Daily movements of desert-dwelling elephants in the northern Namib Desert

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The daily movements of the desert-dwelling elephants, *Loxodonta africana,* residing in the extremely arid northern Namib Desert region of Namibia are discussed. The mean distance moved in a 12-h period during 1981 and 1982 was 12,9 km (range of 4 to 38 km). Distances moved in the wet season were shortest and gradually increased during the cold dry season to reach a maximum during the hot dry season. The daily distances moved were apparently affected by the quality of the available vegetation (food) and the proximity of water-holes to such vegetation which in turn were determined by the amount of rainfall and the occurrence of riverfloods. The overall mean distance of 27,5 km travelled in 24 h is further than that of other elephants studied thus far. The ability of the desert-dwelling elephants to travel such long distances regularly is regarded as one of the important elements in their survival. During the 1981 drought the desert-dwelling elephants' ability to range over long distances between available food and water resources resulted in a better survival during the drought than that of most other large mammals in the desert.

Die daaglikse bewegings van die woestynlewende olifante, *Loxodonta africana,* in die uiters droë noordelike Namib-woestyngebied van Namibia word bespreek. Gedurende 1981 en 1982 was die gemiddelde stapafstand in 'n 12 h-periode 12,9 km met 'n variasie van 4 tot 38 km. Die daaglikse afstande beweeg was die kortste in die nat seisoen. Stapafstande het geleidelik gedurende die koue droë seisoen vergroot om 'n maksimum gedurende die warm droë seisoen te bereik. Die daaglikse stapafstande word deur die kwaliteit van die beskikbare voedselplante en die nabyheid van watergate beïnvloed, beide faktore wat op hulle beurt weer deur die hoeveelheid reën en die voorkoms van riviervloede bepaal word. Die algehele gemiddelde daaglikse stapafstand van 27,5 km in 24 h is verder as dié van die meeste ander olifante wat tot dusver bestudeer is. Die vermoë van die woestynlewende olifante om sulke lang afstande gereeld af te lê word beskou as 'n belangrike faktor in die oorlewing van hierdie olifante in die woestyn. Gedurende die 1981 droogte het die olifante hierdie vermoë benut om lang afstande tussen die beskikbare voedsel en water af te lê. Sodoende het hulle die droogte beter as die meeste ander groter soogdiere in die woestyn oorleef.

Keywords: Elephants, *Loxodonta africana*, movements, Namib Desert

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Introduction

It is generally accepted that African elephants, *Loxodonta africana,* are capable of occupying a wide variety of habitats ranging from semi-desert to tropical forests (Laws 1970). However, the presence of elephants in the extremely arid northern Namib Desert region of Namibia (Viljoen 1987) is in conflict with the general concept of elephant habitat requirements. This has led to many questions regarding their adaptation to, and survival in that desert. In the past it was believed that these elephants migrated seasonally to and from the Etosha National Park in the east (Bigalke 1958; Tinley 1971) to escape the harsh desert environment. However, it has since been shown that the desert-dwelling elephants occupy the northern Namib Desert region permanently (Owen-Smith 1970; De Villiers 1981; Viljoen 1989). By implication these elephants must therefore be adapted to survive even the harsh desert conditions.

Against this background, a study was initiated to investigate aspects of the elephants' adaptation and survival in the desert environment. As part of a study (Viljoen 1988) of the movements and spatial organization of the desert-dwelling elephants, the elephants' daily movements and the possible enviromental factors influencing them are specifically examined.

Study area

The northern Namib Desert of Namibia encompasses western Kaokoland, western Damaraland and the Skeleton Coast Park (between 11°45′ and 14°15′E / 17°00′ and 21°05′S), and covers approximately 4,5 million ha (Figure 1). The region is extremely arid, with a marked gradient in annual rainfall from 150 mm in the east to as low as 19 mm in the west. Topographically the area is mountainous, intersected by large valleys with sandy, gravel or stony plains predominating in the west. Drainage is well defined with dry river courses running mainly from east to west. The woody vegetation is mainly restricted to the dry river courses (Viljoen 1980) with arid-adapted plants scattered over the adjacent plains and mountain slopes. The study area experiences three defined ecological seasons (Viljoen 1988), i.e: the wet season (March to May), the cold dry season (June to August) and the hot dry season (September to February). The northern Namib Desert is practically devoid of people as most people live in and around the main administrative centres located in the east.

Methods

Daily movements are defined as those which the elephants undertook in their normal daily travels between food sources. Movement data were collected on

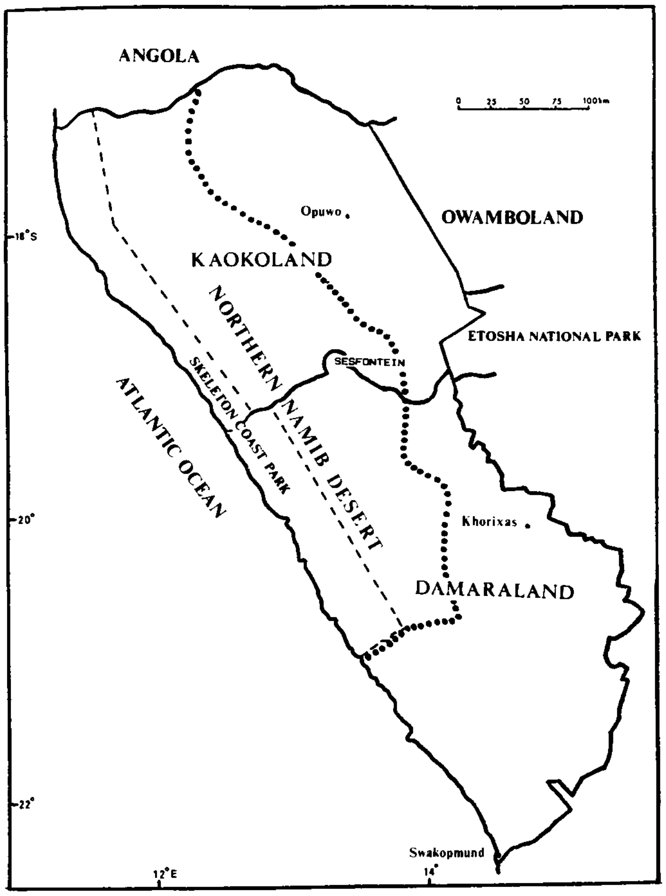

Figure 1 Map of the Kaokoveld, showing the approximate extent (solid circles) of the northern Namib Desert.

a monthly basis during 1981 and 1982. Diurnal movements of the elephants were determined from visually following identifiable individuals on foot whereas the nocturnal movements were determined from following elephant spoor the next day, starting from where the animals were last seen on the previous evening. Ideally, data for the diurnal and nocturnal movements were collected consecutively on a 24-h basis within the same month. However, nocturnal tracks were often obliterated by wind and in such cases only the diurnal movements were recorded. Diurnal and nocturnal movements were recorded in terms of 12-h periods which, although not strictly according to day length, were considered to be more objective and practically more feasible for comparisons. The entire meandering movement was noted and measured directly onto a 1 : 250 000 map, rather than the straight-line distances between consecutive locations.

For comparing rainfall with distances moved on a monthly basis, the river floods were also taken into account, as the effect of the floods on the dry riverbed and flood plain vegetation (although on a smaller scale) are the same. For this purpose an arbitrary rainfall value, equal to the minimum observed amount (68 mm) of rainfall recorded in the east to cause the rivers to flood, was allocated to that particular month for the study area. Mean values are followed by one standard deviation (±).

Results

No significant differences in distances travelled during diurnal and nocturnal movements (t = –0,40; df = 36; p > 0,05) and between 1981 and 1982 (t = 1,44; df = 72; p > 0,05) were found. Thus, all data were grouped to obtain a larger sample of the distances travelled in a 12-h period. The annual mean distance travelled by the desert-dwelling elephants in a 12-h period was 12,9 ± 6,43 km (n = 79). This indicates a distance of 25,0 km in 24 h which compares favourably with the annual mean distance of 27,5 ± 8,7 km (range 9–68 km) obtained over continuously monitored 24-h periods (n = 24).

Between seasons (Figure 2) there was a significant difference (F = 11,86; p < 0,01; df_1 = 2, df_2 = 71) in 12-h distances moved, with the mean distance moved being at its shortest during the wet season ($\bar{x}$ = 9,23 ± 5,61 km), gradually increasing through the cold dry season ($\bar{x}$ = 12,6 ± 4,86 km) to reach a maximum during the hot dry season ($\bar{x}$ = 16,9 ± 6,67 km). At the onset of the wet season there was an abrupt decrease in distances moved following the flush of green vegetation.

A significant negative linear correlation was found between rainfall and floods and mean monthly 12-h distances moved (r = –0,59; t = –3,47; p < 0,01; df = 23). However, because the state of the vegetation in a particular month is more likely to be related to the rainfall or floods of the previous month, a stronger negative correlation (r = –0,64; t = –3,93; p < 0,001; df = 23) existed when mean monthly 12-h distances moved are compared with the rainfall of the previous month in a given area. This correlation is further supported by the short 12-h distances which were recorded in May ($\bar{x}$ = 9,19 ± 5,62 km) when no rainfall actually occurred (Figure 3), but when the effect of the rainfall on the vegetation and temporary water-holes in close proximity to each other was maximal.

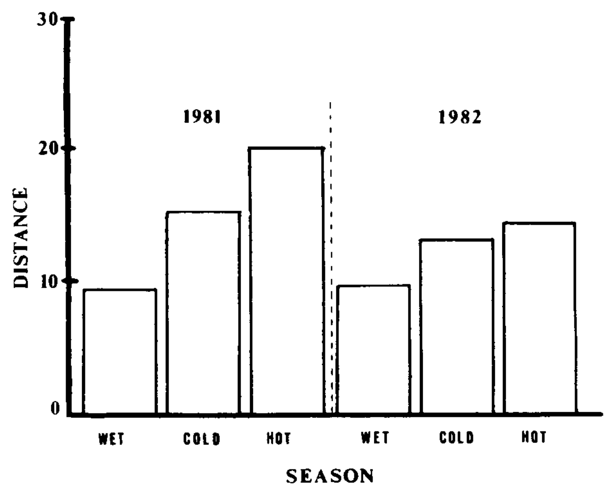

Figure 2 Mean seasonal distances (km) moved in a 12-h period during 1981 (dry year) and 1982 (wet year) by the desert-dwelling elephants of the northern Namib Desert region of the Kaokoveld, Namibia.

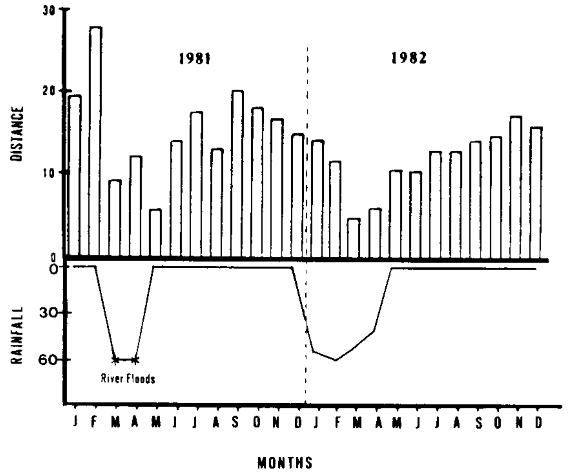

Figure 3 Mean monthly distances (km) moved in a 12-h period by the desert-dwelling elephants with rainfall (mm) and the occurrence of river floods (*) in the northern Namib Desert region of the Kaokoveld during 1981 and 1982.

Discussion

The distances moved by the desert-dwelling elephants were probably affected by the quality of the available vegetation (green grass) and the proximity of water-holes to the vegetation. This can be illustrated by the following examples. Between 1977 and 1981 the total recorded annual rainfall at Sesfontein varied from 31% to 100% below the long-term mean of 108,1 mm per annum. In 1982 the total rainfall was 94% above that mean. The information on the distances moved by elephants in this study therefore represents both years of extreme drought and of abundant rainfall. Even so, the relative patterns of 12-h distances moved in both 1981 (dry year) and 1982 (wet year) were similar (Figures 2 & 3). This was brought about by the flooding of the dry river beds, when even in 1981 with no recorded rainfall, the major rivers flooded because of rainfall in the eastern catchment basins. The resultant flooding caused a flush of green vegetation in the river beds and flood plains and formed temporary water-holes there. However, these water-holes soon dried up. This drying up is reflected in the sudden increase in 12-h distances moved between the wet and cold dry seasons of 1981 (Figures 2 & 3). In 1982, however, rain fell over a wide area causing an abundance of green grass and temporary water-holes away from the riverbeds, conditions which gradually deteriorated in the cold dry season. This changed situation is reflected by the gradual increase in 12-h distances moved (Figures 2 & 3) as the cold dry season progressed.

As the dry seasons progressed the temporary water-holes dried up and food in the immediate vicinity of the permanent water-holes was consumed first, with the result that the elephants thereafter had to move increasingly further away from their water supply to satisfy their food requirements. As the elephants usually returned to the same water-hole, however, the actual shifts in locality during the dry seasons were relatively small. In contrast, during the wet season, the elephants roamed between several temporary water-holes over a large area. Thus although their daily distances moved were relatively short, the actual shift in locality over a period of time was larger than that during the dry seasons. This explains the discrepancy observed between the results of the present study and those of Douglas-Hamilton (1971) and Leuthold (1977), who reported shorter daily movements in the dry season. In these latter studies daily shifts in locality were recorded rather than daily distances moved, since the movements were calculated by dividing the linear distance between two locations by the number of days between successive radio fixes. However, the discrepancy between the current data and those of Young (1970) cannot be explained. It is possible that the shorter distances moved in the Kruger National Park during the dry season may be influenced by the occurrence and distribution of artificial water-holes in that park.

The ability of the African elephant to move over long distances is not unique to the desert-dwelling elephants and there are many reports of elephants in other populations which occasionally moved long distances (e.g. Wing & Buss 1970; Sikes 1971; Leuthold & Sale 1973; Laws, Parker & Johnstone 1975; Leuthold 1977; De Villiers 1981). However, although there are few studies which are directly comparable, the mean distance of 27,5 km moved by the desert-dwelling elephants in 24 h during this study is greater than that of most other elephant populations studied (Young 1970; Wyatt & Eltringham 1974; Williamson 1975; De Villiers 1981; Barnes 1982).

The ability of the desert-dwelling elephants to move long daily distances regularly, may be unique and could conceivably have been acquired through selective pressures. This ability must be one of the important factors in the survival of these elephants in the desert as is highlighted by the extremely long 12-h distances (27,17 ± 9,9 km) recorded during February 1981 (Figure 3). This was a direct result of the drying up of the elephants' usual water-holes which forced them to use water-holes far removed from their food resources. It was during this period when more than 85% (Viljoen 1982) of the desert-adapted herbivores such as the gemsbok *Oryx gazella* and the springbok *Antidorcas marsupialis* (Louw & Seely 1982), died from a lack of available food in the vicinity of the remaining water-holes. As far as could be ascertained, not one of the desert-dwelling elephants died during the drought (Viljoen 1988). This was in contrast to the elephants of eastern Kaokoveld, where at least five elephants died as a result of the same drought. Also, during the same drought, approximately 200 elephants died in the Etosha National Park, presumably ultimately from anthrax, but with nutritional stress as a probable proximate cause (Berry & De Villiers 1982).

Conclusion

The elephants' high degree of mobility is possibly one of the key factors in the survival of the desert-dwelling elephants. The daily movements of the desert-dwelling population are a manifestation of the climatic regime dressed; the dressed carcass being the body of the animal after the head, legs, viscera and skin were removed.

Age was determined by tooth eruption and wear (Rautenbach 1971), and in the older group by tooth sectioning and counting cementum annuli. For the calculation of population age structure all ages were recalculated to an arbitary date taken as June 1976 in the first sample and June 1977 in the second.

Females were examined for reproductive status, and taken to be pregnant if a visible foetus was present, and lactating if milk could be expressed from the teats. All foetuses were collected and birth dates were determined by calculation, after age determination following Hugget & Widdas (1951).

The age structure determined here cannot readily be used to calculate life table statistics and therefore productivity could not be determined in this manner. A rough calculation, however, was attempted based on the following method. The age structure of the female segment was smoothed using a polynomial function. A cropping rate of 20% had been applied and this was mainly on the age groups older than one year. These groups were consequently increased by 20%. Births were then calculated using this structure and the fecundity values determined in the study.

Two-litre random-grab samples of rumen contents were collected and preserved in formalin. These were analysed at the McGregor Museum in Kimberley, where experienced technicians identified plants present from epidermal characteristics of the leaves. Stalks which could not be individually identified were grouped together in a separate category. Results are presented as percentage occurrence, calculated as the number of stomachs containing a species divided by the total number of stomachs.

Rumen samples were collected on a monthly basis and an importance value was calculated as

$$\frac{\text{percentage occurrence} \times \text{months of occurrence}}{10}$$

for all species with a percentage occurrence of more than 1%.

Grass occurrence and use is strongly influenced by rainfall and this varied widely over the study period (Figure 4).

Results

The meat production potential of cropped springbok is detailed in Table 1. Maximum growth rate is attained before the animals are one year old and at this stage males have achieved 88% and females 92% of their respective mean mature body mass of 31,5 and 27,1 kg respectively.

Dressing percentage is high in all age groups and carcasses from 10 kg upwards are acceptable for marketing.

The ages of the animals at the time they were shot (Figure 1) and corrected age structure of the population (Figure 2) indicate that in spite of the cropping being concentrated on animals older than 24 months, survival up to four years of age is high, after which it declines sharply. It is also interesting that although there are fewer males in the older age groups, they in fact survive longer than do females.

Foetal sex ratio was 0,85 f : 1,0 m. In the shot sample this ratio was 0,74 f : 1,0 m. The sex ratio of the standing population was 1,0 f : 0,85 m.

Age-specific fecundity determined as the number of foetuses per female is shown in Figure 2. It can be seen that females can conceive before they are 12 months of age and that maximum fecundity is achieved by an age of 24 months. Because of small sample sizes in the older age groups all animals older than 24 months were lumped together to determine the latter value.

The calculated number of births per hundred females, and the modification of the age structure used to determine it, is shown in Table 2. Taking juvenile mortality to be 42,1% (Figure 2) a productivity figure of 29 lambs per 100 ewes per year is arrived at.

Births during this study were shown to be seasonal (Figure 3). As the study terminated in May 1978 it is not known if another birth peak was experienced in the spring of that year, but judging from the records of lactating females there was no early peak in February–March during 1976 before the investigation commenced.

In attempting to relate the seasonality to environmental factors, the time of conception (mating season) was compared graphically with the distribution of rainfall (Figure 4). It can be seen that the two regular birth peaks resulted from conceptions shortly after good rains; the smaller peaks in March, April and May 1978, however,

Table 1 Meat production potential of the Biesjesfontein springbok herd. Values are means for each age group ± standard deviations

Age group (months)	Live mass (kg)		Dressed mass (kg)		Dressing percentage		Sample size	
	Male	Female	Male	Female	Male	Female	Male	Female
0– 3	11,5 ± 0,7		7,2 ± 0,5		62,3		3	0
3– 6	17,3 ± 3,2	16,3 ± 3,8	9,7 ± 1,8	8,7 ± 1,5	56,1	53,3	20	9
6– 9	21,3 ± 3,3	21,3 ± 2,6	12,1 ± 3,0	11,7 ± 1,8	56,9	55,2	23	24
9–12	24,6 ± 3,9	22,3 ± 3,7	13,6 ± 2,2	13,2 ± 2,0	55,0	58,3	35	20
12–24	27,7 ± 4,3	24,8 ± 3,6	15,1 ± 2,6	13,71 ± 2,1	54,6	55,3	72	59
24+	31,5 ± 3,9	27,1 ± 2,7	18,3 ± 2,5	14,9 ± 2,1	58,8	55,0	144	107

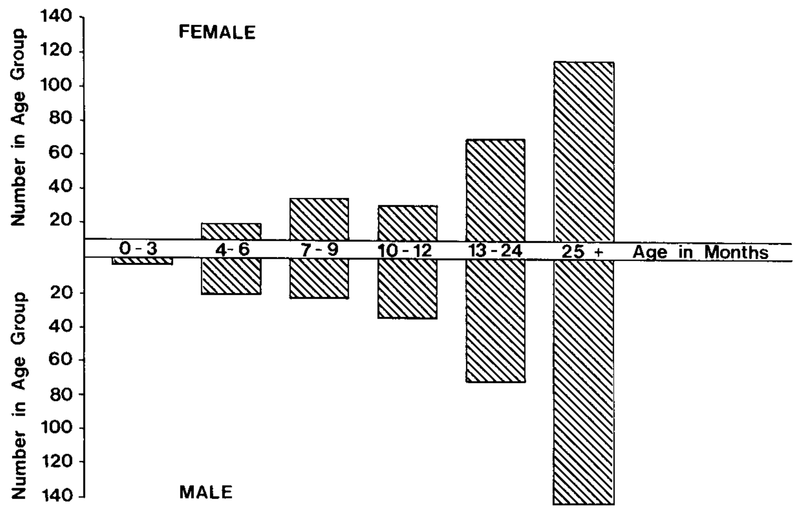

Figure 1 The age distribution of the animals as they were shot. Cropping was aimed mainly at animals older than two years.

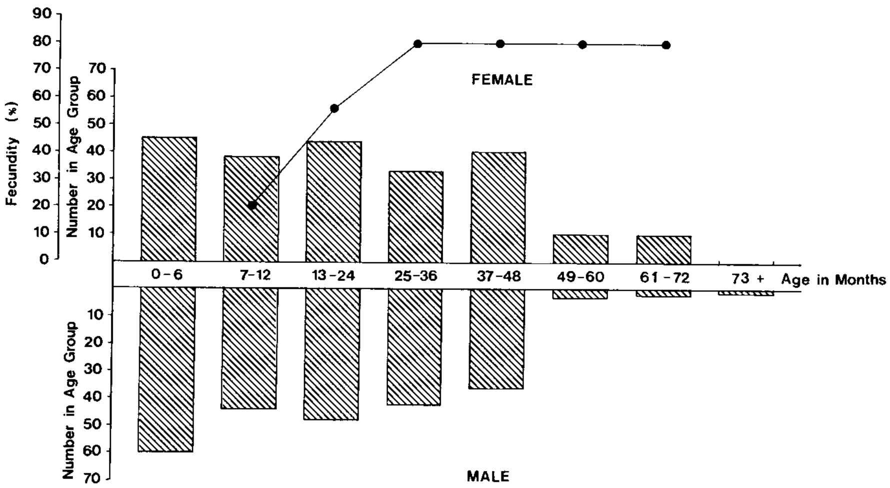

Figure 2 Age structure of the Biesjesfontein springbok herd calculated to an arbitary annual date of June each year. Fecundity is for the female segment.

Table 2 Data used to calculate production in terms of births. The number sampled is the ratio of females actually collected in the different age groups, calculated to a specific time. These data were smoothed by a polynomial function and corrected to account for the number harvested in that year. Births were then calculated from age-specific fecundity

Age group	No. sampled (per 100)	Smoothed	Corrected	Births (per 100)
0–12	40	35	35	3
13–24	21	25	30	16
25–36	16	18	21	14
37–48	19	14	17	12
48 <	4	8	10	6
Total	100	100	113	51

resulted from conceptions that occurred shortly after a dry spell.

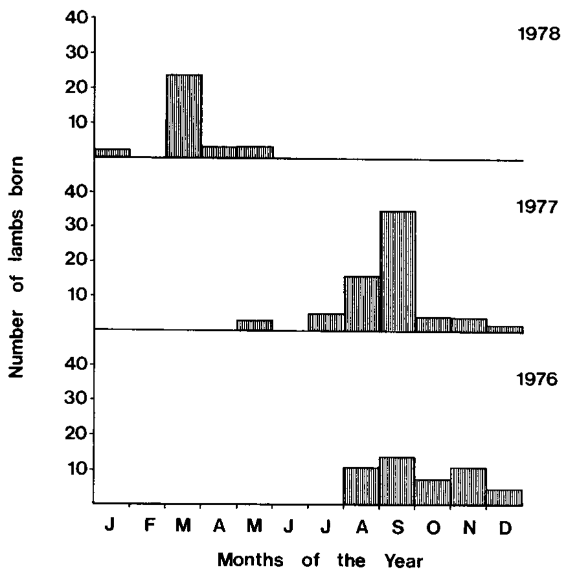

Figure 3 Distribution of births as calculated from embryo sizes, using the formula of Hugget & Widdas (1951).

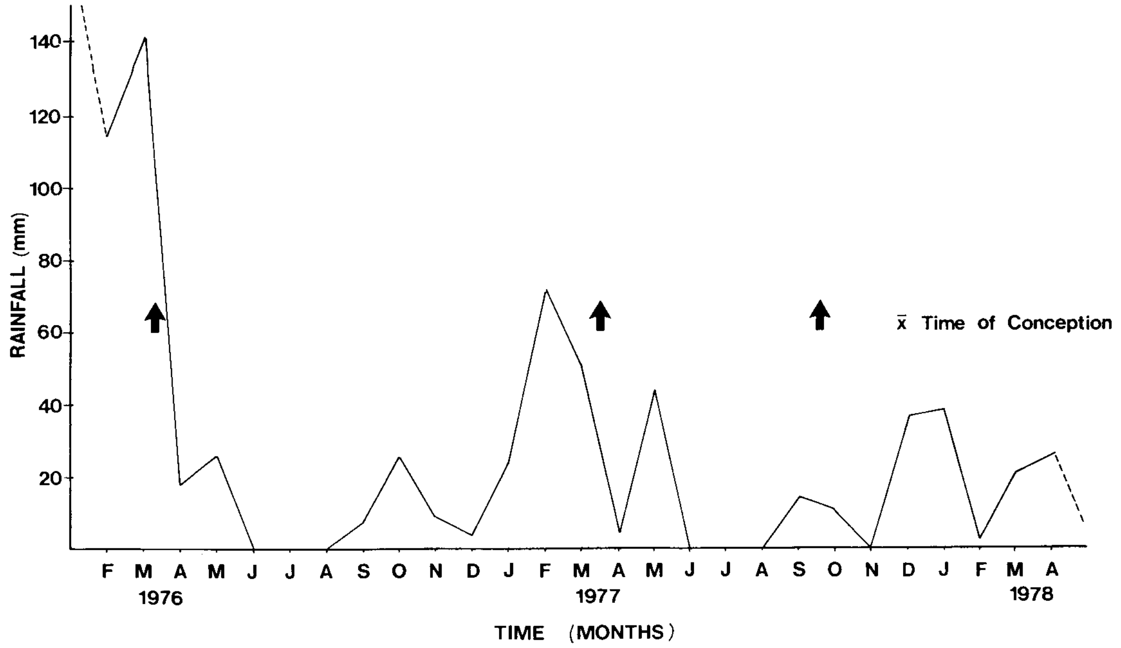

Figure 4 Rainfall distribution during the study period. Arrows indicate the mean date of conception for the three lambing peaks shown in Figure 3.

The composition of the diet (Figures 5 & 6) covers 57 plant species. Of the species eaten, however, only 15 shrubs occurred in more than 3% of the rumen samples and only three in more than 50%. Table 3 is an attempt to rank the main shrub species (and the total grass component) occurring in the rumen in terms of importance.

The ratio of browse and graze components and the unidentifiable stalks in the different months of the study (Figure 7) in terms of the number of identifiable fragments, is a crude measure of the contribution made by the two main dietary components. Although differential digestibility would tend to bias the results in terms of browse, it is apparent that the latter component provides the bulk of the springbok's diet in the study area. The amount of unidentifiable material also acts as a control on the efficiency of the method of diet determination.

The number of species in the samples shown in Figure 7 indicate a trend for more species of a particular component to be used when there is more of this component in the diet (Figure 8). This trend is more pronounced in the grasses, indicating less selection here, a result that concurs with the species composition of the rumen samples

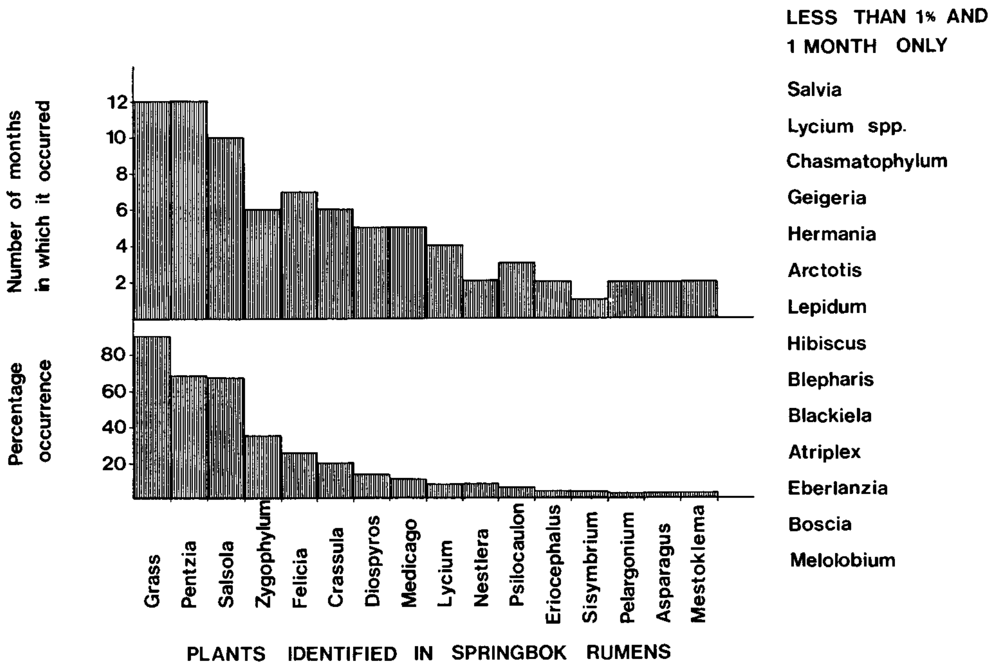

Figure 5 The plants identified in springbok rumen contents and the number of months in which each item occurred.

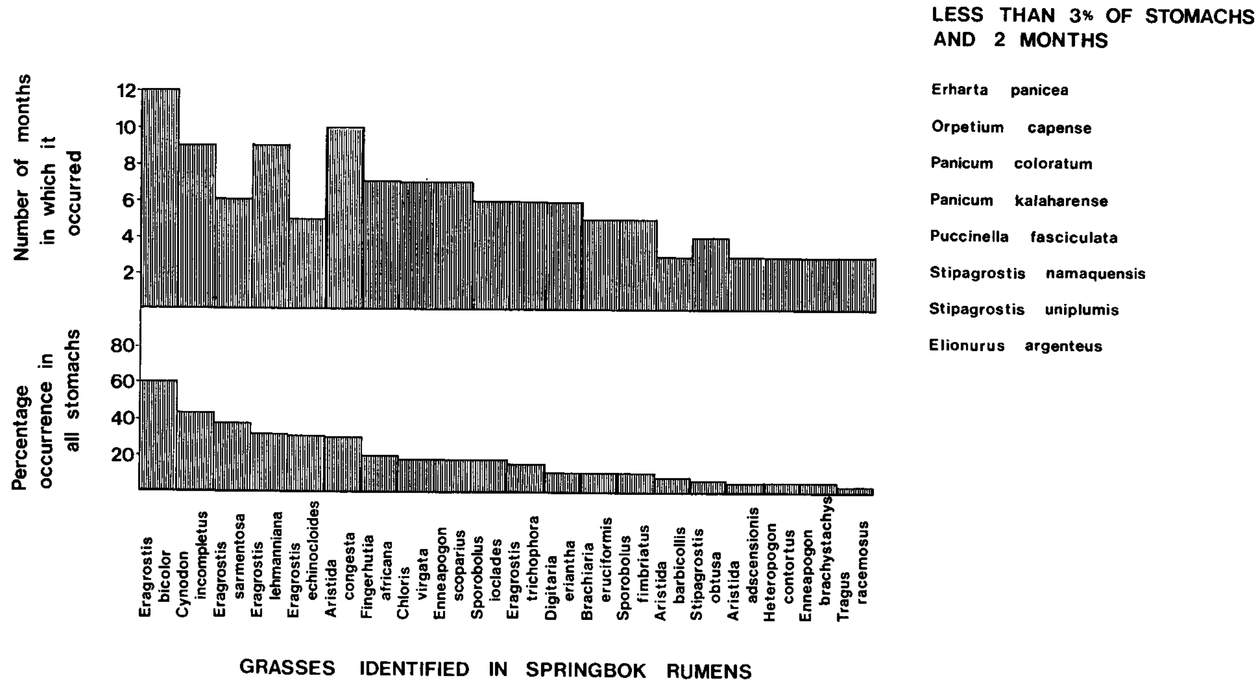

Figure 6 Individual grass species identified in springbok rumen and the number of months of occurrence.

Table 3 Food components of the springbok diet ranked according to the calculated importance value

Plant species	Importance value (rumen)
Grass	10,80
Pentzia sp.	8,16
Salsola nigrescens	6,70
Zygophyllum incrustatum	2,10
Felicia muricata	1,75
Crassula muscosa	1,20
Diospyros afro-australis	0,65
Medicago hispida	0,55
Lycium cinereum	0,32
Nestlera prostrata	0,16
Psilocaulon absimile	0,18
Eriocephalus spinescens	0,08
Sisymbrium sp.	0,05
Pelargonium sp.	0,06
Asparagus sp.	0,06
Mestoklema arboriforme	0,06

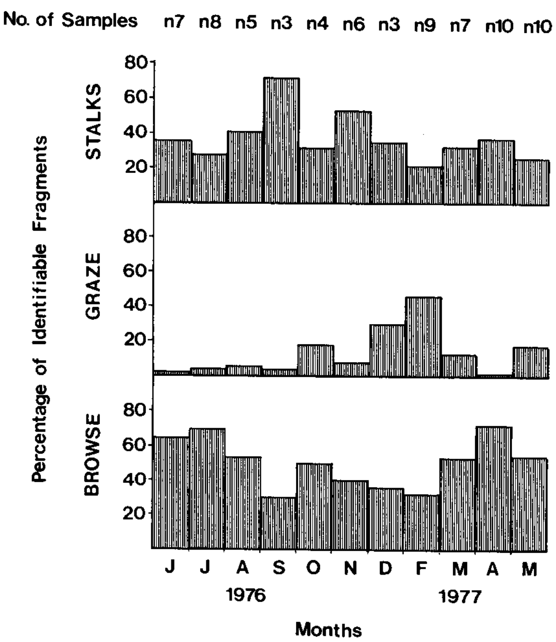

Figure 7 Browse and graze components of the diet as the ratio of identifiable fragments per rumen with an indication of the unidentified component in the form of stalks.

(Figures 5 & 6).

Figures 7 and 8, taken together with Figure 4, also show that the importance of grasses increases during the rains; the highest values being attained during October and November and again in February, March and May, which coincide with rainfall peaks in 1977 (Figure 4) when the samples were obtained.

Discussion

The importance of the springbok as a game-farming species has been emphasized in previous papers (Jooste 1980; Conroy & Gaigher 1982), mainly in terms of distribution and numeric abundance of the animal. Evaluating the full potential requires that its productivity, adaptability and veld utilization also be considered.

The mature live mass and growth rate values found in this study are essentially the same as those reported previously for another Karoo region (Penzhorn 1978), and for the western Transvaal grassveld (von la Chevallerie 1970), indicating that the study population can be

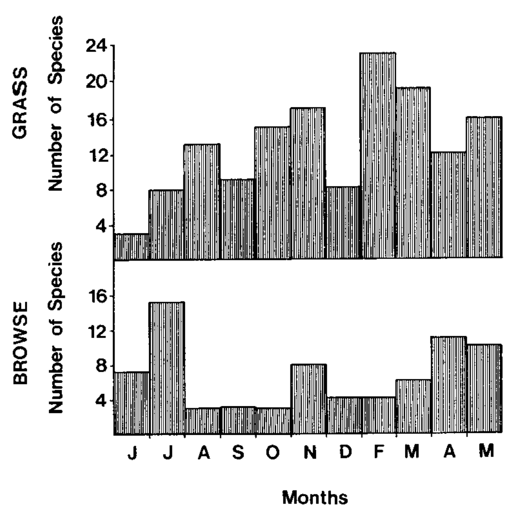

Figure 8 Monthly variation in number of species of the browse and grass components of the springbok diet.

used to evaluate the productivity of springbok in a more general sense. Mass in males increased at a rate of 77 g/day up to an age of six months; this gain constitutes 55% of the mature live mass of the springbok. Merino sheep in this area have a mass of about 20 kg at six months of age giving a growth rate of 94 g/day with a mean mature live mass of 40 kg, this is 50% of the mature mass in this case, thus while the springbok have a lower absolute growth rate, on a relative scale they are competitive with merinos. Dressing percentage is high at all ages as is the case with game generally and corresponds to that quoted in the literature (von la Chevallerie 1970). This, coupled with the lower fat content of the carcass (van Zyl, *et al.* 1969), is a major advantage in today's market if the two animals were to be evaluated on an equivalent basis. The dressing percentage results again emphasize that this study can be generalized with reasonable confidence.

Growth and yield data show that cropping would be most efficient at an age of between six months and one year for both males and females, in contrast with the actual results (Figure 1). Most of the animals shot were older than two years, this means that as far as males are concerned, too many animals are being carried for an unproductive year in which only 4 kg or 12% of live mass is added. Cropping a part of the male segment at one year would allow more females to be carried for a higher productivity or conversely a lower stocking rate with no loss of productivity. For impala *Aepyceros melampus* it has been shown theoretically that productivity can be increased by between 30% and 100% purely by manipulation of the sex ratio (Fairall 1985), and the same should be possible with springbok.

Fecundity as determined here is as high as has been reported in the literature (Skinner 1984). Because some females could have lambed in the years under investigation, but were collected outside the period where either a foetus or milk could be detected, the fecundity values presented must be considered minimal.

The calculated productivity of 29% indicates that the cropping rate applied during the study period (20%) could easily be sustained, and that the population was probably exhibiting positive growth. Davies (1985), in a subsequent study of the same population, calculated a recruitment rate of 35% and feels that cropping at 30% is safe. This study supports his finding.

There does not seem to be an overall age-specific difference in mortality between the sexes except in the older age classes where the low numbers, and more difficult age determination, make speculation dangerous. This finding and the fact that cropping had been carried out for a number of years before the study, means that harvesting can be done without much sexual bias, should this be required.

Davies (1985) gives the only other data on springbok age structure and cropping rate, but rates of between 20% and 30% based on recruitment estimates (Dasmann & Mossman 1962; Berry 1974) or on age structure and lifetable analysis (Fairall 1969; Fairall 1983; Fairall 1985) are available for other game populations, and point to the estimate for this springbok population being at least as good as for other game. Lambing percentages of 75% are common for the merino sheep on this farm, and survival up to the age of one year is in the region of 85%. This compares favourably with that of the springbok.

Conroy & Gaigher (1982), in an evaluation of the future of game farming in South Africa, point out that the field of population manipulation would probably provide the most rapid results in terms of increased productivity with relatively small managerial inputs. The research to provide the management base, however, is reasonably complex and time consuming, hence the dearth of data in this field. The level and quality of management will also determine the success with which population manipulation can be implemented (Mentis 1972; Fairall 1984). It is clear from this study, however, that gains can be achieved in springbok productivity along this course.

One of the problems in using conventional demographic analysis in springbok is the determination of the breeding system. This is usually described as either a birthflow or birthpulse model, and these models impose reasonably severe restraints on how the demographic parameters are calculated (Caughley 1977). Springbok have been described as breeding throughout the year (Skinner 1984; Skinner, van Aarde & van Jaarsveld 1984). The data presented in Figure 3, however, indicate seasonality and this spring peak has been reported by a number of other authors (Mentis 1972). As the study was concluded before the spring of 1978, it is not known whether there were two lambing peaks in that year, but the available data show that the autumn peak is not a regular occurrence. Suggestions that lambing is related to rainfall do not seem to be borne out by this study, but there is evidence for at least some ewes having two lambs in one year as suggested by Bigalke (1970). Even if such an event were to occur sporadically, it would effectively increase the productivity of the population, as it would automatically increase the calculated cropping rate.

Accurate quantitative studies of reproduction and age structure of springbok populations are urgently needed to provide the base for formulating effective production models for this important agricultural resource. In the interim, however, the data presented here can be used for such work as long as the limitations are realized.

While productivity of the animal forms the basis of the cropping enterprise, the whole system is based on the veld and the effective use of this base will determine whether the system is productive or not. As the major income from this enterprise is derived from the Merino sheep, springbok should complement the latter in veld utilization in order to increase overall efficiency.

Grass is an important component of the springbok's diet (Figure 5) and practically all species are used (Figure 6, Table 3). As a whole, however, the browse (dicotyledon) component is more important (Figure 7, Table 3) even if it is accepted that grass fragments will be damaged to a greater extent than browse during the digestion process thereby artificially enhancing browse values. A far greater proportion of grass relative to shrub species was utilized (Figure 6), and only three shrubs occurred in more than 50% of all rumens. Judging from the number of months in which a species occurred, and the overall occurrence in the rumen, grass seems to be utilized when available, with 12 species being recorded in more than six months and 20 species in more than three months. Considering the ephemeral nature of grasses in the Karoo this is extremely high. Browse on the other hand is much more selectively used, with only six species being recorded in more than six months, even though the large majority of these plants are perennial.

Studies with Merino sheep (Botha 1981; Botha, Blom, Sykes & Barnhoorn 1983), and Merino sheep and springbok (Liversidge 1972), show that grass is a relatively more important component of the sheep's diet, but that springbok use a larger variety of grasses and in terms of direct comparison there is only a small overlap in terms of species selected. Utilization of grass and browse in the present study was complementary (Figure 7) and most of the grass was taken in summer; this concurs with the findings for Merino sheep in the Karoo (Botha 1981). In contrast, in the False Upper Karoo and Kalahari Thornveld grass is taken equally throughout the year by sheep (Liversidge 1972), but the species diversity of grass taken in summer by springbok is greatly increased (Figure 8). This could lead to lessened competition and a more efficient utilization of the veld, if it can be accepted that the same conditions found in the only direct comparison of springbok and sheep (Liversidge 1972) apply.

Only 29 species of dicotyledon were found in the rumens, although many more occur in the Karoo flora of this area. Only 15 shrubs occurred in more than 3% of the rumens (Table 2) which reflects a high level of selection, although a wide range of plants can be used, and probably are, under stress conditions.

Of the shrubs selected *Pentzia* spp. must rank as the single most important food item. This genus is considered a less palatable shrub in terms of agricultural use and does not constitute an important part of the diet of the Merino sheep in the Middelburg area of the Karoo (Botha 1981). Similarly *Zygophyllum incrustatum* is considered an unpalatable shrub for sheep but is highly selected for by springbok. Other unpalatable shrubs that rank highly in the diet of the springbok are *Lycium cinereum, Psilocaulon absimile, Pelargonium* spp. and *Asparagus* spp.

Only two species considered palatable for sheep, *Salsola nigrescens* and *Felicia muricata,* are selected by springbok and both are important dietary components. Both are important in the diet of the Merino sheep in the Middelburg Karoo (Botha 1981) and this can be accepted to be the case on Biesjesfontein as well.

While there is overlap in the diet of the springbok and Merino sheep in the palatable categories of the browse component as well as in the grass component, the most important characteristic of the springbok diet is the positive selection for what are normally considered to be less palatable species. Springbok also used 29 species of dicotyledonous plants at Biesjesfontein as opposed to only 19 species quoted for Merino sheep in the Middelburg Karoo (Botha 1981).

The findings of this study confirm what has previously been reported for multi-species animal populations, namely overlap in terms of the more palatable species of food plants but an overall increase in the number of species used by the grazing animals as a whole (Taylor & Walker 1978). Springbok also exhibit wider use of the vegetation and from this a greater flexibility in utilization can be deduced, as is also generally accepted for multi-species mixes (Walker 1979). This may account for the observation that the presence of springbok does not seem to reduce the number of sheep that can be kept on a specific area on this farm (Conroy & Gaigher 1982).

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