individuals from engaging in certain activities and from which it excludes individuals of comparable social status through active repulsion".

Fig. 23: Location of sightings of territorial gemsbok males TM05 (▼) solitary, ▽ with a herd, ▼ displaced, TM13 (●) TM15 (■) TM16 (◆) and TM 17 (▲) for the period May 1976 to June 1977

Fig. 24: Location of sightings of adult gemsbok females AF02(●) and AF04(○) for the period May 1976 to June 1977

Fig. 25: Location of sightings of a territorial gemsbok male TM10 (◬ sharing, ○ solitary, ● with a herd, ◉ displaced and bachelor male AM09(▲) for the period May 1976 to June 1977

The results are presented under the following features which incorporate the criteria listed above:

1. The territorial male
2. The territory
3. Attachment to territory and replacement of territorial male
4. Intolerant behaviour or defence of territory
5. Territorial advertising
    a) Static optic advertising
    b) Demonstration-threat advertising
        i) Defaecation
        ii) Pawing
        iii) Shrub-horning
6. Herding.

THE TERRITORIAL MALE

Leuthold (1970) points out that the occurrence of many single adult males in gregarious species is "unusual and likely to have special significance" and that it may indicate territorial behaviour. All solitary gemsbok males were found to be territorial males (TM)*. Sightings of solitary territorial males comprised 13,1% of the total of all gemsbok sightings from May 1976 to June 1977 (Table 13) and 19,2% of the sightings of territorial males while they were still territorial (Table 15). The low values may be attributed to the low population size (±64, June 1977) and the nature of the habitat. Seventy five comma eight per cent of the sightings of territorial males (while territorial) were recorded while the animals were in the company of a mixed herd and 4,9% as the only male

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* These males, TMs 5, 10, 13, 15, 16, 17 and 25 will be called territorial males, also after they were displaced from their territories.

Table 13: Sightings of gemsbok groups in the HMNR during the period May 1976 to June 1977

Kind of group	Number of sightings	Percent
Solitary territorial males	54	13,1
Mixed herd + territorial males	213	51,4
Mixed herd without territorial males	95	23,0
Nursery herd + territorial males	14	3,3
Nursery herd or female herds with=out males	33	8,0
Female herds (2 - 4 animals)	4	0,9
Total sightings	414	99,6

with a nursery herd (Table 14). Sightings of the displaced territorial males (TMs 5, 10 and 13), comprised 11,0% of all the sightings of territorial males (Table 15).

The number of recorded sightings of seven territorial males from May 1976 to June 1977 are summarized in Table 16, and Figure 23 shows the localities at which these observations were recorded. All territorial males had distinctive characteristics and could be recognized as follows: TM5 was the smallest of the territorial males with comparatively short horns and was the only male with no black stripe connecting the black patch at the horn base with the black pattern of the muzzle.

TM10 had long horns with about 10cm of the right horntip bent outwards.

TM13 had only one straight horn while the other spiralled and grew out at an angle over the neck. This deformity possibly resulted from an injury sustained while he was a calf.

TM15 also had short horns, longer than TM5, which were perfectly symmetrical when seen from the front. He had a black stripe connecting the black patterns on the face (Fig. 26).

TM 16 had horns which were slightly asymmetrical when seen from the front and the right horn lay behind the other when seen from the side.

TM 17 (Fig. 26), was the male with the longest horns, more like those of a female, with the horn tips exceptionally wide apart.

TM25 was the most difficult male to recognize, with straight long horns growing close together.

Table 14: Sightings of territorial gemsbok males in association with other gemsbok groups

	Kind of group and associations												
	Territorial								Non territorial				Total
	Solitary		+ Mixed herd		+ Nursery herd		Total		Sharing		Displaced		
Territorial male	No of sightings	%	No of sightings	%	No of sightings	%	No of sightings	%	No of sightings	%	No of sightings	%	No of sightings
5	8	22,8	12	34,2	-	-	20	57,1	-	-	15	42,8	35
10	5	4,8	48	46,6	1	0,9	54	52,4	39	37,8	10	9,7	103
13	1	1,9	34	65,3	7	11,2	42	80,7	-	-	10	19,2	52
15	9	27,2	21	63,6	3	9,0	33	99,8	-	-	-	-	33
16	24	41,3	32	55,1	2	3,4	58	99,8	-	-	-	-	58
17	7	18,9	29	78,3	1	2,7	37	99,9	-	-	-	-	37
25	-	-	37	100,0	-	-	37	100,0	-	-	-	-	37
Total	54	19,2	213	75,8	14	4,9	281	79,1	39	10,9	35	9,8	355

Table 15: Sighting of territorial gemsbok males main=taining a territory and after displacement

Status	No of sightings	Percent
Territorial	281	88,9
Displaced	35	11,0
Total	316	99,9

Table 16: Monthly sightings of six territorial gemsbok males in their territories during the period May 1976 to June 1977

Territorial male				1976								1977			Total sightings on territory
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	
5	4	3	2	3	-		3	-	-	-	-	-	-	-	15
10	-	-	-	-	-	10	12	6	11	5	6	4	-	-	54
13	-	6	7	15	13	1	-	-	-	-	-	-	-	-	42
15	-	3	1	7	-	3	2	4	-	2	4	5	2	-	33
16	-	3	2	6	4	11	7	3	10	2	-	4	5	1	58
17	-	-	-	1	3	5	2	5	2	8	5	3	1	2	37
Total	4	15	12	32	20	30	26	18	23	17	15	16	8	3	239

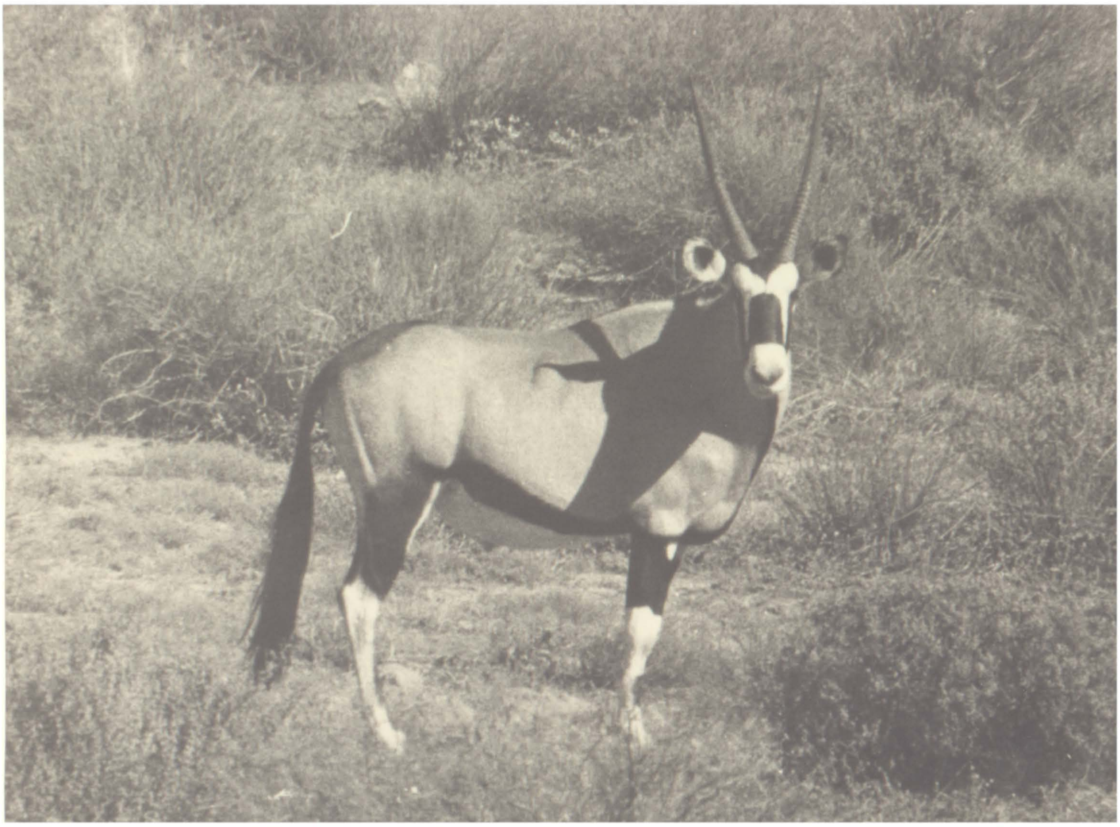

Fig 26: Two territorial males, TM15 above and TM 17 below

A comparison of the estimated age, (judged according to the thickness of the horn bases and body size) of the entire male population (25 in June 1977) showed that the territorial males were probably five to seven years old. Non-territorial or bachelor males, between the age six months and five years, remained with the females in mixed herds. An absolute dominance hierarchy was established among the bachelor males which in turn were subordinate to the territorial male in whose territory they occurred at that particular time.

Courtship and mating were found to be largely the privilege of the territorial males and were rarely performed by the bachelor males. This was probably not the result of any physiological incapacity of the bachelor males. Flehmen was in one instance exhibited simultaneously by a bachelor and a territorial male on a urinating female with no sign of aggression from the latter male. This was attributed to the female being anoestrous. Unsuccessful mounting of oestrus females by bachelor males was also observed on occasions where the territorial male was otherwise occupied or when two oestrous females were present in the herd.

THE TERRITORY

The territories were spaced out throughout the reserve with the exception of the central, south-western and south-eastern regions (Fig. 23). This was attributed to the nature of the terrain in these areas, which seemed to be unsuitable gemsbok habitat. No territories were established in these areas during the study.

The approximate minimum size of the territories was calculated by linking the outer plotted points and determining the area thus enclosed. This gave a figure ranging from 4,2 to 9,8km^2 (mean - 7,6km^2)(TM5 - ±6km^2, TM13 - 9,6km^2, TM15 - 9,8km^2, TM16 - 7,5km^2 and TM17 - 4,2km^2).

The actual areas as delimited by koppies and drainage lines are probably considerably larger.

As a consequence of the exceptionally large size of the territories, which included the entire home range of the territorial males, the boundaries were not well defined and no attempt has been made to define them. In some instances however, the boundaries were found to be natural geographic features such as drainage lines and steep koppie slopes or artificial features such as roads. This was demonstrated by the following observation: On 3 August, 1976 a large mixed herd with TM13 as the dominant male, was chased toward the territory of TM15 in the northern part of the reserve. The herd crossed the road near the watering point (Fig. 2) and were joined by TM15. TM13, however, did not accompany the herd across the road and walked along it as the herd moved parallel to it for about 500m. He was not seen to cross the road which apparently formed the boundary between the two territories. TM13 eventually walked back toward the core area of his territory.

The territories contained certain areas within which most sightings were clustered. These centres of activity (clearly shown by Figure 23) were found to be open sandy spaces with a sparse vegetation cover consisting mostly of short ephemerals. Each territory also contained at least one natural or artificial watering point.

ATTACHMENT TO TERRITORY AND REPLACEMENT OF TERRITORIAL MALE

Intrusions by territorial males into neighbouring territories were rarely recorded and seemed to occur most frequently when the territorial male followed a herd into the other territory while the incumbent was not nearby. Territorial males also left their territories after long periods of isolation, possibly as a result of a desire for social contact. An example of this behaviour was shown by TM5. During the wet season in 1976 the gemsbok restricted themselves to the northern part of the reserve and specifically to the territories of TMs 13, 15 and 16 due to the more abundant growth of ephemerals in that area. During the period 10 June to 13 August 1976, TM5 was never seen in the company of other gemsbok. On 18 August 1976 he left his territory and joined a mixed herd of about thirty-eight gemsbok in the southern part of TM16's territory while the latter male was not in the vicinity. From 19 August to 21 August 1976 TM5 followed the herd through the territory of TM16 and into TM13's territory. During this time he was the dominant male in the herd. On 22 August he was chased off the territory by TM13 and then subsequently chased back to his own territory by TM16.

The term of occupation of a territory by a specific male is linked with his physical and psychological ability to defend the territory against potential territorial males and is also influenced by the competition for space.

Table 16 shows the number of monthly observations of territorial males and where it was possible to establish it, the period of occupation. The low number of sightings of gemsbok, particularly of solitary males may be attributed to their behaviour and to the nature of the habitat. Solitary territorial males were found to be more shy and have a greater flight distance than when they were with a herd.

With the exception of TM10, the term of occupation of a territory by the territorial males could not be determined. TM5, 13, 15, 16 and 17 were occupying territories when they were first sighted at the beginning of the study. TM15, 16 and 17 maintained their territories throughout the study and still occupied the same territories during a subsequent visit to the reserve in October, 1977.

TM5 was sighted on his territory for the last time on 18 November 1976 and was seen again in the north eastern section of the reserve on 12 January 1977. When sighted he was with a mixed herd of which TM10 was the dominant male. TM25 was the first seen in TM5's old territory on 11 December 1976 and still occupied the territory in October 1977. TM10 and 13 were "sharing" the territory when first sighted in June 1976 with TM13 being the territorial male and therefore the more dominant of the two. From 11 June 1976 to 2 October 1976, while they were "sharing" the territory, TM10 was sighted twenty-three times with TM13 and sixteen times as a dominant male in a mixed herd while TM13 was with another herd in the same territory. During this time TM10 was treated like a territorial male by neighbouring territorial males while TM13 had become habituated to his presence.

TM13 was displaced from the territory after 2 October 1976 and was subsequently seen on 11 January 1977 in the vicinity of the watering point in the north of the reserve. At this stage he was in a poor physical condition with the ribs visible and two large lumps behind his shoulders. These were probably scars from wounds which he had received during the territorial fight. The insecurity which resulted from the loss of the territory and from the intolerance shown by other territorial males as well as being forced into unsuitable habitat (he probably remained in the koppies until he was sighted again), probably contributed to the deterioration in his condition. TM13 eventually joined a mixed herd as a very low ranking individual. Even juvenile males were more dominant. He was last sighted on 23 May 1977 and was assumed to have died. TM5 also did not regain his social status and no attempt to regain a territory by either male was witnessed.

TM10 was sighted fifty-four times in his territory after he had displace TM13 (Table 14). He was in turn displaced by an unnumbered male after 25 April 1977 and had there=

fore occupied the territory as a territorial male, for approximately seven months. On 23 June 1977 he unsuccessfully attempted to regain a territory. This was shown by the following observations: TM10 and TM17 were sighted near each other in the vicinity of a waterhole near what was probably the boundary of TM17's territory. Both individuals were bleeding from minor flank wounds and TM10 was shortly afterwards chased out of the territory. He eventually rejoined a mixed herd as a high ranking bachelor male and was seen on 3 July 1977 with TM15 in the latter's territory.

All three replacements of territorial males mentioned above did not alter the territorial limits of these territories. The gemsbok territories therefore appeared to be geographic entities which existed independently of the occupying males. No marked seasonal variation with relation to the occupation of the territories was evident from the results obtained (Table 16). This phenomenon may be attributed to the aseasonality of the gemsbok reproduction in the reserve.

INTOLERANT BEHAVIOUR

Intolerant behaviour by territorial males is directed mostly towards other territorial males and sometimes towards high ranking bachelor males, as was the case with TM10 while he was "sharing" the territory with TM13. Interactions between neighbouring males were infrequent due to the large size of the territories and only two such interactions were observed. Both took the form of a high intensity fight and did not result in an obvious change of boundary. On June 12, 1976, a mixed herd, with TM10 as the dominant male. was feeding in the southern part of his territory near that of TM16. The latter male also with a mixed herd, was near the boundary and when the two males saw each other they left their herds and met, displaying with a stiff neck and head held high posture which accentuated the conspicuous facial markings. Both males tossed their heads then shrubhorned violently. TM10 ran off without a fight having taken place. In the meantime TM13, which had been nearby, wandered over what was assumed to be the boundary with TM16's territory. TM16 walked toward him and a high intensity fight took place after proud displays and shrub-horning behaviour. The fight lasted for about two minutes with no injuries received by either male and ended when both individuals began to graze (displacement) and move apart. TM16 then walked off toward the core area of his territory, while TM13 followed the herd into his own territory. On 29 August 1976, TM10 (still "sharing") and a mixed herd were observed near the boundary of TM16's territory. TM16, which was solitary, joined the herd with dominance displays and walked toward TM10, ignoring the other animals. TM10 ran off towards the centre of the territory and was chased by the other male. Both individuals stopped twice and shrub-horned vigorously before TM 10 eventually turned around approximately 1,5km from the herd, displaying as above. The fight that ensued lasted for about two minutes until TM10 ran off again. TM16 followed the latter animal for approximately 800m and then rejoined the herd which remained where it was first sighted. TM10 also rejoined the herd a while later, was chased around the herd by TM16 and was eventually tolerated while the latter male attempted to drive the herd towards his territory.

As a consequence of the large size of the territories and the resulting rare interactions between neighbouring males, territorial advertising possibly functions as a form of threat, or rather as intolerance, towards other territorial males.

TERRITORIAL ADVERTISING

Schenkel (1966) criticizes the use of the term "marking" in its relationship with territoriality in mammals, unless the "mark" set by an individual is perceived by and is of some significance to a conspecific. He questions the use of dung and urine as scent markers unless these excretory functions are performed while following a ritualized be= haviour pattern or ritualized posture. These postures and movements, which can be conspicuous and unambiguous in meaning, commonly also function as visual displays (Estes, 1969). Schloeth (1958), cited by Estes (1969) and Walther (1967), explains that a display can have two functions i.e. advertisement or threat depending on whether or not it is directed at a specific individual. The term "territorial marking" has therefore been replaced by the less defini= tive term "territorial advertising" or more specifically "demonstrative-threat advertising" which is what Estes (1969) has called the ritualized behaviour patterns func= tioning as significant social displays. He gives examples of ground horning, pawing, defeacating and rolling as ag= gressive actions which serve as advertisements in wilde= beest territorial males.

Static optic advertising

The most basic form of territorial advertising is just being there (Estes, 1969) and has been described as sta= tic-optic advertising by Hediger (1949). The gemsbok territorial or dominant male could be easily recognized by his size and posture. Walther (1966 in Estes 1974) suggests that the distinctive horns and conspicuous mark= ings which accentuate the head and body contours in oryx probably also function as species-specific recognition characters. This was evident from the observations re= lated previously of the encounter between TM5 and 16 on 29 August, 1976. TM16 walked through the mixed herd of approximately thirty-five gemsbok, directly towards TM10, ignoring the other gemsbok. He had noticed and possibly recognized the other territorial male from approximately 50m because of his size, posture and possibly his markings.

David (1973) suggests that the proud posture could possibly be interpreted as threat or intolerant behaviour when it is perceived by, or successfully intimidated, other males some distance away. He describes this form of advertising in bontebok and it has also been described in other members of the Alcelaphinae (Estes, 1969; Joubert, 1972; Von Richter, 1972 and Lynch, 1974). The gemsbok were cryptic in certain habitats but became conspicuous as soon as they turned their heads toward the observers as the facial markings could be seen from a considerable distance.

Demonstration-threat advertising

The following features have been interpreted as functioning in demonstration threat or intolerance advertising in the gemsbok in the H M N R: defaecation, pawing and shrub-horning.

Defaecation

Territorial male gemsbok exhibit a specialized and conspicuous defaecation posture in the form of a low crouch (Fig. 27), during which the dark rump patch becomes more conspicuous. This exaggerated defaecation stance also ensures that the dung, which is usually in the form of pellets, is deposited in a small pile - approximately 16cm in diamter and 4 - 8cm high (Fig. 28). During the normal defaecation posture shown by bachelor males and females, the gemsbok walk or stand, scattering the pellets over a larger area. The pellets in the centre of the small piles were found to be moist 24h after being deposited during the dry season. They therefore retained their odour for that long, while the scattered pellets dried out within a few hours and possibly lost their odour very rapidly. Dung piles were also more conspicuous than scattered pellets. These dung piles were often deposited at the site of older piles but middens or dung patches as found in some ungulate

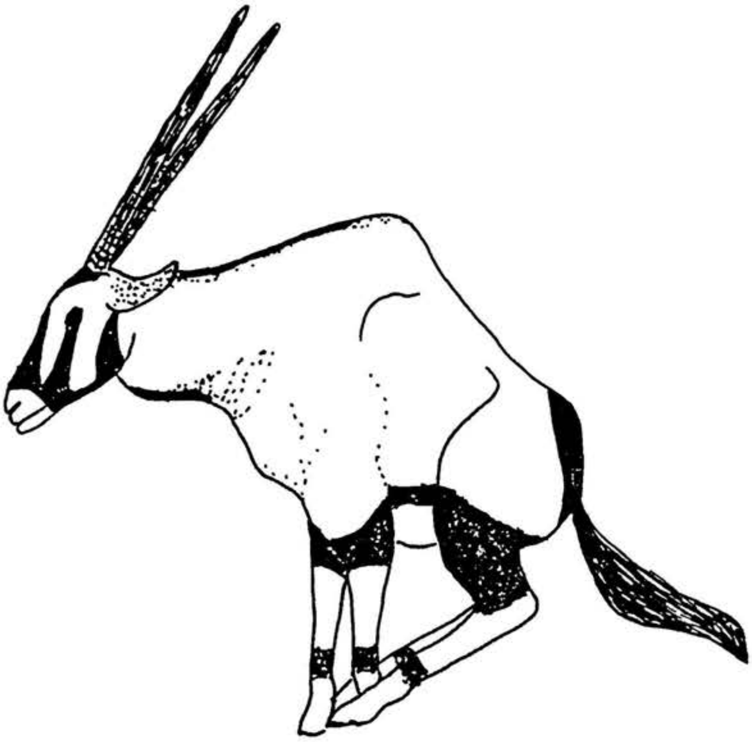

Fig. 27: Crouching gemsbok male, after Walther (1958) above, and showing conspicuous rump patch, below

Fig. 28 a and b: Dung piles at dunging sites, of gemsbok in HMNR showing pawing mark, above and shrub horning site, below species were not formed. Some dung sites contained as many as four dung piles of different degrees of freshness which may have been deposited by different males, particularly in those near the boundaries which were possibly shared by neighbouring males. The dung sites and piles were scattered throughout the territory at low densities and showed no higher frequencies along the assumed boundaries. They were more abundant in the activity zones, as could be expected, as well as in other open areas such as sandy patches, roads and ephemeral river courses. A thorough search of the territories confirmed this fact and Kok (1975) observed a similar phenomenon in red hartebeest.

Bachelor gemsbok males were observed to crouch and defaecate on two occasions. One was TM10 while he was sharing the territory with TM13, a short time before he displaced the latter male, while the other was the most dominant male in a mixed herd. Both gemsbok appeared not to crouch as low as the territorial males. Leuthold (1977) points out that behaviour patterns associated with territoriality are exhibited with increasing frequency by males near the top of the bachelor hierarchy, suggesting the important psychic changes accompanying the step from bachelor to dominant male.

The frequency of squatting increases when oestrous females are present in the herd.

Walther (1958) and Van der Hoven (1975) described defaecation crouching in Beisa oryx dominant and captive gemsbok males respectively. The Beisa oryx male crouched regularly after antagonistic encounters with another male. Walther (1978) also observed this posture in the fringe-eared oryx (<u>O. beisa callotis</u>) for solitary and "alpha-bulls" but did not interpret it as a sign of territoriality. A crouching defaecation posture has also been described in other bovids: gerenuk (Leuthold, 1971) dik dik (Hendricks and Hendricks, 1971) and Thomson's gazelle, where it is linked in a urination defaecation sequence (Walther, 1964 and

1967). In the latter species Walther found that this conspi= behaviour pattern was often adopted before or after a fight, in combination with ground pawing, in which case it was interpreted as threatening. Defaecation, pawing and shrub-horning linked in a sequence was sometimes observed in gemsbok territorial males.

Pawing

As a prelude to defaecation the territorial males were ob= served to paw the ground with either of their forehooves, sometimes in the vicinity of older dung piles, and then crouch and defaecate on the same spot (Fig. 28b). It is evident (Fig. 28a) that when the animal paws, the digits of the hoof are forced apart more than usual. This action may increase the flow of interdigital gland secretions, impregnating the soil between the digits. The glands have a similar morphology to the interdigital glands of _Hippo= tragus niger_ and _H. equinus_ (Pocock, 1910; Joubert, 1974) (Fig. 29).

The secretions are probably consistently left on the ground while the gemsbok is walking, but by pawing, the male is actively depositing the secretions at a particular spot. The significance of such secretions functioning in terri= torial advertising was explained by Burger* (pers. comm.), who found that certain volatile substances in the interdi= gital gland secretions of bontebok and blesbok could be detected by conspecifics up to three days after deposition.

Shrub-horning

Although shrub-horning was not performed exclusively by the territorial males, they appeared to do so more often than the other age and sex classes. Two intensities of shrub-horning patterns could be distinguished. During the less vigorous pattern, performed when the gemsbok was standing, the shrub was beaten with the horns in forward and side=

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* Prof. A. Burger, Department of Chemistry, University of Stellenbosch

Fig. 29: Interdigital glands of a sub-adult male

way strokes, with the top of the head sometimes pushed into the shrub. The more aggressive horning was per=formed during territorial fights or antagonistic encoun=ters between high ranking males. Individuals knelt on their carpals beating the shrub in the same way as in the above pattern, but more vigorously, sometimes rubbing the side of the head against the shrub with violent strokes. The shrubs were badly damaged by this action (Fig. 30) and were sometimes destroyed completely.

The following observations of shrub-horning were recorded on 26 June 1976: TM13 joined a mixed herd of which TM10 was the dominant male. The latter male walked toward him and when he recognized TM13, TM10 turned and ran back in=to the herd with TM13 following for a short distance. The territorial male then shrub-horned very vigorously while kneeling and appeared to rub the side of the head and base of the horns against the shrub. He performed this pattern of shrub-horning three times within about five minutes at three different shrubs leaving only a small stump at the last shrub. The fourth time he shrub-horned while standing and beat the horns into the shrub.

On July 11, 1976 TM10 was observed to shrub-horn while he was sub-dominant to TM13 in a mixed herd. He horned two shrubs in succession for about four minutes continously while kneeling. He once sniffed and pawed the shrub be=fore continuing.

Shrub-horning sites were evident in the vicinity of dung piles and pawing sites (Fig. 28b), and in some cases the shrubs had been horned on three different occasions, which could be determined from the degree of freshness of the broken twigs. The dung piles had also been deposited at different times.

The following observation was made of shrub-horning per=formed in sequence with defaecation and pawing. On 11

Fig. 30: Effects of shrub-beating by gemsbok males

July 1976, TM13 was observed to shrub-horn while standing, paw the ground and then crouch and defaecate at the same spot. It was observed that shrub-horning, in sequence with defaecation and pawing, was performed either before or after defaecation, regardless of whether any dung piles were present at that particular site. It was not possible to determine whether the smell of urine could induce the defaecation sequence.

When trees were horned by the territorial males, the bark was scraped off and the branches were broken, up to 1,5m above the ground.

Shrub-horning by bachelor males and females was not performed as vigorously as by territorial males, and seemed to function mostly as a scratching technique.

HERDING

Herding behaviour, which is one of the features of territoriality in ungulates, was shown by the territorial male gemsbok in two situations. A territorial male could drive a mixed herd or nursery herd from a neighbouring territory into his own or he may prevent a herd from leaving his territory, the latter being more frequently observed than the former. A recorded behaviour has previously been discussed (page 117) in association with intolerant behaviour.

On 12 June 1976 a large mixed herd dominated by TM10 walked, while feeding, towards the assumed boundary with TM16's territory. TM10 followed until TM16 appeared near the boundary, he then persistently attempted to retrieve the members of the herd. This was done by running to the front of the herd with sweeping horns and other dominance displays. The herd was spread out over about 50m with the result that some individuals continued to walk toward the boundary while the male was retrieving the others. The male gave up after about 15 minutes, seemingly very tired, and the herd moved closer toward the boundary where it was joined by TM16. After a high intensity fight with TM10, TM16 successfully herded the mixed herd into his own territory.

DISCUSSION

It must be emphasized that the data presented were obtained exclusively from the relatively small and restricted (sedentary) gemsbok population in the H M N R. The gemsbok territorial system was characterized by the large size of the territories and by the tolerance of the territorial males toward bachelor males. It would appear that these territories are areas in which reproductive behaviour can continue without disturbance from other high ranking males. Courtship and mating is largely the privilege of the territorial males and is rarely performed by the bachelor males who pose no threat to the territorial male as they are subordinate to him and keep their distance from copulating males. The territory itself functions as a mating territory, since the territorial male shares his food reserves with other potential territorial males (Owen-Smith, 1972).

Territorial intolerance and domainance by the territorial gemsbok males may be expressed in a number of ways. As mentioned earlier, Schenkel (1966) suggested that the mark set by an animal can only be considered to be of significance in territorial advertising if it is set in combination with a ritualized behaviour pattern. However, the precise relationship between the "marks" set, and the postures involved, and territorial advertising in gemsbok is uncertain, as no behaviour pattern connected with reaction to these marks and postures by conspecifics were seen. TM10 was once observed to smell at a fresh dung pile of TM13 and then walk away, while they were sharing the territory. TM16 was also seen to stop and smell a dung pile at a dung site with pawing and shrub-horning marks, while running away from a vehicle.

The sites are possibly of greater significance to the incumbent himself and serve to maintain the male's familiarity with his environment, rather than to ward off intruders. David (1973) suggested that the scent of the male's own dung, concentrated in small areas scattered about his territory, could serve to reinforce the self-confidence the male requires to maintain his territory.

The behaviour patterns involved with the setting of the marks, or the demonstrative threat advertisements as they have been called, express dominance to conspecifics in a herd and possibly intolerance to gemsbok of equal social status when it is perceived by them. They function in territorial advertising either by reinforcing the self-confidence of the territorial male when they are performed by solitary territorial males or by intimidating conspecifics in a herd. The effect may not be perceived directly by an observer but may be obvious from the ultimate behaviour of the other gemsbok.

Territorial advertising is a means by which the frequency of antagonistic interactions between territorial males and potential territorial males, i.e. bachelor males, as well as between neighbouring territorial males, is reduced. In a similar way ritualized dominance displays such as the proud posture or stiff neck posture are used to replace potentially dangerous fights.

Shrub-horning in gemsbok is assumed to be a relic behaviour pattern, derived from preorbital gland marking in an ancestor, which has become ritualized and may now come to have a visual display function. Although gemsbok do not possess preorbital glands, non-functional glands, which are a primitive characteristic (Vrba pers. comm.*) were found to be present in two members of the genus Oryx: _O. gazella beisa_

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*Dr E. Vrba, Transvaal Museum, Pretoria.

(Walther, 1976) and O. dammah (Ansel, 1971). Shrub-horning could possibly also function as a form of redirected aggression in gemsbok when performed by males during or after antagonistic interactions. Estes (1969) witnessed ground-horning during antagonistic confrontations between wildebeest males and suggested that it serves as a high intensity threat. He points out that it seems to function primarily as a visual display which probably arose as redirected aggression rather than from scent marking.

Shrub-horning has also been observed in the sable and roan antelopes. Grobler (1975) found that the horning site of sable territorial males correlated well with the territorial boundary while the adult roan, in particular the males, "mark" their activity zone by shrub-horning as well as by defaecation and interdigital gland secretions (Joubert 1974). Neither author described any reaction by conspecifics to the shrub-horning sites, with the result that their function as territorial "markers" may be questioned.

The territorial system of the gemsbok in the H M N R may be a result of their restricted existence but could possibly also occur in a sedentary wild population of gemsbok. Estes (1974) points out that the formation of mixed herds is an adaptation to nomadism in gemsbok and that the social organization as a whole is specialized for nomadism.

The social organization of a nomadic gemsbok population would differ from that of a sedentary population and it is postulated that two types of social organizations would exist in a wild gemsbok population. During short migrations, temporary or movable territories around mixed herds could be established. The latter situation would in fact be an example of a hierarchial system with a dominant male and bachelor males ranked below him. In a sedentary population fixed territories could be established, similar to those found by Estes (1974) in the Etosha and Iona National Parks and in the present study.

The hypothesized social organization for a nomadic gemsbok population was described by Walther (1978) for "wandering groups" of fringe eared oryx (O. gazella callotis) in Serengeti, which also existed in large mixed herds. The alpha males recognized by Walther were of a similar social status as the solitary males although neither were recognized as territorial males. The expression of dominance and the general behaviour of the above males is similar to that of territorial gemsbok males as described in this study.

In the words of Eisenberg (1966) "the social organization is potentially the most variable structure characterizing a given species. It is variable because it reflects the sum total of all the adjustments to the environment in terms of habitat exploitation and energy budget".

A comparison with other ungulates

There is a certain similarity between the territorial system of the gemsbok in the H M N R and that of two equid species. Klingel (1972 and 1974) found that the Grevy zebra (Equus grevyi) near Wamba in N. Kenya, had territories ranging in size from 2,7 - 10,5km², while the wild ass (E. africanus) of the Danakil region in Ethiopia had even larger territories. In both species the territorial males tolerated the presence of bachelor males within their territories. All three species occur in semi-desert or arid environments and this type of territorial system may be an adaptation to this habitat. These factors need further investigation.

Klingel (1974) does not give an explanation for the large size of the territories but considers the tolerance shown by the territorial males toward subordinate bachelors to be a consequence of the large territories.

CHAPTER 9: CONCLUSION

The gemsbok, having adapted to a harsh arid environment and in the case of this study, to a restricted existance, shows some unusual physiological and behavioural adaptations. These include an aseasonal reproductive pattern, tolerance of high diurnal temperatures and limited water supply, variations in the feeding pattern and the social organization.

REPRODUCTION

In a habitat that is characterized by unpredictable rainfall the gemsbok has developed an aseasonal breeding system. Although this system places a heavy physiological strain on the females which lactate for approximately six months during pregnancy, it improves the chances of the calf being born during a "wet" period with a favourable food supply. The reproductive pattern is interrupted during extended unfavourable conditions. The wasted energy expenditure resulting from the death of an abandoned calf, when the importance of the cow's survival disrupts the mother-young bond, is compensated for during favourable conditions, when theoretically a female can produce five calves in four years. Under more natural circumstances, where gemsbok would migrate when conditions become unfavourable in a specific area, they possibly have a lower calf mortality.

Conception in gemsbok is related to rainfall as females will come into oestrous only when conditions are favourable. Reproduction is therefore regulated by proximate factors rather than ultimate ones, i.e. the female may conceive when present conditions are favourable although the calf may be born at a time with poor food supply which is the opposite to what may occur in seasonal breeders. Females conceive when food supply is low with the "knowledge" that conditions will be favourable when the calf is born i.e. predictable system. The variations in mother/calf behaviour exhibited by the gemsbok in the HMNR may be an adaptation to a sedentary as well as a migratory existance. The concealment phase is possibly more obvious in a sedentary population while the formation of nursery herds would have obvious advantages for migrating population.

FEEDING

The gemsbok in the HMNR have adapted to a habitat and food supply, which in the past was probably utilized only seasonally by migrating gemsbok i.e. when the ephemeral plants were available.

Faced with seasonal variations in quantity, nutritional quality and palatability of the plants, the gemsbok utilized a diversity of food plants (in species composition as well as structurally). As a result of this they have become opportunistic feeders, and a major factor determining whether a plant is utilized, is it's availabilty, particularly in the dry season.

TERRITORIALITY

The territorial system maintained by the gemsbok in the HMNR is also related to their sedentary existance. In natural gemsbok populations, temporary, territories are possibly established only when the herd remains in a particular area for a certain length of time and are therefore not as stable as was found in this study. During migrations the ordering of reproductive competition within a mixed herd, is maintained by means of a well developed social hierarchy within which mating becomes the privilege of the dominant male.

The large territories in the HMNR are an adaptation to the poor carrying capacity of the veld, where the territorial male remains in his territory throughout the year and on occasion shares it with a mixed herd or nursery herd.

MANAGEMENT CONSIDERATIONS AND RECOMMENDATIONS

The conservation status of the gemsbok in almost its entire former distribution range, is secure, a factor which may be attributed largely to its increasing popularity for game farming. Unfortunately however, this has also lead to gemsbok being introduced into areas far outside their former range where existing habitats are considered unsuitable.

The general body condition of such gemsbok often appears unaffected while the unsuitability of the habitat is usually reflected by low productivity.

Tighter control measures, particularly by Provincial Conservation Departments are required to prevent these indiscriminate introductions by private landowners of gemsbok as well as other game species. Although, as was found in this study, gemsbok adapt well to habitats which may be seasonally optimal it is important that careful consideration be given to habitat suitability as well as surface area of the proposed reintroductory site. Where gemsbok are introduced onto private land the minimum size of the farm or game camp for a viable gemsbok population with at least one adult male and three adult females should be set at 400 ha which was found to be approximately the size of the smallest territory in this study.

HABITAT SUITABILITY

Under natural conditions gemsbok show a preference for open sandy grassland, open bush savannah and open woodland with semi arid to arid climatic conditions.

Marginal habitats such as in the H M N R would possibly be uitlized only when conditions there are favourable, i.e. during seasons with good ephemeral plant growth. As discussed earlier, gemsbok possibly migrated from the False Desert Grassveld, a pure grassveld with a predominantly summer rain= fall pattern in the east of the HMNR westwards into the Nama=

qualand Broken Veld with a predominantly winter rainfall pattern. Ideally therefore, if the aim of the HMNR is expanded to include the conservation of some indigenous ungulate species under ecological viable conditions (in addition to conserving three veld types) the reserve should be enlarged to include a portion of the False Desert Grassland veld type which lies almost at its eastern boundary. The alternative would be to reduce the existing large mammal population as suggested below.

CARRYING CAPACITY AND STOCKING RATES

The carrying capacity of an area has to be judged by what it can support at the driest time of the year and in this sense the concept of carrying capacity is directly applicable to a nature reserve where the upper limits at which herbivores can be stocked without damage or drastic change to the habitat, are of immediate concern.

The determination of carrying capacity based on accepted agricultural standards is not applicable to game animals on a nature reserve. Agricultural assessments are based on strictly controlled and often ideal conditions, and at most consider only a few animals not in direct competition for grazing. This becomes especially true when dealing with veld in arid areas where there is a marked decline in the palatability and nutritional value of the plants during the dry months. Because of the reduction in palatability and nutritional value, domestic stock run in these areas during the dry period must be given supplementary feeding while wild herbivores, particularly in nature reserves should normally exist from the veld resources with a minimum of supplementary feeding e.g. game licks.

Determinations of agricultural capacities are also based on intensive management practices such as the division of the land unit into camps and the application of a rotational grazing system. These practices serve to increase the carrying capacity, that is, they allow for a higher stocking rate. On nature reserves, although managed, carrying capacities must be based on a continuous free range grazing system.

A further consideration when computing stocking rates for wild herbivores is the role and contribution of the mixed feeders and browsers to the standing crop. The small antelope associating under this category, for example, steenbok, duiker and klipspringer, are regulated naturally by behaviour mechanisms and by the availability of their preferred food. These tiny antelope are usually highly selective feeders, selecting for a high quality food plant in terms of protein and soluble carbohydrate.

Determinations of carrying capacities for nature reserves in terms of game units must also take into account that many of the game animals are relatively selective feeders while species such as gemsbok and springbok under optimal conditions utilize the same plant species as domesticates, they may select for different plant parts. As a result of the homogeneous character of the vegetation in the HMNR however, the gemsbok, springbok and possibly the Hartmann's zebra probably show similar feeding strategies, when the food supply becomes limiting as in the dry season, which may be comparable with that of sheep, with the result that they are all utilizing the same resource and are therefore potential competitors. By using metabolic mass we can compare animals in terms of energy consumed, but not in terms of their impact on the environment, and great care must be taken so as not to overestimate the stocking rate for game animals.

In order to calculate carrying capacities in terms of large herbivore standing crop, small herbivores were equated with large herbivores on the basis of estimated relative energy requirements using metabolic body mass (body mass 0,75) (Brody, 1945 in M.T. Mentis and R.R. Duke, Carrying capacities of natural veld in Natal for large wild herbivores. S. Afr. J. Wildl. Res. 1976 6(2)65-74). The agricultural large stock unit is considered to be a mature cow (454 kg) or the equivalent based on the average daily forage consumption of 11,8 kg dry matter per day. The formula applied in the conversion of large stock units to game units or large stock unit equivalents is:

$$\frac{454^{0,75}}{(\text{mean body mass for species x})^{0,75}}$$

STOCKING RATES

Agriculturists set the carrying capacity of the veld in the vicinity of the reserve at approximately one small stock unit (S.S.U. = 45 kg) per 12ha under average climatic conditions but suggest a carrying capcity of at least 50 per cent of the above during extended dry periods as have been experienced in the past years. As the carrying capacity of an area has to be judged by what it can support at the driest time it is recommended that the carrying capacity of the reserve be set at a minimum of the equivalent of 1 S.S.U per 32ha (a third lower than that recommended by agriculturists). This is the equivalent, on the basis of relative energy requirements, of one large stock unit (L.S.U.) per 186ha.

With the surface area of the reserve taken as approximately 5000ha the stocking rate in L.S.U. equivalents would be 26,9. The following is an example of how the recommended stocking rate can be subdivided among the three larger ungulate species on the reserve which utilize the same food resource. Klip=springer, duikers and dassies are not considered here as they probably compete to a lesser extent with the above species.

Species	Mean body weight (kg)*	No. per L.S.U. (game units)	Recommended population size	Total L.S.U. equivalents (game units)
Gemsbok	200	1,9	30	15,7
Springbok	32	7,3	50	6,8
Zebra	250	1,6	7	4,4
Total				26,9

* Figures compiled from several African workers.

The sex ratio for all the above species should not be allowed to distort beyond one male to three females with at least one adult and one juvenile male for each territorial or dominant male and two thirds of the female population consisting of adults and the remainder juvenile, when surplus animals are removed from the reserve.

CAPTURE AND TRANSPORT

Various capture techniques have been used for gemsbok with variable rates of success. These include

a) chasing gemsbok with vehicles until they can be seized by the tail and eventually handled

b) using a trained "gemsbok dog" to pull the gemsbok down so that it can be handled

c) using attractants such as lucerne to entice the gemsbok into a boma and

d) driving the gemsbok into a boma with a helicopter.

The latter two techniques are probably the most successful as they do not require physical handling of the gemsbok, a factor which may contribute largely to mortalities due to capture myopathy. The use of attractants is practicable mainly during periods with a sparse natural food supply when gemsbok will readily eat lucerne. However during these perriods careful consideration must be taken of the gemsbok's physical condition before any translocation is considered, particularly over long distances. The use of a helicopter to drive gemsbok into a boma is therefore the technique recommended here albeit more expensive. Gemsbok can be captured when in peak physical condition and within a relatively short period, as required. A temporary boma and funnel of plastic sheeting with a netting backing was used successfully during a capture operation in the HMNR in October 1978.

To minimize injuries from horn poking inside the boma, territorial, dominant or large adult males, where these can be recognized should be separated from the herd before being chased into the boma. Where this has not been possible it may be advisable to tranquilize or even shoot these gemsbok as soon as possible.

TRANSLOCATION

Moving the gemsbok from the capture to the relocation site is possibly the most important factor to be considered when translocating gemsbok as it is during this period that the majority of mortalities occur.

Once in the boma the gemsbok should be transported as soon as possible unless a quarantine period is required. Two methods for transporting gemsbok have been used i.e. individually in wooden crates or mass transport, with similar rates of success. In both cases gemsbok should not be handled, i.e. no plastic piping should be placed on the horn=tips as this can result in serious damage to the horns. This is particularly true for young gemsbok where the horn sheath can be twisted off the core during a slight movement of the head. Furthermore, handled gemsbok have a far greater chance of dying from shock or capture myopathy. During mass transport, which is the quicker and cheaper loading method gemsbok should be loaded so that they stand against each other minimizing chances of injuring each other with their horns.

SUMMARY

In the review of the taxonomic status of the genus three species are recognized, while three subspecies are recognized within the species gazella. Gazella and beisa from the Southwest arid and Somali arid zones respectively are geographically separated by an intervening moist savanna biome but were possibly one population as recently as the Pleistocene.

Formerly distributed throughout the arid regions of southern Africa the gemsbok has shown a steadily decreasing range of distribution and declining numbers. Re-introductions and an increase in numbers have however ensured that they are again becoming well represented in their former range.

Eight age classes could be recognized in the field using morphological criteria such as height, change in pelage colour and horn growth. The gemsbok has a high reproductive potential and theoretically, females can produce a calf every nine months as there is no post partum anoestrus. This however is dependent on the physical condition of the female and therefore indirectly on climatic factors. They give birth for the first time at 30 months, have a gestation period of 264 days and an inter-calving interval of approximately 289 days. Reproductive strategy and behaviour are adapted to erratic desert climatic conditions. Mother/young bond is loose and calves remain concealed during early stages. Infant mortality is high during drought conditions which also interrupts the breeding cycle. High infant mortality is indirectly related to restricted existence.

Gemsbok occur in mixed herds, the sizes of which are governed by availability and nutritional value of food plants, and ultimately climatic conditions.

They ranged the entire reserve but showed preference for

flat open areas and their distribution was influenced by the distribution of ephemeral plants. Known as bulk-rough=age feeders, as they are essentially grazers in preferred habitats, the gemsbok in HMNR have adapted to a shrubby habitat with a low grass biomass, eating browse and ephe=merals, the latter constituting the largest portion of their diet. One hundred and forty five food plants were recorded. Food preference is governed by availability of the food plant.

The gemsbok diurnal activity pattern was influenced by a number of interrelated meteorological variables. Patterns were also specific to age and sex classes and social status.

Territoriality was a feature of the gemsbok social organi=zation and may be related to their restricted existence. The territories are among the largest known for ungulates with a mean size of 7,6km². Ownership is advertized in a number of ways. Territoriality in the gemsbok was also characterized by the tolerance of the territorial male toward bachelor males but nonetheless had the primary func=tion of ordering reproductive competition among males.

OPSOMMING

Drie spesies word erken in die oorsig van die taksonomiese status van die genus, terwyl drie subspesies herken word in die spesies gazella. Gazella en beisa, onderskeidelik van die suidwestelike droë- en somali droësones, word deur ŉ tussenkomende vogtige savanne bioom geografies geskei, maar was moontlik so onlangs as die Pleistoseen een bevolking.

Vroeër versprei dwarsdeur die droë dele van suidelike Afrika, het die gemsbok ŉ geleidelike afname in verspreidingsgebied en in getalle getoon. Hervestiging en ŉ toename in getalle verseker nietemin dat hulle weer goed verteenwoordig word in hul vroeëre verspreidingsgebied.

Agt ouderdomsklasse kan in die veld herken word met die gebruik van morfologiese kriteria soos hoogte, verandering in huid-kleur en horinggroei. Die gemsbok het ŉ hoë voortplantings potensiaal en die wyfies kan teoreties ŉ kalf elke nege maande produseer aangesien hulle direk na geboorte weer in estrus kom. Hierdie is nietemin afhanklik van die wyfie se fisiese kondisie en dus indirek op klimaatsfaktore. Die wyfies kan met die ouderdom van 30 maande vir die eerste keer geboorte gee en het ŉ dragtigheidsperiode van 264 dae met ŉ tussen-kalf periode van ongeveer 289 dae. Voortplantingsstrategie en -gedrag is aangepas tot wisselvallige woestyn klimaatstoestande. Moeder/kalf bande is los en kalfies bly versteek gedurende vroeë stadiums. Kalf mortaliteit is hoog gedurende droogte toestande wat ook die voortplantingssiklus onderbreek. Hoë kalf mortaliteit is indirek gekoppel aan ŉ beperkte leefruimte.

Gemsbok kom voor in gemengde troppe waarvan die groottes beheer word deur die beskikbaarheid en voedingswaarde van voedselplante en dus uiteindelik, klimaatstoestande.

Die hele reservaat is gebruik maar voorkeur is getoon vir die plat oop gebiede en verspreiding is beïnvloed deur die

verspreiding van efemere plante. Bekend as massa-ruvoer voeders, aangesien hulle hoofsaaklik weiers is in voorkeur habitats, het die gemsbok in HMNR aangepas tot 'n struikagtige habitat met 'n lae gras biomassa en vreet struike en efemere, die laasgenoemde vorm die grootste gedeelte van hulle dieët. Eenhonderd vyf en veertig voedselplante is aangeteken. Voedselvoorkeur word bepaal deur die beskikbaarheid van die voedselplant.

Die gemsbok se daaglikse aktiwiteitspatroon is beïnvloed deur 'n aantal meteorologiese veranderlikes wat in onderlinge verband is met mekaar. Patrone is ook spesifiek vir ouderdoms- en geslagsklasse en vir sosiale status.

Territorialiteit is 'n kenmerk van die gemsbok se sosiale gedrag en mag gekoppel wees aan hulle beperkte leefruimte. Die territoriums is van die grootste bekend vir hoefdiere met 'n gemiddelde grootte van 7,6km². Eienaarskap word geadverteer op 'n aantal maniere. Territorialiteit in die gemsbok is ook gekenmerk deur die verdraagsaamheid getoon deur die territoriale mannetjie teenoor vrygesel mannetjies maar het nietemin die primêre doel om die voortplantingskompetisie tussen mannetjies te reguleer.

***

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APPENDIX: Gemsbok feeding records from the Hester Malan Nature Reserve based on field observations from May 1976 to June 1977 giving monthly records and plant parts eaten

			1976								1977				Leaves/Terminal buds	Twigs/Stems	Inflorescence	Fruit	Roots	Food Class
			WET						DRY				WET							
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	L	T	I	F	R	C
POACEAE (GRAMINAE)																				
Ehrharta barnidonids	x	x	x	x	x			x			x	x			x					C
E. calycina	x		x	x	x	x									x					C
E. longifolia	x											x			x					D
Setaria pallide	x	x													x					D
Pentashistis tomentella	x	x		x			x		x			x			x					C
Chaetobromus dregeanus					x	x									x					D
Stipagrostis brevifolia	x	x	x	x	x			x		x	x	x		x	x					A
S. namaquensis	x	x								x	x	x	x		x					C
S. zeyheri					x										x					D
S. ciliata								x		x		x	x	x	x					C
Aristida dasydesmis					x										x					D
Cynodon dactylon	x														x					D
Chloris virgata	x	x													x					C
Enneapogon scaber			x								x				x					D
E. desvauxii												x			x					D
Schmidtia kalahariensis	x	x								x					x					C
Fingerhutia africana	x	x										x			x					C
Schismus barbatus					x										x					D
CYPERACEAE																				
Scirpus dioecus	x	x	x						x	x		x			x					B

APPENDIX: Gemsbok feeding records

	M	J	J	A	S
LILIACEAE					
Trachyandra falcata	x				
T. laxa	x				
Massonia depressa		x			
POLYNGONACEAE					
Polygonum lapathifolium		x			
CHENOPODIACEAE					
Chenopodium cf. murale	x				
Blackiella inflata		x			
Monochlamys albicans	x		x	x	x
Salsola kali		x			
S. tuberculosa					
AMARANTHACEAE					
Hermbsteadtia glauca	x	x			
PHYTOLOCACEAE					
Lineum africanum			x		
L. aethiopicum	x	x	x		x
AIZOACEAE					
Pharnaceum aurantiacum	x	x	x		x
Galenia africana		x	x		
G. namaense					
G. sarcophylla	x	x	x	x	x
Aizoon canariense	x		x		
Tetragonia cf. macroptera	x		x	x	x
T. microptera		x	x	x	
T. cf. reduplicata	x	x	x	x	x
Tetragonia sp.			x	x	

O	N	D	J	F	M	A	M	J	L	T	I	F	R	C
									x					D
						x	x	x						E
									x					D
								x	x					D
									x	x				D
		x		x	x	x		x	x	x				D
	x	x	x	x	x	x	x	x	x	x			x	A
						x		x	x	x				D
	x	x				x			x	x				D
		x	x	x	x		x		x	x				B
									x					D
	x	x	x	x	x			x	x	x				A
x									x	x				C
									x	x				C
						x			x	x				D
	x	x	x	x	x	x	x	x	x	x	x			A
									x	x				C
x	x		x						x	x				C
							x		x	x				
x	x		x	x	x	x	x	x	x	x				A
									x	x				C

APPENDIX: Gemsbok feeding records

	M	J	J	A	S
MESSEMBRYANTHEMACEAE					
Cheiridopsis dentata				x	
Drosanthemum sp.		x	x		
Lampranthus godmanniae		x	x	x	x
Leipoldtia pauciflora		x	x	x	x
Mesembryantheum karroense			x		x
Ruschia brevibracteata	x	x	x	x	
Herrea blanda	x		x		
Aridaria sp.		x			
CAPOPHYLLACEAE					
Spergularia glandulosa					
Silene burchelli			x	x	
CRUCIFEREAE					
Heliophila cornuta	x		x		
H. latisique var. macrostylis	x	x	x	x	x
CRASSULACEAE					
Crassula incana			x		x
C. muscosa var. muscosa			x		
C. muscosa var. rigida		x			x
ROSACEAE					
Grielum humifusum	x	x	x	x	x
LEGUMINOSAE					
Lebeckia sericea				x	x
Wiborgia monoptera	x	x	x	x	x
Melolobium humile		x	x		x
M. microphyllum	x				
Psoralea striata		x			

O	N	D	J	F	M	A	M	J	L	T	I	F	R	C
									x		x			D
x				x					x	x				C
	x					x			x	x				C
x	x						x	x	x	x	x			C
			x			x	x	x	x					C
x	x	x					x		x	x	x			C
									x		x			C
									x		x			D
x									x					D
									x					C
									x	x				C
									x	x				C
									x	x				C
									x	x				D
									x	x				C
				x					x		x	x	x	C
x	x		x			x			x		x	x		B
x			x		x		x		x	x	x			A
									x	x		x		C
									x	x	x			D
		x	x		x	x	x		x	x				D

APPENDIX: Gemsbok feeding records

	M	J	J	A	S	O
Lessertia diffusa	x					
L. spnescens	x					x
Lotononis brachyloba	x	x	x	x	x	x
GERANIACEAE						
Erodium moschatum		x				
Pelargonium dasyphyllum		x	x	x	x	x
P. incrassatum			x			
P. quinatum			x		x	
P. senecioides	x	x		x	x	
OXALIDACEAE						
Oxalis pes-caprae	x		x			
ZYGOPHYLLACEAE						
Zygophyllum divariatum	x				x	
Z. meyeri			x	x		
Z. morgsana		x	x			
Z. retrofactum						
Tribulus zeyheri	x	x				
EUPHORBIACEAE						
Euphorbia decussata		x		x		
E. mauritanica		x				
ANACARDIACEAE						
Rhus viminalis		x				
STERCULIACEAE						
Hermannia meyeriana						x
H. cuneifolia		x	x			x
H. cuneifolia var. cuneifolia			x		x	
H. dissermifolia	x	x	x	x	x	x

N	D	J	F	M	A	M	J	L	T	I	F	R	C
								x	x				D
x								x	x				D
x							x	x	x	x			C
								x					D
								x	x				C
								x					D
								x	x				C
x								x					C
					x	x		x					C
			x	x		x		x	x				B
x				x			x	x	x				B
				x	x	x	x	x	x				C
			x	x				x	x				D
x	x		x	x	x			x	x	x	x		B
		x						x					C
								x					D
			x		x		x	x	x				C
x								x	x				D
x								x	x	x			B
								x	x	x			C
x				x	x	x	x	x	x	x			C

APPENDIX: Gemsbok feeding records

	M	J	J	A	S
H. gariepina	x	x	x		
H. trifurca	x	x	x	x	x
EVENACEAE					
Diospyros ramulosa	x	x			
ASCLEPIADACEAE					
Microloma sagittatum	x	x	x	x	x
BORAGINACEAE					
Trichodesma africanus	x	x	x		
SOLANACEAE					
Lycium austrinum					x
SCROPHULARIACEAE					
Aptosimum indivisum	x	x	x	x	
Peliostomum virgatum	x	x	x		x
Manulea benthamiens	x			x	
M. cheiranthus			x		
Zaluzianskya benthamiana		x			
Hebenstreitia crassifolia		x			
Dischisma spicata	x				
Selago minutissima	x	x	x	x	x
RUBIACEAE					
Nenax dregei	x			x	
CUCURBITACEAE					
Citrullus lenatus	x				
Cucumis africanus	x				

O	N	D	J	F	M	A	M	J	L	T	I	F	R	C
	x	x		x	x	x	x	x	x	x	x			B
x	x	x	x	x	x	x	x	x	x	x	x			A
				x			x		x	x				C
									x	x	x			C
		x		x		x		x	x	x				C
			x						x	x				D
x	x	x	x	x	x	x			x		x			A
	x	x	x	x	x	x		x	x	x	x			A
		x					x		x		x			C
									x	x	x			D
									x					
									x	x				D
									x	x				D
					x		x		x	x				C
x	x					x			x	x				B
												x		D
												x		D

APPENDIX: Gemsbok feeding records

	M	J	J	A	S	O
CAMPANULACEAE						
Wahlenbergia acaulis		x				
Lightfootia thunbergiana	x		x	x		x
COMPOSITAE						
Pterenia oblanceolata	x					
Pterenoia sp.			x			
Felicia brevifolia			x			
Amphiglossa tomentosa	x					
Leyssera gnaphalioides		x	x			
Pentzia albida		x				
P. grandiflora		x				
Senecio arenarius		x				
S. cardaminifolius		x	x	x		
S. niveus		x				
Euryops multifidus			x			
Othonna floribunda	x	x	x	x		
O. lasiocarpa				x		
O. macrophylla	x			x		
Dimorphotheca polyptera	x	x				
D. sinuata	x		x	x		x
Castalis tragus	x					
Osteospermum amplectens	x	x	x	x	x	x
O. grandiglorum		x	x	x		
O. hyoceroides	x	x	x	x	x	x
O. sinuatum	x	x	x	x	x	
Ursinia cakelifolia	x			x	x	
U. chrysanthemoides				x		
Arctotis fastuosa	x	x	x	x	x	x
Arctotheca calendula		x				
Gazania heterochaeta		x				
G. lichtensteinii	x	x	x		x	
G. tennifolia		x	x			
Hirpicium alienatum	x	x	x	x	x	x

N	D	J	F	M	A	M	J	L	T	I	F	R	C
								x		x			D
x								x	x				C
								x	x				D
								x	x				D
								x	x				D
				x				x	x				B
								x	x				C
										x			D
								x					D
													D
								x	x	x			C
				x				x	x	x			D
								x					D
			x	x				x	x				C
								x		x			D
										x			C
x	x	x			x	x	x	x	x	x			B
						x	x	x		x			C
								x					D
x	x	x	x	x	x	x	x	x	x	x	x		A
								x		x			C
x	x	x	x	x	x	x	x	x	x	x	x		A
	x	x	x	x	x	x	x	x	x	x	x		A
								x		x			C
										x			D
								x		x			C
								x					D
								x					D
							x	x					C
								x					D
x								x	x	x			C

APPENDIX: Gemsbok feeding records

	M	J	J	A	S
H. schinus			x		
Berkheya fructicosa		x	x		x
Didelta carnosa	x				
D. spinosa		x	x		x

O	N	D	J	F	M	A	M	J	L	T	I	F	R	C
									x					D
x						x		x	x	x				C
						x		x	x	x				D
x						x		x	x	x				C