OBSERVATIONS ON THE BEHAVIOUR AND FEEDING HABITS OF THE SPRINGBOK, *ANTIDORCAS MARSUPIALIS*.

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ABSTRACT

The stance and attitudes of the springbok are found to be similar to those of other gazelles. Gaits used are a rack-like walk (passgang), a trot and a gallop; display trot, the stott and the pronk are considered to be ritualised gaits of increasing intensity. Urination and defecation and comfort behaviour are described. Social behaviour is discussed and mixed herds, bachelor herds and solitary territorial males are shown to occur. Territorial marking is performed by taking up conspicuous positions, horn sweeping and ritualised defecation-urination. Mating behaviour resembles that of other gazelles and harem herds are common although some copulation was seen in larger groups. Agonistic behaviour involves little ritual display. Females and young form temporary herds; the young lie out and thereafter associate in "kindergarten" groups. Communication is by various calls and by visual signals of which the erection of the dorsal fan is the most striking. Morning and evening peaks of activity occur.

Previous studies of food eaten are reviewed and the results of rumen sample analysis presented. Karroid shrubs and the leaves of several bushes and trees were found to be the dominant food in June and July. Springbok drink but can survive in waterless areas. Open or semi-open habitats are preferred and the factors influencing the preference are discussed.

In a previous publication (Bigalke 1970), some results of a general study of the springbok, *Antidorcas marsupialis*, were presented. The account dealt with body weight, reproduction, herd composition and the structure of several populations. The purpose of this paper is to describe various aspects of springbok behaviour observed in the course of the same study. Particular attention is given to the composition of the diet, as deduced from analysing rumen samples collected during the winter months.

Since the field work was terminated in 1964, a general account of the behaviour of the gazelles, among which the springbok is included, has appeared (Walther 1968). The springbok was not studied in detail and observations were confined to captive animals. Despite these limitations, there is close agreement between the behaviour patterns described for the gazelles in general, and for the springbok in particular, and my own findings.

Walther uses the term 'gazelle' for the six genera *Antilope, Antidorcas, Procapra, Gazella, Ammodorcas,* and *Litocranius.* He regards them as members of the bovid subfamily Gazellinae, sensu Haltenorth (1963), except that this author separates *Ammodorcas* from the other five – which Walther considers a mistake. Walther equates his Gazellinae with the traditional subfamily Antilopinae.

In the most recent taxonomic account of the African Bovidae, Ansell (1968) rejects Halternorth's terminology and reverts partly to Simpson's (1945) classification, using subfamily Antilopinae with the tribes Antilopini and Neotragini. However, Ansell excludes *Ammodorcas* and *Aepyceros,* both of which were included in Antilopinae, Antilopini by Simpson.

Walther's "Gazellinae (=Antilopinae)" is almost exactly equivalent to Simpson's Antilopinae, Antilopini but excludes *Aepyceros*. In this paper we follow Walther (1968), and use 'gazelle' for those antelope belonging to the six genera listed above.

PROCEDURE

Field work was done by the methods and in the areas previously described (Bigalke 1970), most observations being made in the Etosha Game Park, South West Africa and in the Kalahari Gemsbok National Park, as well as on the farms Rooipoort and Benaauwdheidsfontein (here abbreviated to Benfontein), near Kimberley, Cape Province.

Springbok in the Etosha and Kalahari Parks belong to the large race, *A.m. angolensis*, the others studied to the smaller *A.m. marsupialis*. No indications were found of behavioural differences between the two subspecies.

Rumen samples were collected from 61 animals in the Kimberley area. Twenty were shot on Benfontein and 14 each on Rooipoort and Retreat. The remainder came from Brakpan (2), Susanna (3), Platfontein (4), Secretarius (1), Soutpansfontein (1) and the Mining Area (2). All except three were collected during the months of June and July. The exceptions (Brakpan, 2; Retreat, 1) were taken at the end of April. The samples therefore indicate the composition of the diet during the dry, winter season.

The rumen contents were thoroughly mixed before taking a sample, which was preserved in dilute formaldehyde. Sample volumes ranged from 310 ml to 430 ml, with a mean of 378 ml. Before analysis, each sample was washed through a set of three sieves of mesh size 5,66 mm, 3,36 mm and 2,00 mm respectively. Finely divided material, not readily identifiable, was removed in this way. The total volume of the remainder ranged from 14,5 ml to 80,0 ml with a mean of 36,3 ml, or approximately 10% of the mean sample volume. Most of this was retained by the coarse sieve (mean 16 ml, range 4,5 – 32,0 ml) and the medium-sized sieve (mean 11,4 ml, range 5,0 – 24,0 ml). The fine sieve contained only a small fraction (mean 8,9 ml, range 5,0 – 24,0 ml).

The contents of each sieve was sorted into species, or, where this was not possible, into one of two broad categories, "unidentified woody stems" and "grass". Of these two, "grass" proved to be a category of minor importance. A mean of 62% by volume (range, 40% – 88%) of the material retained by the three sieves together, was placed into species or categories. The remainder was unidentifiable. Data collected by this relatively simple technique served to indicate important food plants, but was not suitable for sophisticated quantitative interpretation.

STANCE AND ATTITUDES

The normal stance of the springbok when undisturbed, is like that of the other gazelles, with the neck held loosely forward and quite sharply angled upward. The nose points forward and downward and the ears are erect with the pinnae directed laterally. The ears may however also be held pointing backward with the pinnae directed downward – a point not made by Walther. The hindquarters are slightly higher than the forequarters. The tail usually hangs down vertically, but

may, as in some other gazelles, be drawn in along the curve of the haunch.

Under conditions of discomfort, as for example when the animals are cold, ill or out in the rain, the stance also resembles that of other gazelles. The fore- and hindlimbs are close together, the back hunched and the neck bent, giving the head the appearance of being drawn in. The ears are laid back. Walther does not remark on the fact that the hair is erected. During rain, springbok may stand or lie down. They usually do so in the open and were rarely seen to take cover under trees or shrubs.

Resting animals which remain alert, move their ears about, as Walther has noted. Springbok have also been seen to move their heads about a good deal. On two occasions, undisturbed springbok were watched briefly while feeding and the times spent feeding, looking about and grooming were noted. Grazing periods were interrupted by short spells of looking around and, occasionally, by bouts of grooming. The times (in seconds) devoted to each activity were as follows:

	Feeding	Looking	Looking and grooming
Observation 1	709 s = 63%	251 s = 22%	165 s = 15%
Observation 2	222 s = 75%	71 s = 24%	5 s = 1%

When alert and tense ("sichernd"), springbok behave like the other gazelles and hold the neck stiffly erect with the ears pricked and turned forward. In the investigating position ("Untersuchungsstellung" – Zeeb 1959, quoted by Walther 1968) head and neck are stretched forward at body height.

On several occasions, springbok were watched when extremely tense as a result of the presence of an observer whom they could not distinguish clearly. After looking fixedly at the half-hidden observer, the animal turns the head to the side and looks away, then looks at the object of suspicion again. This may be repeated several times. The animal may also take a few steps forward, or turn through 90° and walk a few steps before again turning towards the observer. The reactions appear to be the result of conflict between a strong flight tendency and another drive – possibly that of aggression. Hinde (1966) quotes several workers who have shown that mobbing displays given to predators depend on ambivalence and the behaviour of the tense springbok described above may contain an element of mobbing. Turning the head aside probably indicates appeasement. Aggressive male Grant's gazelle use a ritualised threat, in one phase of which the contestants turn their heads aside. According to Ewer (1968), this may signify "the offer of a truce – or signifies at least that if the opponent withdraws he will be permitted to do so unmolested."

TAIL MOVEMENTS

Walther points out that the tail of all gazelles is an extremely mobile organ. In the springbok, the tail is moved from side to side incessantly while the animals feed or walk about. Tense situations, as for example when a resting herd is disturbed and the animals rise and watch the intruder, also produce active tail wagging. In flight, on the other hand, the tail is pressed up against the body between the haunches, as in Grant's gazelle (Walther 1968).

HEAD TOSSING

Unlike Thomson's and Grant's gazelles (Brooks 1961), the springbok has not been observed to flick the skin in the region of the lateral stripe before fleeing. However springbok often toss the head as they move off, commonly at a fast trot, when alarmed. The movement is pronounced, the head being lowered to near the ground and raised again repeatedly. It appears in other gaits as well and will be discussed further below.

GAITS

Unless moving very slowly or in difficult terrain, springbok, like other gazelles, have a "rack-like walk" (Harrison Mathews 1969) for which Walther (1968) uses the term "passgang". The fore- and hindlegs of one side are moved simultaneously, or nearly so, while the legs of the other side remain stationary. As in the giraffe, the fall of the hind foot usually precedes that of the forefoot very slightly.

The trot which, as Walther (1968) has shown, is usually employed when gazelles are moving rapidly with a particular goal in view ("going places"), is an important gait frequently adopted by springbok. While they may leap and then race away from a source of danger at a gallop, and can maintain this pace for long distances, they usually slow down quite soon to a fast, business-like trot. The tail is then held up against the curve of the haunches.

Walther uses the term, prelltrab – literally "bouncing trot" – for a springy, exaggerated, high-stepping gait which he has found to be widespread among the gazelles. It occurs as well in some other Bovid subfamilies, such as the Alcelaphinae and Hippotraginae. Springbok also employ this gait, and it is usually accompanied by head tossing. It may be termed proud trotting or regarded as a trotting display.

The gallop calls for no special comment. When moving at an extended gallop, springbok lay their ears back. Speeds of the order of 88 km/h are attained.

When suddenly alarmed, as, for example, by a shot or by perception of human scent, the animals often perform gigantic leaps. The legs are held far apart, the forelegs angled forward and the hindlegs partly extended. Metacarpals and metatarsals are flexed. The animals rise perhaps 2 m above the ground and cover a considerable horizontal distance. Members of a herd may respond to a fright by leaping wildly in different directions and then running in zig-zags for a short distance before settling down to flee at a gallop, and, eventually, at a trot.

When in flight, springbok not uncommonly leap over roads, a fact on which early travellers such as Millais (1899) remarked. It is of particular interest that they do not however usually leap over even quite low vertical barriers. This is evidenced by the fact that conventional 4 ft. farm fences contain springbok quite satisfactorily. Only when extremely hard pressed do they clear fences. Walther (1968) notes that gazelles in general very rarely jump over vertical barriers and can be kept in pens with fences only 1,50 m high.

The pronk is perhaps the best known gait and has been described by many early hunters and travellers as well as by modern writers such as Harrison Mathews (1969) and Walther (1968). A well known sketch by Millais (1899) is reproduced by Wynne-Edwards (1962). Some of the

animals are shown in quite unnatural positions, but others are faithfully portrayed. The back is arched, the legs hang down, either vertically or with the feet drawn close together, and the dorsal fan is usually expanded. The animal reaches the ground with all four legs simultaneously and shoots up into the air again, repeating the process a number of times. The head is usually described (e.g. Walther 1968) as being held low during a pronk, but it is by no means always in this position.

Before taking this point further, it is necessary to describe one more kind of gait. This is the "Stott" – a term not usually used in South Africa. It is of East African origin and has been adopted by Walther who uses it as an alternative to "prellsprung" – literally bouncing jump. In the springbok, the gait resembles the stotting described in other gazelles, and consists of a series of jumps executed with stiff legs, sometimes with the dorsal fan slightly open. Head tossing may also be performed.

The proud trot, the stott and the pronk are probably best interpreted as ritualised gaits of increasing intensity. Walther (1968), in my opinion rightly, considers the pronk to be functionally related to stotting in other gazelles, but he was apparently not aware of the occurrence of stotting in the springbok.

He describes accurately how stotting occurs mainly in situations of increasing or decreasing tension, but not when the animals are thoroughly alarmed. He also notes its use in play, and remarks that females and young are particularly prone to using the gait.

In the springbok, proud trotting is sometimes accompanied by a slight show of the dorsal fan. It was observed in a yearling springbok which had been alarmed by a jackal. On one occasion, a rutting male in pursuit of a female was seen to proud trot briefly. Lambs have been seen to perform the proud trot with expanded fans. Stotting is commonly seen when springbok flee from a source of disturbance. They often trot and stott alternately, but only in the case of lambs is the fan usually opened.

Head tossing is an important element of the stott and also appears in the proud trot. When pronking, the dorsal fan is usually opened wide and head tossing may precede adoption of the classic posture in which the head is held low while the animal is in the air. However females being pursued by rutting males frequently pronk and here the head is held up. Males may pronk as they retreat from a chase by another male who has ceased serious pursuit. Lambs are particularly prone to pronk, even when very slightly disturbed. In lamb groups, as in groups of adults, pronking by one animal often sets off most if not all of its companions. Pronking appears to be a common response to a predator and may be elicited by a dog.

URINATION AND DEFECATION

Walther's (1968) description of the different positions in which male and female gazelles urinate and defecate exactly fits the springbok. Females spread the hind legs a little and go into a slight crouch both when urinating and defecating. They may also defecate while walking. Urination and defecation are not necessarily linked. Urinating females elicit the immediate attention of males, who sniff the urine and lip curl (flehmen). It was not established whether urination took place more frequently than usual during the rut.

Springbok males urinate with the hind legs far back and widely spread, belly close to the ground. The legs are then brought forward and the animal squats deeply, anus near the ground, to

defecate on the same spot. This linked urination-defecation ritual, which Estes (1967) and Walther consider to be a display of territorial behaviour, is typical of adult males, not of immatures. David (1970) has already drawn attention to its existence in the springbok and his observation that pawing precedes the sequence is borne out by my study. Tail wagging ends the display, as in other gazelles.

Territorial male springbok have large, conspicuous dung heaps in their territories and usually use them. They must be presumed to serve a marking function, and perhaps also to reinforce the territory owner's sense of dominance. The distinctive patches of green vegetation growing around these heaps is characteristic of country inhabited by springbok. The grass *Cynodon dactylon* and a small species of *Solanum* are typical plants. Dung heaps of this kind are also used by other gazelle males (Walther 1968).

COMFORT BEHAVIOUR

This study can add little to the description of comfort behaviour given for the gazelles as a group by Walther (1968). Springbok groom themselves frequently and actively. The hind foot is used to scratch the anterior parts of the body. Shoulders, flanks and hindquarters are groomed by rubbing with the side of the muzzle and especially with the incisor teeth, or, sometimes, with the horns. The coat is kept in excellent condition and springbok usually appear clean and sleek. No mutual grooming was observed.

When shaking themselves, for example after standing in the rain, springbok often erect the dorsal fan slightly and shake the long hairs. Stretching, when rising after a rest, follows the normal gazelle pattern.

SOCIAL BEHAVIOUR

Herd formation and social structure

The sporadic appearance of enormous congregations of springbok, commonly referred to as 'trekbokken', in the Cape Colony up to the end of the nineteenth century, is well known (see e.g. Cronwright-Schreiner 1925, for a collection of descriptions). Wynne-Edwards (1962) agrees with early observers in interpreting springbok treks as mass-irruptions following a period of unfavourable conditions in the arid regions inhabited by the species. He discusses the treks as an example of the irruptive behaviour evolved by species inhabiting regions where the physical environment is unstable and conditions for life often become extremely adverse – the high boreal, steppe or desert regions – to ensure their survival. He finds nothing inconsistent between the idea of a homeostatic control of numbers and the existence of fluctuations occurring in a variable environment.

Child and le Riche (1969) have described two recent treks which took place in south-western Botswana and neighbouring parts of the Cape Province in 1946 and 1950. All sex and age groups were represented. They believe the treks to have been spectacular dispersal movements from areas of high population density, but thought that the possible role played by the social hierarchy in

selecting which animals trekked, and the possible importance of habitat conditions, required further consideration. Reports of a later trek in south-western Botswana and the adjacent regions of South West Africa reached the present writer in 1957. Unfortunately it was not documented. Eloff (1961) records another trek in the same area in 1959.

a) Summer concentrations

The social behaviour of the springbok is of particular interest in view of the occurrence of treks. In several of our study areas, large assemblages were found during the summer (rainy season), when the animals congregated in localities with fresh, green vegetation. All ages and sexes were represented in these large herds.

The low, erratic precipitation of the arid regions, in which the work was done, often falls as local showers. Consequently green vegetation is more often than not patchily distributed, and this profoundly affects springbok distribution in summer.

In the Etosha Game Park, aggregations of up to approximately 2 000 springbok moved erratically about the wet season dispersal area west of Etosha Pan during the rainy seasons of 1956/57 and 1957/58 (Bigalke 1961). On Rooipoort, a large calcareous pan was the most favoured summer feeding ground. On a number of occasions, when the short grasses, ephemeral forbs and karroid shrubs on the pan were green after rain, counts and estimates gave totals of 1 000 and over and, occasionally, up to 2 000 springbok. The higher figure represented a large proportion of the entire springbok population on the property.

These animals were mobile and the large concentrations often dispersed or moved elsewhere within a short while. For example, on 2nd February, 1960, approximately 2 000 springbok were seen on the pan. Eighteen days later the vegetation was dry and wilted and only approximately 50 animals could be found.

Similar, but smaller congregations of springbok were also found elsewhere on Rooipoort when local rain showers had brought on a flush of green vegetation. The pattern of opportunistic mobility was confirmed on Benaauwdheidsfontein, where most of the springbok population, which numbered approximately 2 000 – 2 200, was often seen massed in a fairly small area of good grazing.

It seems likely that feeding aggregations of the kind described may have been the nuclei from which the massed treks started in the past.

b) Winter dispersal

The summer picture of large herds concentrated in a few areas is quite different from that seen at other times of the year. During the dry season, the springbok populations studied were widely dispersed and groups were smaller. At this time the social structure could be most easily observed.

It has been shown in an earlier publication (Bigalke 1970) that springbok, like many other gregarious bovids, occur mainly in mixed herds of adults and juveniles of both sexes, in bachelor herds and as solitary males.

c) Mixed herds

After the end of the rut, which usually extends from March to May in the Northern Cape, and

TABLE 1
COMPOSITION OF 17 MIXED HERDS FROM A SAMPLE COUNTED IN THE KALAHARI GEMSBOK PARK, SEPTEMBER, 1959 (DRY SEASON)

Males	*Females*	*Juveniles*	*Total*
2	8	–	10
4	4	2	10
4	5	1	10
1	8	1	10
9	5	1	15
9	7	2	18
10	9	1	20
3	21	–	24
18	11	1	30
5	25	2	32
5	27	5	37
9	24	6	39
8	27	5	40
7	32	4	43
18	49	3	70
23	54	8	85
29	56	8	93

from June to August in the Etosha Park (Bigalke 1970) mixed herds of females, young and varying numbers of males were the commonest groups encountered.

The herds were extremely variable in size. A few of over 200 (the largest numbered approximately 250) were seen in the Etosha Park, and some of over 150 in the Gemsbok Park (maximum 183) whereas on Rooipoort, the largest mixed herds seldom exceeded 100. Most consisted of less than 100 animals and more than half of the groups in several samples, numbered less than 50. Within these limits, the variability is such that a mean value has little significance.

The overall proportion of males (other than lambs) in several population samples from the Etosha and Gemsbok Parks has been shown to vary from 22% to 27,6% (Bigalke 1970). The composition of some individual dry season mixed herds is illustrated in Table 1.

The rarity of groups with only one mature male, also seen in other areas at this time of year, emphasizes the point that harem herds are typical of the rutting period (Bigalke 1970). The fact that they do occur thereafter may signify that some female herds remain on male territories at least until the rainy season grazing concentrations form.

The onset of lambing, usually between September and November in the Northern Cape (Bigalke 1970), and the start of the rainy season are the most important events influencing social behaviour during summer. Mixed herds are disrupted as the females congregate with their lambs. The composition of bachelor herds is also altered by the influx of year-olds which, as will be shown below, become increasingly obvious as they leave their mothers and seek other social contacts.

d) Bachelor herds

Bachelor herds were seen in all study areas throughout the year. They are quite common and constituted 23% of 22 groups (excluding solitary males) sampled in the Gemsbok Park, and 25% of 76 groups in the Etosha Park. They numbered from 2 to over 50 and one report was received of a group of approximately 300 seen on Rooipoort. Such large herds are exceptional.

While small bachelor herds often consist only of mature rams, larger ones are usually made up of a few large adults and a number of younger animals. This is particularly noticeable in the early summer, when most year-old males seem to leave their mothers as new lambs are born, and join up with the older males. Examples of bachelor herds recorded at this time are: 3 Nov. 2 adults, 10 yearling male; 29 adults, 13 yearling male; 25 Nov. 8 adults, 15 yearling male; 16 Dec. 5 adults, 12 yearling male; 21 Dec. 11 adults, 11 yearling male.

Some juveniles become independent at an earlier age. On 27th March, 1962, seven estimated to be six months old, were seen in a bachelor herd totalling 47 on Benfontein. They may have been the offspring of ewes which lambed for a second time in autumn, since in the year in question there was a distinct autumn lamb crop (Bigalke 1970). No further similar observations were made, and it must be concluded that juvenile males usually join bachelor herds rather later in their first year, most of them probably when about one year old.

On a few occasions, bachelor herds were found to be accompanied by small numbers of adult females or yearling females.

Bachelor herds are common among the gazelles (Walther 1968) and also known in other Bovid groups (Ewer 1968). In the case of the springbok a few observations indicated that bachelor herds inhabit territories or home ranges as they do in Grant's gazelle (Walther 1965), but if this behaviour is general, the territories are probably temporary and less well defined than those of solitary males.

e) Solitary males

Solitary males were second only to mixed herds in frequency of occurrence in the Etosha and Kalahari Park populations (Bigalke 1970). They were also numerous on the Kimberley farms. For example, in the course of an aerial census at Rooipoort on 4 May, 1964, springbok were seen on 148 occasions. Solitary animals, most of them almost certainly males, comprised 47 or 31,7% of the sightings.

These males occupy territories. This became obvious in the course of the study, in spite of the fact that long-term observations of marked animals were not possible. Two animals were ear tagged in the Etosha Park and watched over a period of twelve days. They both remained in the immediate vicinity of the places where they had been darted and tagged, often lying in exactly the same places. In most of the study areas, solitary males were often seen to run along with a passing herd, only to lag behind and eventually to turn back to the area where they had first started. The evidence for territoriality provided by the existence of a ritualised urination-dunging sequence has already been discussed.

On the Kimberley farms Rooipoort and Retreat, the attachment of lone males to particular areas could be particularly clearly seen. The farms have areas of quite dense shrub savanna, dominated by *Tarchonanthus*, a habitat not much favoured by springbok. Small pans, similar to those described by Leistner (1967) as calc-pans, are quite common. They provide miniature islands

of open country in the otherwise dense bush. The pans are partly bare and support a sparse vegetation of grasses and karroid shrubs. Each one is usually occupied by a solitary adult male. This phenomenon is so well known that hunting tracks have been made, running from pan to pan. On the Provincial farm De Hoop, similar pans in an otherwise quite different habitat were also found to be occupied by territorial males. After being disturbed, the animals return to their pans with little delay.

This study has confirmed Walther's (1968) supposition that territorial behaviour probably occurred in *Antidorcas* (and other gazelles about which he had no information). He reported its existence in *Antilope cervicapra, Gazella thomsoni, G. granti, G. dorcas* and *G. subgutturosa.*

As it was not possible to mark territory holders, no evidence on the length of territory occupation was obtained. My impression was that conditions remained settled after the autumn rut, at least for the remainder of the dry season. The pattern of summer congregations on green grazing must be expected to disrupt the territorial system to some extent. However solitary males were also encountered during the summer. For example, 14 were seen on Rooipoort in January, 1961, and constituted 35,9% of the 39 groups encountered. No quantitative data were obtained to determine whether there was a consistent seasonal difference between the proportions of this class in the population. In any event, it can be said that in the springbok, as in some other gazelles described by Walther (1968), territoriality is not simply associated with mating.

Our data do suggest an increase in the number of solitary males during the rut. At Etosha, they comprised 27 of 103 sightings (26,2%) in July, when active mating was in progress. In April, on the other hand, only 3 (5,9%) of 17 groups seen were lone males. Similar observations were made in the Gemsbok Park, where 11 (33,3%) singleton rams out of 33 groups were seen in March, shortly before the main rut, but only 2 (5,7%) out of 35 were noted in September. The figure of 47 singles in 148 sightings (31,7%) at Rooipoort, already noted, was obtained during the rut in May. The high proportion in the Rooipoort January sample, mentioned above, is however contradictory and more data are needed to confirm this point.

It will be shown below that harem herds are the most important mating groups. Some evidence was obtained showing that harem males do not simply defend their females, as did the impala studied by Schenkel (1966, quoted by Ewer 1968), but defend territory in which rutting takes place. On some occasions, males were seen to take no active interest in females until these approached quite closely. Males were also seen to cease herding when female herds moved away. On five successive visits to one study area, over a period of nineteen days during the rut in April, an adult male was seen in the same place with a group of between 12 and 16 females and their lambs. Most of the females seem to have been the same individuals each time.

This assumption is supported by the fact that there were seven lambs about six months old with the group on each occasion. In addition, some of the females were giving birth to autumn lambs (discussed elsewhere). On the first visit there were none, but the number increased from two to five over the period of observation. The adult male drove off other solitary males and bachelor herds, sometimes running up to 450 m from the ewes to see off other males which were grazing past.

f) Territorial marking

As in the case of some other gazelles (Walther 1968), male springbok in their territories tend to

take up conspicuous positions, probably announcing their presence in this way. Territories are often, perhaps always, situated in open areas. In the small calc-pans mentioned above, male springbok usually lie down on the most sparsely vegetated ground, not seeking the shade of trees and bushes.

Walther also considers horn sweeping ("weben") to play a role in making males more conspicuous, so that it can be considered as a form of "dynamic-optic" marking. Springbok do perform this display, and the horns of adult males are often stained green by the chlorophyll of vegetation crushed while sweeping. It was observed in situations where it could be interpreted as redirected aggression. On one occasion, a male which had been tending an oestrous female was driven off by another male. The first animal thereupon indulged in a vigorous bout of horn sweeping. In another case a male was seen to chase another and then to turn back, presumably re-entering his territory, and horn sweep among some low shrubs. Further study is needed to confirm these indications that horn sweeping is to be considered an element of territorial behaviour.

The ritualised urination-defecation sequence already described is a conspicuous element of the territorial behaviour. In the springbok, as in some other gazelles, there does not appear to be any other form of obvious olfactory marking. No evidence was found for marking with the secretions of the preorbital glands. This confirms Walther's (1968) observation that he did not see captive springbok using their preorbitals in this way. The gland does not appear to secrete actively.

During the rut, adult male springbok are extremely vocal and their loud, grunting bellows probably assist in announcing their territorial dominance. Walther (1968) also considers that the sounds made by male gazelles when rutting, and sometimes when chasing a rival, might serve to emphasize their presence.

Mating behaviour

During the autumn rut, harem herds are the most frequently occurring association (Bigalke 1970). They consist of one adult male, with a variable number of females and their offspring, approximately 6 months old. Herds contain between 2 and 35 adult females but in most cases these appear to number from 8 – 10. The mean size of 32 herds during the rut was 18,7 (Bigalke 1970).

The male is extremely active in herding females and, as noted elsewhere, probably defends the territory in which they are, rather than simply the harem as such. The possibility of an increase in the number of territorial males during the rut has also been mentioned. Since territorial males constitute a rather small proportion of the total male population at other times of year, it seems necessary to postulate the formation of rutting territories by some of the males from the bachelor herds. Only in this way can one explain the large number of harem herds scattered over the countryside during the autumn.

The posture of a herding male resembles the attitudes described for other gazelles by Walther (1968). The head is stretched forward, the horns laid back and the tail held stiffly horizontal. With mounting excitement, the tail is lifted to the vertical or even curled forward. A series of loud, grunting bellows, rising to a penultimate crescendo on a higher note, is commonly heard. The sounds carry far and one is impressed by the noisiness of a population in rut.

In the early stages, distinguished as the *Vorphase* by Walther (1968), the male incessantly

chases individual females. The pace is fast, usually a fast trot or extended gallop, and the pair follows a devious zig-zag or circular course, eventually leading back to the herd. Ewes may also stott and quite often they pronk with head held high. Males do not stott or pronk and only on one occasion was the proud trot seen. Other members of the herd react to a chase by moving about, and sometimes stotting or even pronking briefly. Lambs are particularly prone to do so. The male seldom pays attention to the lambs although slight aggression was occasionally observed.

Sedate following, with urination by the ewe and lipcurl displays (flehmen) by the ram follows the pattern of the "Kontakt-und-Kontroll-phase" of Walther. In the "Demonstrative Treibphase", the male extends the head and neck horizontally, often holds the tail horizontal, and also lifts the nose from time to time. He thus displays two of the three elements which Walther considered to be basic to this phase of behaviour in all gazelles. The third element, drumming with the forelegs, appears in the springbok only as a slight stiffening of the forelegs as the animal walks. In this it appears to resemble Walther's description of Sömmering's gazelle most closely. The response of an unwilling female was simply to turn through 90°, not through 180° as Walther found in other species.

The mating march is a quiet phase, as in the other species, and springbok also fit the gazelle pattern in attempting to mount while walking. The leg tap (Laufschlag) consists merely of raising one foreleg and moving it laterally a few times, without touching the female. Copulation is performed while the male stands vertically, his forelegs bent but not touching the female, and is of extremely short duration. By Walther's definition, this stance alone qualifies the springbok for inclusion in the gazelles, since it is absolutely typical of the other species.

After copulation, both partners stand still for a while, the female with legs slightly spread and tail raised.

It was particularly interesting to find that mating was not entirely confined to harem herds. On both Benfontein and Rooipoort large groups were encountered in which several males exhibited rutting behaviour. In a herd of approximately 120, several males were seen herding. Two males were active in a herd of 28. In another herd of 110, there were 4 adult males, two of which were seen rutting. One herd of 54 was seen at Etosha in which two males both herded; although they sometimes showed aggression toward one another, both remained in the group. In this sometimes rather languid approach to the presence of rivals, springbok males appear to resemble those of Grant's gazelle (Estes 1967).

During the rutting activity which is seen in spring, when the main lamb crop is born and those females which lamb the following April are mated, harem herds are not conspicuous. Autumn lamb crops are seldom large (Bigalke 1970), and not many ewes come into oestrus in spring. There is therefore probably little stimulus for the intense activity characteristic of the autumn rut and the spring mating seems to be performed more or less incidentally. On 27 October, two mixed herds, one of 43 adults and 16 lambs, the other of approximately 80 adults and 30 lambs, were watched on Benfontein. In both, there were several adult males displaying active rut behaviour. Skinner and van Zyl (1970) have shown that the male reproductive organs demonstrate a sexual cycle with a peak in autumn (May) but that there were always rams capable of breeding at any time of year. The decline in reproductive capacity was marked in spring; this would account for the rather low-key spring rutting observed in this study.

Agonistic behaviour

Males threaten with the horns but do not have a highly ritualised display comparable with that of Grant's gazelle (Estes 1967). Fighting follows the pattern described by Walther (1968), with horns interlocked and hard wrestling from side to side.

On a few occasions, most of them during the autumn rut, dead males were found. They had apparently been killed in intraspecific fights. One which could be closely examined, had a small hole behind the shoulder, presumably caused by a horn tip.

Fighting at low intensity, perhaps best described as playful sparring, was frequently observed among young males. On occasion most members of a bachelor herd would engage in this activity.

Females exhibiting aggression toward other females, young or members of the opposite sex, threaten by lowering the horns or make stabbing movements.

Relations between females and young

As in other gazelles, newly born springbok lambs go through a lying out period. In the early stages directly after birth, the young animals remain immobile ("Freeze") when approached by an observer and may be captured quite easily. This phase does not seem to last very long in the springbok, perhaps only a day or two. Thereafter the lambs jump up when approached by a human observer and run off at great speed.

The females usually graze some distance away from the young, and approach them from time to time. The young then leave their sheltered resting places – in a hollow, under a bush or in other suitable cover – and come to suckle. Gradually the length of time spent lying in hiding decreases and the active periods increase until the lambs run with the maternal herds – probably from the age of three or four weeks.

Females with young lambs show a strong tendency to form herds of their own – as in some other gazelles. In the vicinity of these female herds, the young lambs which have passed the early immobile stage of the lying out period, rest in groups. A number of these "kindergarten" assemblages were observed, with from 2 to 15 young animals.

It usually proved possible to approach them quite closely by vehicle. The animals lie prone with head down and ears back, until, when approached too closely, they all spring up more or less in unison. In most cases they pronk with widely expanded fans, jumping in all directions in a fashion which probably confuses a potential predator. After a spell of pronking, the animals become quiet and soon lie down again. Kindergarten groups were seen with a few adult females in the immediate vicinity, with the remaining mothers grazing further away.

When older and running with the maternal herds, lambs often tend to congregate and may be seen resting in a group with the herd. The female – lamb herds tend to be far more cautious than other groups and exhibit a very long flight distance.

Young females do not appear to leave the maternal herds as easily as young males, and may indeed remain with the adults indefinitely. There was some evidence for a severance of the mother – young bond at the age of approximately six months, but most lambs probably remain with their mothers for a longer period. During the winter months, when the spring lambs are 8–10 months old, young males showed a tendency to appear in small groups with a few adults. However the birth of the next lamb crop is the main stimulus to independence. Year old animals, mainly males, form conspicuous small herds in spring. For example, 21 of both sexes were seen with 2 adult

females on 6 October and 10 with 2 adult rams on 3 November. The tendency for young males to join bachelor herds at this time has been mentioned elsewhere.

Communication

Springbok are not particularly vocal animals and have indeed been described as "almost silent." (Cronwright-Schreiner 1925). Contact calls in the form of short, low-pitched, grunt-like bellows made with slightly open mouth, were recorded however. For example, on one occasion a large herd, estimated to number 400–500, slightly alarmed and running through thick bush in the twilight of early evening, produced a notable chorus. The fact that visibility was poor on this occasion supports Walther's (1968) remark that some other gazelles tended to be more vocal in the dark than in the light.

The contact call is very similar to the call made by females in the presence of lambs. In the case of most other gazelles, Walther considers this maternal call to be the same as the contact call.

No threat sound was noted in springbok, although Walther describes it as a characteristic of the gazelles and found it to be similar to the rutting bellow of other species. When alarmed, springbok emit a forceful, high-pitched whistling snort. As in other gazelles, where there are considerable species differences, it is a nasal sound.

Fear and pain are indicated by a loud call which seems to be identical to the one which Walther (1968) describes for the other gazelles – a loud, prolonged "ÖÖÖÖÖ" emitted with open mouth.

Visual communication is effected by taking up the alarm stance, previously described, and by moving off. The pronk is a particularly effective signal and if one animal starts pronking it is frequently followed by most others within sight.

The dorsal gland, situated at the anterior end of the dorsal fan, secretes actively and produces a strong sweet smell. This is presumably released when springbok pronk and, if so, probably enhances the effect of the visual signal.

ACTIVITY RHYTHMS

The pattern of daily activity was found to show two peaks, one in the early morning and one in the late afternoon and early evening. Most feeding took place at these times but weather conditions and the state of the vegetation influenced the timing and extent of the peaks. On hot summer days, grazing ceased early, often between 0800 h and 0900 h, and the animals sought the shade of trees and bushes where they stood or lay down until the late afternoon, resuming their feeding activity between 1600 h and 1700 h. Herds were commonly seen tightly clustered together in the shade of large trees. As noted elsewhere, the use of shade is probably an important aid to thermoregulation and water conservation. On cool days, and particularly after rain when green vegetation was freely available, springbok frequently fed throughout most of the day.

In winter, the early morning feeding period tended to end rather later than in summer, animals bedding down from approximately 1000 h or later and becoming active between 1500 h and 1600 h. Little use was made of shade in winter, the animals commonly lying down in the open. Resting animals quite frequently rose, stretched and groomed, urinated or defecated and even fed

for a short while before again lying down. Those observed closely remained alert and did not appear to be sleeping.

Some evidence was obtained for nocturnal activity. Observations made on two moonlit nights showed that feeding proceeded at least until 2130 h and reports were received of springbok seen grazing at about 0500 h on summer mornings.

FOOD AND FEEDING BEHAVIOUR

Sclater, quoted in Shortridge (1934), described the food plants of springbok as consisting of the "various small bushes with which the Karroo is clothed", adding that in Bechuanaland "where the country is covered in grass, springbok find their nourishment from this". Gentry (1964) suggested that the springbok might be predominantly a grazer. He did so on the argument that an increase in molar tooth row length relative to the premolar row, appeared to accompany a greater proportion of grass in the diets of a series of other gazelles. Eloff (1959 a, b; 1961; 1962) recorded a number of plant species on which springbok were seen to feed in the Kalahari Gemsbok National Park.

Van Zyl (1965) was the first to deal in any detail with the feeding habits of springbok. In the Lombard Reserve, Western Transvaal, he found that they took 68 plant species, representing 25,9% of the species in the reserve. Only 20 species were taken during three or more months of the year, and these were considered to be the main food plants. Nine (45%) were grass and 11 (55%) shrubs, the former being of greater importance during the rainy season and the latter being favoured in the dry season.

Leistner (1967) lists 57 species of plants which he found springbok to take in the Kalahari Gemsbok Park. These include grass, shrubs and ephemerals. The grasses *Stipagrostis obtusa, Schmidtia kalahariensis,* the shrubs *Monechma australe* and *Rhigozum trichotomum* and the small legume *Psoralea obtusifolia* were seen to be eaten very often while another 14 species, mainly shrubs and ephemerals, were taken frequently. He found that the animals fed mainly on short karooid vegetation which is found on limestone, in and along river-beds and in pan areas. Ephemerals, in important item, are often pulled out by roots and grasses are taken mainly while young and green. Leistner also observes that springbok can raise themselves on their hindlegs, like goats, to reach attractive leaves, shoots and pods of tall shrubs. This behaviour was confirmed in the present study. Walther (1968) reported that blackbuck and Dorcas gazelle, and particularly gerenuk and dibatag, also feed in this way. Springbok also dig for roots to a limited extent (Eloff 1959b; Smithers 1971) which I have also observed.

Liversidge (1970) identified grasses in rumen samples taken from springbok and Merino sheep on a farm near Belmont, C.P., situated in the Transitional Karoo veld type. There was a close similarity in the preferences-shown by the two animal species for the more important grasses. However springbok fed on a wider spectrum, taking 33 species, compared with 20 species identified in rumen samples from sheep. Lack of material precluded a satisfactory determination of seasonal preferences. However both springbok and sheep appeared to take a greater variety of grasses in early summer, from August to December.

In a subsequent paper, Liversidge (in press) discusses the results of further quantitative studies, both on material from the Belmont farm and on rumen samples from springbok and Dorper sheep

TABLE 2
PLANT SPECIES IN SPRINGBOK RUMENS, CLASSIFIED BY LIFE FORM

Key	Category	Total spp. Identified No.	Total spp. Identified %	% spp. above trace
1	Grass	2	2,5	—*
2	Annual herb	6	7,6	4
3	Perennial herb	25	31,6	11
4	Chamaephyte	30	38,0	21
5	Shrub or tree	15	19,0	11
6	Succulent	1	1,3	1

* The macerated grasses were not identified. Had they been, one or both of the species which were identified from larger fragments might have fallen in this category.

taken on a farm in the Kalahari Thornveld – *Tarchonanthus* veld near Campbell. At Campbell, springbok took 68 grass species and Dorper sheep took 34. Of the total of 78 different grasses identified in the study, only eight were present in any quantity in the rumens. These were *Aristida congesta, Enneapogon brachystachyus* and six species of *Eragrostis.*

The proportion, by weight, of grasses and of dicotyledons in springbok rumens tended to fluctuate seasonally, although the author concludes that no consistent seasonal variation of feeding habits was detectable. The tables and figures show a preponderance, and in some cases a dominance, of grass between October and March. From June to August, dicotyledons constituded 88%–10%, by weight, of the food examined.

The rumen samples analysed in the present study indicate that dicotyledonous plants are the springboks' mainstay during the winter months of June and July on the Kimberley farms. A taxonomic list of the 74 plant species identified is given in Appendix 1. A list, in which the species are arranged by life form, and their occurrence in rumens from the 9 farms indicated, forms Appendix II.

In Table 2, the total number of species identified is summarised by life forms. In addition, those found in quantities greater than traces, are listed separately to show the percentage of species falling in each life form category. From Table 2 it is seen that chamaephytes constituted the greatest percentage of the species identified, followed by perennial herbs. Shrubs and trees were less important and few annual herbs, grasses and succulents were found. Reduction of the number of species by eliminating those found in trace amounts, reduced the relative importance of perennial herbs, which take up a position equal to that of shrubs and trees, both well below the percentage of chamaephytes.

In Table 3, the results of quantitative analyses of rumen samples from three farms, Rooipoort, Retreat and Benfontein, are compared. The results have been greatly simplified. We have eliminated not only 'trace species' but also all species found in amounts less than 5% of the volume of each rumen sample analyses. From this reduced list of species, the *percentage occurrence* of each in the group of rumen samples from each of the three farms was calculated.

From Table 3 it is seen that there are a few interesting similarities between rumens from the three properties. But differences in the importance of various species are the most striking feature of the table, and are probably related mainly to their availability.

The karroid shrubs (chamaephytes) *Pentzia incana* and *P. calcarea* were found in most or all stomachs. This may be because they are abundant in the field, or because they are highly favoured food plants, or both. A great deal of the material classified as 'unidentified woody stems', appeared also to consist of *Pentzia* fragments, emphasising the importance of these plants. The leaves of the small tree *Zizyphus mucronata* were also found in stomachs from all three areas. Van Zyl (1965) has noted that springbok pick the fallen leaves from the ground with relish during the winter months. On Rooipoort the scarcity of fallen leaves under the trees was most striking at this time of year. The karroid shrubs *Chrysocoma tenuifolia, Pentzia globosa* and *P. lanata, Lycium spp.*, the shrub *Rhus ciliata* and the tree *Acacia tortilis* were found in many stomachs from two of the three properties and must therefore also be considered to be important items in the diet.

Noteworthy differences between rumens from the three farms outnumber the similarities. More shrub and three species were of frequent occurrence in Rooipoort rumens than elsewhere. This reflects the existence of large tracts of shrub savanna where *Acacia mellifera, Rhigozum trichotomum* and *Tarchonanthus camphoratus* are locally dominant. *Zizyphus mucronata* is common in moist depressions and *Acacia tortilis* is abundant on deeper soils. *Euryops multifidus* is prominent in some sandy grassveld. Karroid shrubs are found on calcrete and these expanses of short veld are particularly favoured by springbok.

Retreat lies on the Karstic Ghaap plateau, with scrub bushveld where *Tarchonanthus* and *Rhus* species are dominant. *Olea africana* and *Zizyphus mucronata* are common shrubs or trees and springbok took both species. *Pentzia spp., Chrysocoma* and *Lycium* found in many of the samples are among the common plants of pans and drainage lines where springbok are often seen. The presence of grass in fair quantity in the only rumen collected in April is noteworthy. It confirms van Zyl's and Leistner's observations that grasses are fed on mainly in the rainy season.

The great variety of karroid shrubs found to characterise the Benfontein samples is of particular interest. These plants grow mainly on the low lying section of the farm surrounding a large pan, where the vegetation has halophytic characteristics. The rumen analyses suggest that the high-lying areas of Kalahari sand with Kalahari thornveld and much perennial grassland provide little food during the dry season.

Very few rumen samples were taken from the other six farms which appear in Appendix II. It is therefore noteworthy that a number of species found to be important in the larger collection of material from Rooipoort, Retreat and Benfontein, also appeared in limited amounts of material from other properties. The importance of the karroid shrubs *Pentzia* (5 species), *Chrysocoma tenuifolia*, and probably *Aster, Barleria* and *Eriocephalus* to a lesser extent, as well as the shrubs and trees *Acacia tortilis, Zizyphus mucronata* and *Rhus ciliata*, as winter foods is emphasised.

In summary, it can be said that the winter food of springbok in the vicinity of Kimberley appears to consist largely of the shoots and leaves of karroid shrubs, and of the leaves of several shrubs and trees. Grasses appear to be of little importance. This choice of food reflects the feeding value of the plants.

As Louw (1969) has pointed out, karroid shrubs "will apparently supply the protein requirements for maintenance of ruminants during winter", although the crude protein levels may

TABLE 3

PLANTS IDENTIFIED IN RUMEN SAMPLES FROM ROOIPOORT (14 SPECIMENS), RETREAT (11 SPECIMENS) AND BENFONTEIN (19 SPECIMENS), PLACED IN ORDER OF IMPORTANCE. THE ORDER OF IMPORTANCE WAS DETERMINED BY CALCULATING THE PERCENTAGE OF SAMPLES WHICH HAD A PARTICULAR SPECIES OR CATEGORY PRESENT IN A QUANTITY OVER 5% OF THE SAMPLE VOLUME

Rank	ROOIPOORT Category/species	Percentage	RETREAT Category/species	Percentage	BENFONTEIN Category/species	Percentage
1.	Woody stems (unidentified)	100,0	Woody stems (unidentified)	100,0	Woody stems (unidentified)	94,7
2.	*Euryops multifidus* ..	78,6	*Pentzia incana* and *calcarea*	100,0	*Pentzia incana* and *calcarea*	78,9
3.	*Pentzia incana* and *calcarea*	50,0	*Chrysocoma tenuifolia* ..	36,4	*Salsola glabrescens* ..	31,6
4.	*Acacia mellifera*	35,7	*Olea africana*	27,3	*Nestlera minuta*	21,1
5.	*Rhigozum trichotomum* ..	28,6	*Rhus ciliata*	27,3	*Chrysocoma tenuifolia* ..	15,8
6.	*Rhus ciliata*	21,4	*Pentzia globosa* and *lanata*	18,2	*Pentzia globosa* and *lanata*	15,8
7.	*Zizyphus mucronata* ..	21,4	*Zizyphus mucronata* ..	18,2	*Zizyphus mucronata* ..	10,5
8.	*Tarconanthus camphoratus*	21,4	*Lycium* sp.	18,2	*Lycium pilofolium*	10,5
9.	*Zygophyllum microphyllum*	14,2	Grass (unidentified)* ..	(9,1)	Grass (unidentified) ..	10,5
10.	*Babiana hypogaea*	7,1	—		*Psilocaulon absimile* ..	10,5
11.	*Acacia tortilis*	7,1	—		*Eriocephalus ericoides* ..	10,5
12.	*Barleria rigida*	7,1	—		*Acacia tortilis*	10,5
13.	*Aster muricatus*	7,1	—		*Salsola nigrescens*	5,3
14.	—		—		*Aptosimum marlothii* ..	5,3
15.	—		—		*Lycium hirsutum*	5,3

* This percentage would be zero if specimen "Retreat 0" was excluded. It was shot in April 1964. All other Retreat specimens were shot in June 1959.

be too low for optimal productivity by the animal. Most grasses, on the other hand, are extremely low in crude protein, as well as having a low energy value, during winter.

Leistner (1967) has summarised the position as follows ". . . . most grasses have a satisfactory nutritional value as long as they are green. In their dry state they are of little or no importance as fodder plants as both their protein and phosphate content are very low. The same applies to both summer and winter annuals as well as perennial herbs: they provide an excellent source of feed while they are green, but are worthless when dry. Low shrubs, on the other hand, retain much of their feeding value throughout the dry season. Leaves, shoots and fruits of most shrubs and trees tested are rich in protein and phosphate, and provide an important source of fodder during the driest months of the year".

The summer aggregations of springbok on areas with green vegetation, described elsewhere in this paper, are probably largely for feeding on newly sprouted grasses and herbs.

It is of interest to compare these findings with those of Stewart (1971) for Grant's and Thomson's gazelles in East Africa. Dicotyledonous plants formed a large part of the diet of Grant's gazelle early in the rains, and were the major source of food both at the end of the rains and at the end of the long dry season. In Thomson's gazelle, dicotyledons also formed a significant part of the diet, increasing in importance as the pasture matured and dried out. However grasses remained important at all stages.

WATER REQUIREMENTS AND DRINKING BEHAVIOUR

Shortridge (1934) quotes several older naturalists who reported that springbok drink little or no water. Penrice, for example, stated that the animals "seldom if ever drink" while Sclater wrote "They are able to go without water for a considerable time, though if it should be present they drink every second day." Shortridge's own view was that springbok seldom drink. Greenwald (1964) mentions numerous reports that the animals exist without drinking water. In a recent paper, Child *et al.* (1971) state that springbok "can live for long periods without surface water". However, they found them to be attracted to boreholes along the Nossob river and in adjacent areas of the south-western Kalahari.

In the course of the study reported here, springbok were seen to drink at natural waterholes in the Etosha Park as well as at troughs at artificial waterpoints in the Kalahari Gemsbok National Park and on the Kimberley farms. Drinking was observed at all times of day and there was some evidence that it also proceeded at night. Animals were seen at the water at all seasons, but drinking ceased during and after rain, and there was usually little activity at waterholes when the weather was cold. Although no quantitative data were collected, these general observations on the influence of weather conditions were repeatedly substantiated. Child *et al.* (1971) also found that ambient temperatures had a marked influence on the numbers of springbok and other antelope drinking at boreholes in the Kalahari.

Springbok were also observed in an area of south-western Botswana where surface water was absent and this, together with the evidence of other workers mentioned above, suggests that the animals are able to adapt, at least temporarily, to extremely dry conditions.

Greenwald (1964) compared the water economy of captive springbok with that of several other species. Springbok were unable to survive indefinitely without drinking water while eating food containing 10% moisture. The parameters total water intake, water drunk, urine volume and evaporative water loss were compared at 21°C and at 35°C. Urine concentration, faecal water content, total faecal water loss and daily loss of body weight during acute dehydration were determined at 21°C. The relative medullary thickness was investigated and the concentration of NaCl solutions with which constant body weight could be maintained, was established.

The author concluded that springbok are physiologically equipped to resist the stresses of a potentially dehydrating environment better than either desert or non-desert races of domestic goats. However the springbok is less well adapted to arid conditions than the kangaroo rat, which can survive indefinitely without drinking water, and the camel. It is more conservative in the use of water than the steenbok, *Raphicerus campestris* (except for the fact that the steenbok has a more powerful kidney) but no better adapted than the grey duiker, *Sylvicapra grimmia,* to aridity. The fact that the ranges of both steenbok and grey duiker include waterless areas, such as much of the Kalahari (Smithers 1971), was not sufficiently well appreciated. The author erroneously considered that these species "would not be expected from their habitats to be desert adapted". This led him to the questionable conclusion that because the springbok was not markedly better able to conserve water by physiological means than the steenbok and grey duiker, it could not be considered to possess "any extra-ordinary desert adaptations".

Greenwald goes on to note that springbok seek shade during hot days (see also below) and suggests that this behaviour is an important aid in conserving moisture. He also reports – without providing supporting evidence – that springbok in the Kalahari Gemsbok Park prefer the river bed (the Auob) where boreholes provide the most dilute drinking water. This is contradicted by the findings of Child *et al.* (1971). Springbok drank highly mineralised water at boreholes along the Nossob river bed. The maximum salinity of water used by these animals was 42,579 p.p.m. T.D.S. and only two other species, gemsbok and black-backed jackal, drank at this highly saline borehole. No correlation could be found between the number of springbok using various boreholes, and the concentrations of the dissolved ions, either separately or as T.D.S., in the water. Greenwald's conclusion that springbok can only survive in the Kalahari Gemsbok Park because artificial sources of water are provided, appears questionable.

Drinking behaviour was observed in some detail on several occasions. It was often characterised by extreme caution. The animals moved slowly to the water, with many pauses. Frequent lowering of the head to the ground is probably to be interpreted as a displacement movement. Active tail-wagging and, on one occasion, urination, denoted tension. Although the members of a herd appeared more relaxed when one had begun to drink, they were nevertheless vigilant while drinking. Frequently the animals would take fright for no apparent reason, and run off some distance before again approaching the water. Springbok were seldom observed to spend much time at the water and usually departed soon after they had finished drinking. Child *et al.* (1971) record similar behaviour along the Nossob River.

MINERAL LICKS

Springbok were frequently observed to visit the salt licks provided on Rooipoort and were also

found to use licks on other farms. Under natural conditions in the Kalahari Gemsbok Park, Eloff (1962) found good springbok habitat to be characterised by, among other things, the presence of mineral licks in pans and river beds. However, Leistner (1967), writing of the same region, considers that this species appears to make less use of natural "brak" licks than gemsbok, possibly because of the higher mineral content of their diet.

HABITAT PREFERENCES

General statements on the habitat preferences of the springbok appear in a number of older publications, that of Shortridge (1934) being perhaps the most comprehensive. He writes "Springbok are typically open high-veld antelope . . . They may be met with either in grassveld – whether open or with bush – or the more arid plains . . . they sometimes wander into the fairly thick belts of bush that intersect open grasslands . . . they avoid unbroken tracts of bush or forest."

In the course of the present study, habitat preferences were investigated in several different areas. In the Etosha Park, springbok were distributed mainly in open grassland and low shrub savanna. Some use was made of mopane *(Colophospermum mopane)* savanna and woodland and of grassland along drainage lines in the mopane veld.

A clear preference was noted for the beds of the two dry rivers, the Auob and the Nossob, and adjacent banks in the Kalahari Gemsbok Park, as already documented by Eloff (1959a) and Leistner (1967). Recently Child *et al.* (1971) reported counting 79 springbok defecations in three transects on the bed of the Upper Nossob, compared with 4 defecations in three transects run on sand dunes c. 550 m from the river. However in spite of this finding, which confirms the scarcity of springbok in the dune veld noted by the present writer, Eloff and Leistner *(op. cit.)*, Child *et al.* also record that fair numbers of springbok used the three waterholes in dune veld which were studied. These boreholes have only been in existence since 1963 and may have attracted springbok into areas not previously utilized to any extent.

On Rooipoort, springbok were markedly more abundant on a large pan and on areas with short vegetation over surface calcrete and on gravelly alluvial deposits, than in perennial grassland on Kalahari sand, *Tarchonanthus* dominated shrub savanna and on rocky hills with shrub savanna dominated by *Acacia* species. On Benfontein the pan and its environs, as well as other parts of the property with short vegetation were heavily used. In parts of the farm with perennial grassland and *Acacia* savanna on sand, springbok were encountered mainly around small pans.

Factors which are probably most important in the choice of habitat are: availability of preferred food plants; mineral content of food; physical attributes of the vegetation, such as density and height, affecting the ease with which the animals can move about; psychological preference for open areas. The availability of palatable and nutritious food is clearly of basic importance. On Rooipoort, springbok were found feeding on fresh green grass in quite dense *Tarchonanthus* savanna, a habitat otherwise avoided, when local rain showers had resulted in a grass flush. Leistner (1967) records a comparable observation. In the Kalahari Gemsbok Park he saw large herds "only rarely among the high dunes and then only where rains had brought on a good crop of annuals".

Pans, areas of surface calcrete and other shallow soils support preferred short grasses and herbs, as well as karroid shrubs which, as already noted, are especially important as winter food. The

mineral content may be an additional factor of importance. Child *et al.* (1971) consider that the year-round concentrations of springbok (and other species) attracted by pans in the Kalahari, may be due to the availability of salts, from the alkali soils, that are scarce in surrounding areas. The mineral content of Kalahari sand, and especially the phosphate content, is low (Leistner, 1967).

Tall grassland was not found to be favoured in any of the areas studied. Eloff (1959b, 1962) confirms this observation, noting of one part of the Kalahari Park "the grass is too dense and tall for their liking" and stating in the second paper that springbok are rarely found where grass is high or dense. Apart from the fact that springbok probably have physical difficulty in feeding on tall grass, the plants appear to be unpalatable, partly perhaps as a result of the low mineral content where they grow on sand. In addition, springbok run awkwardly in dense grassland and probably feel ill at ease there. In one sandveld area on Rooipoort, where the tall grasses had been well grazed by cattle, springbok were markedly more numerous than in similar veld without cattle.

Rocky hills were found to be avoided but some use was made of *Acacia mellifera* var. *detinens*, which flowers in early spring and produces palatable pods, growing on the slopes of hills on Rooipoort. When stressed during a hunt, springbok were also seen to take to rocky hills otherwise avoided.

Finally, it should be noted that springbok are able to adapt successfully to densely vegetated habitat. Animals introduced to dense *Tarchonanthus* savanna on Retreat and surrounding farms have fared well.

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APPENDIX I

TAXONOMIC LIST OF PLANT SPECIES IDENTIFIED IN SPRINGBOK RUMEN SAMPLES

GRAMINEAE
Cenchrus ciliaris
Enneapogon brachystachyus
Eragrostis echinochloidea

LILIACEAE
Asparagus sp.

IRIDACEAE
Babiana hypogaea

SANTALACEAE
Thesium hystricoides

CHENOPODIACEAE
Chenopodium album
Salsola glabrescens
Salsola nigrescens

AMARANTHACEAE
Alternanthera repens
Cyphocarpa angustifolia

AIZOACEAE
Galenia pubescens
Plinthus karooicus
Psilocaulon absimile
Ruschia canonotata

CRUCIFERAE
Coronopus integrifolius
Erucastrum griquense
Erucastrum griquensie
Lepidium divaricatum

CAPPARIDACEAE
Boscia albitrunca

LEGUMINOSEA
Acacia karoo
Acacia mellifera
Acacia tortilis
Melolobium macrocalyx
Medicago aschersoniana
Psoralea obtusifolia
Tephrosia capensis

OXALIDACEAE
Oxalis depressa

ZYGOPHYLLACEAE
Zygophyllum microphyllum

EUPHORBIACEAE
Euphorbia inaequilatera

ANACARDIACEAE
Rhus ciliata

RHAMNACEAE
Ziziphus mucronata

TILIACEAE
Grewia flava

STERCULIACEAE
Melhania griquensis
Hermannia coccocarpa
Hermannia resedifolia

OLEACEAE
Menodora africana
Olea africana

ASCLEPIADACEA
Microloma massonii

CONVOLVULACEAE
Convolvulus ocellatus

BORAGINACEAE
Ehretia rigida

VERBENACEAE
Chascanum pinnatifidum

LABIATAE
Acrotome inflata
Lasiocorys capensis

SOLANACEAE
Lycium pilifolium
Solanum tomentosum

SCROPHULARIACEAE
Aptosimum albomarginatum
Aptosimum marlothii
Sitera albeflora
Sutera atropurpurea
Walafrida paniculata

BIGNONIACEAE
Rhigozum obovatum
Rhigozum trichotomum

ACANTHACEAE
Barleria rigida
Blepharis marginata
Ruelliopsis setosa

CAMPANULACEAE
Lightfootia nodosa

COMPOSITAE
Aster muricatus
Berkheya pinnatifida
Chrysocoma tenuifolia
Dimorphotheca cuneata
Eriocephalus ericoides
Euryops asparagiodes
Euryops multifidus
Gazania krebsiana
Geigeria africana
Gnaphalium glomerulatum
Hertia pallens
Hirpicium echinus
Nestlera minuta
Osteospermum muricatum
Pegolettia retrofracta
Pterothrix spinescens
Tarchonanthus camphoratus

APPENDIX II

PLANT SPECIES IDENTIFIED IN RUMEN SAMPLES, BY LIFE FORMS, SHOWING OCCURRENCE IN SPECIMENS FROM DIFFERENT FARMS

Plant Species and Life Forms	Occurrence on Farms								
	Ro	Re	Be	Br	Su	MA	So	Pl	Se
GRASS									
Enneapogon brachystachyus ..	t	t	t	—	—	t	t	t	—
Eragrostis echinochloidea ..	—	—	—	—	t	—	—	—	—
ANNUAL HERB									
Acrotome inflate	—	—	—	—	M	—	—	—	—
Chenopodium album	—	t	t	—	—	—	—	—	—
Erucastrum griquensis ..	—	M	—	—	—	—	—	—	—
Geigeria africana	—	M	—	—	—	—	—	—	—
Gnaphalium glomerulatum ..	—	—	t	—	—	—	—	—	—
Lepidium divaricatum	M	—	—	—	—	—	—	t	—
PERENNIAL HERB									
Alternanthera repens ..	—	t	t	—	—	—	—	—	—
Asparagus sp.	t	M	t	t	—	t	M	t	—
Babiana hypogaea	M	—	—	—	—	—	—	—	—
Berkheya pinnatifida	—	—	t	—	—	t	—	—	—
Chascanum pinnatifidum ..	t	—	—	—	M	—	—	—	—
Coronopus integrifolius ..	t	—	—	—	—	—	—	—	—
Convolvulus ocellatus	—	—	t	—	—	—	—	—	—
Cyphocarpa angustifolia ..	t	—	—	—	—	—	—	—	—
Euphorbia inaequilatera ..	—	t	—	—	M	—	—	—	—
Galenia pubescens	—	—	t	—	—	t	—	—	—
Gazania krebsiana	—	—	t	—	—	—	—	t	—
Hermannia coccocarpa ..	—	—	t	—	—	—	—	—	—
Hermannia resedifolia ..	—	—	—	—	—	—	—	t	—
Hirpicium echinus	—	—	—	—	—	—	t	M	—
Lasiocorys capensis	t	t	M	—	—	—	—	—	—
Medicago aschersoniana ..	—	—	t	—	—	—	—	M	—
Menodora africana	—	—	—	—	—	—	t	t	M
Melolobium macrocalyx ..	—	—	M	—	—	—	—	—	—
Osteospermum muricatum ..	—	—	t	—	—	—	—	—	—
Oxalis depressa	—	t	t	—	—	—	—	—	—
Psoralea obtusifolia	—	t	t	—	—	—	—	—	—
Ruelliopsis setosa	—	—	—	—	t	—	—	—	—
Solanum tomentosum	—	—	—	—	M	—	—	—	—
Tephrosia capensis	—	—	—	—	M	—	—	—	—
Walafrida paniculata	—	—	t	—	t	—	—	—	—

Plant Species and Life Forms	Occurrence on Farms								
	Ro	Re	Be	Br	Su	MA	So	Pl	Se
CHAMAEPHYTE									
Aptosimum albomarginatum ..	M	—	—	—	—	—	—	—	—
Aptosimum marlothii	—	—	M	—	—	—	—	—	—
Aster muricatus	M	t	M	—	—	—	—	M	—
Barleria rigida	t	t	t	—	—	—	—	t	—
Blepharis marginata	—	t	—	—	—	—	—	—	—
Chrysocoma tenuifolia	t	M	M	M	—	M	—	t	—
Dimorphotheca cuneata ..	—	—	—	—	M	—	—	—	—
Eriocephalus ericoides ..	—	t	M	—	—	M	—	t	—
Euryops asparagoides	—	—	t	—	—	—	—	—	—
Lightfootia nodosa	—	—	t	—	—	—	—	—	—
Lycium pilifolium	t	t	M	—	—	—	—	—	—
Lycium hirsutum	t	—	M	—	—	M	—	—	—
Melhania griquensis	—	—	—	—	M	—	—	—	—
Microloma masonii	—	t	M	—	—	—	—	—	—
Nestlera minuta	—	—	M	—	—	—	—	—	—
Pegolettia retrofracta	M	—	—	—	t	—	—	—	—
Pentzia calcarea	M	M	M	t	—	M	t	M	—
Pentzia globosa	t	M	M	—	—	M	t	M	—
Pentzia incana	M	M	M	t	—	M	t	M	—
Pentzia lanata	t	M	M	—	—	M	—	M	—
Pentzia viridis	M	M	M	—	—	—	t	M	—
Plinthus karooicus	—	—	t	—	—	—	—	—	—
Pterothrix spinescens	—	t	t	—	—	—	—	—	—
Ruschia canonotata	t	—	t	—	—	t	—	—	—
Salsola glabrescens	t	—	M	—	—	M	—	t	t
Salsola nigrescens	—	—	M	—	—	—	—	—	—
Sutera albiflora	—	—	M	—	—	—	—	—	—
Sutera atropurpurea	—	—	t	—	t	—	—	—	—
Thesium hystricoides	—	t	—	—	—	—	—	—	—
Zygophyllum microphyllum ..	M	M	t	—	—	t	M	t	—
SHRUB OR TREE									
Acacia karroo	—	—	—	—	t	—	—	—	—
Acacia mellifera	M	—	—	M	M	—	—	—	t
Acacia tortilis	M	—	M	—	M	M	—	M	—
Boscia albitrunca	M	M	—	—	M	—	—	—	—
Ehretia rigida	—	—	M	—	—	—	t	—	—
Euryops multifidus	M	—	—	t	—	—	—	—	—
Grewia flava	t	t	—	—	—	—	t	—	—

Plant Species and Life Forms	Occurrence on Farms								
	Ro	Re	Be	Br	Su	MA	So	Pl	Se
Hertia pallens	—	—	—	—	—	—	M	t	—
Maytenus cymosus	—	t	—	—	—	—	—	—	—
Olea africana	—	M	t	—	t	—	—	—	—
Rhigozum obovatum	t	—	—	—	—	—	—	—	—
Rhigozum trichotomum ..	M	—	—	—	—	—	—	—	—
Rhus ciliata	M	M	M	t	—	—	M	M	—
Tarchonanthus camphoratus ..	M	M	—	t	t	—	—	t	—
Zizyphus mucronata	M	M	M	t	—	—	M	—	—
SUCCULENT									
Psilocaulon absimile	—	—	M	—	—	M	—	—	—

Note: Brakpan (2 specimens) specimens shot in April 1964. Retreat specimen "O" omitted.
M Measurable quantities.
t traces only.

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