OBSERVATIONS ON TERRITORIAL BEHAVIOUR OF SPRINGBOK, *ANTIDORCAS MARSUPIALIS*, IN THE BONTEBOK NATIONAL PARK, SWELLENDAM

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Accepted: October 1977

ABSTRACT

Some adult males defended territories of up to 40 ha in size all year round. Most males were seen both alone and with females on their territories. Males did not have permanent harems, since groups of females were fluid in composition and highly mobile. Groups of females moved into and out of male territories at will, despite attempts by the male to prevent them leaving.

For ten marked males the minimum period spent on a territory ranged from 6,5 to 26 months. These males appeared to cover a wide age-range from young adult to old. Results of a quantitative study of daily activity of selected territorial males are presented. Males were observed for 12 consecutive daylight hours for a total of 13 days. The most important activity on a year-round basis was grazing. Courtship and defence of territory were second in importance.

Aspects of territorial behaviour, such as courtship displays, defence of territory (by chasing out trespassing males), and advertising of territory by means of linked urination-defaecation displays on discrete dung-sites, are described.

INTRODUCTION

This is the second of two papers reporting the results of a part-time study of springbok in the Bontebok National Park. See David (1978) for details of the study area.

METHODS

The data were gathered during 78 separate day visits to the Bontebok Park between 4.3.72 and 7.3.76. All observations were made from a motor vehicle. Information was gained on territorial behaviour, including quantitative daily activity of selected males. Observations were aided by marking 15 adult males with numbered, white, 'Sterkolite' nylon collars. The drugs Fentanyl, Etorphine hydrochloride (M-99), and Xylazine (Rompun) were all used with success for capturing the animals. The collars were extremely durable, though some became torn or turned over due to the activities of the animals - fighting, moving through dense thorn bushes, etc. To the best of my knowledge no male lost his collar during the study period.

RESULTS

According to Burt (1943, citing Noble 1939), the best definition of territory is 'any defended area.' Spinage (1969) considered that an area within which a male spent 95% of his time and from which competing males were excluded, would be his territory, whether or not the boundaries were shown to be defended.

Due to the part-time nature of this study, I could only obtain relatively few observations on individual males and several males which were considered to be territorial were never actually seen defending territorial boundaries. Elements of both definitions of territory have therefore been incorporated when deciding whether a given male was territorial or not. If a male was never seen defending any boundaries but was seen 10 or more times in the same restricted area of the Park either alone or with females this was considered good evidence of territorial status. This will be discussed further below.

The 15 adult males were marked between 25.9.72 and 20.2.73. Sufficient observations were subsequently obtained on 12 of these to enable an estimate of their status to be made. Ten of them appeared to hold territories for some or all of the study period. In addition, there were another 5 unmarked males which were identified by their attachment to a specific area. One of these was individually identifiable. All 15 males confined their activities to the western section of the Park - an area of about 1 280 ha. This gave a density of about 1,2 territorial males per km^2. This is a comparable density to what was found for bontebok in the same study area (David 1973) and to what Spinage (1969) found for defassa waterbuck, *Kobus defassa ugandae*.

Analysis of the data for 10 marked males and 3 unmarked males for which there were at least 10 observations showed that most males were seen both alone and with females on their territories. Out of a total of 243 observations for these 13 males (mean: 19 observations per male), they were seen 93 times with females (38%) and 119 times alone (49%). The balance of 31 observations was made up of occasions when the males were seen away from their territories (either alone or with bachelor groups) or on territory but associating with bachelor males. It was interesting that 6 out of 10 marked territorial males were seen away from their territories (either alone or associating with bachelors) 17 times (13,5%) out of a total of 126 observations for those 6 males, during the time they were territorial. It was also noticeable that though 11 out of 13 males, for which there were at least 10 observations, were seen with females at least once, yet the bulk of the observations were recorded for only 5 of the 13 males. These 5 males (Nos. 17; 0; 5; 6 and 10) were seen with females 77 times (68%), and alone only 27 times (24%), out of the total of 113 observations.

It is possible that the reason some males were seen with females more frequently than others was that the home ranges of females included some male territories and excluded others. However, since the habitat in the Park was fairly uniform there did not appear to be a good reason why this should be so. Observations of males away from their territories, sharing their territories with bachelors and not showing defence of territory suggested that some males were not very intensely territorial (eg. males 3; 4; 7 and 8). It is possible that there were two categories of male - males that were truly territorial and those that were

restricted to a limited home range but did not defend it. Novellie (1975) also observed territorial males which left their territories or did not defend them outside the rut in the Jack Scott Reserve, Transvaal.

Although a springbok male will normally court and herd any females appearing on his territory, yet he apparently spends much time alone. Thirteen male springbok were alone in 49% of 243 observations. This may partially be explained by the apparently fluid, inconstant nature of springbok nursery herds. The females making up these herds seemed to form quite transient associations with each other and groups would constantly split up and change. Unfortunately, it was not possible to document this properly as there were no marked females. These nursery herds were also very mobile and would normally spend only a few hours in a male's territory before moving on elsewhere.

Size of territory

To give an estimate of territory size is difficult when there are no visible boundaries. Boundaries are not always consistently defended. Some of the springbok occupied territories that appeared to coincide fairly closely with those of male bontebok. Areas were estimated by observing the approximate boundaries within which each male confined his activities. This gave territory sizes of roughly 10-40 ha (25-100 acres). Male 0 had the largest territory of the marked males. The approximate boundaries of his territory were paced out and found to enclose an area of 41 ha. In general, the springbok territories were fairly well spaced and most territory holders did not appear to have more than one territorial neighbour. Mason (1976), who studied a small herd of springbok in the Jack Scott Reserve, Transvaal, gave territory sizes for the males of between 27 and 70 ha. Novellie (1975) gave a range of from 7-43 ha with a mean of 22 ha for six springbok territories in the same reserve.

Time spent on territory by males

Although a seasonal breeder (David 1978), the springbok appears to be territorial throughout the year in the Bontebok Park. In the Jack Scott Reserve, Transvaal, Mason (1976) found four males to be territorial for 4-11 months. There may be some evidence for increased territoriality during the rut, as suggested by Bigalke (1972), who also found that territoriality was not simply associated with mating. Assuming solitary males and single adult males accompanying female herds to be territorial, I recorded nearly 50% more territorial males during the rut (February-March), than during the lambing season (September). The evidence from numbers of solitary males should be treated with caution since some of these were probably wandering bachelors. The evidence from the marked males was that they were territorial throughout the year and some were seen defending their territories at all seasons. Table 1 shows the minimum period spent on the same territory for 10 marked males for which there were at least 10, and a maximum of 30, observations. The minimum period that a male spent on the same territory varied from 6,5 to 26 months in this sample (mean 17,5 months). This year-round territoriality is interesting in a seasonal breeder.

The age of territorial males

The study was terminated before any hard data on this topic could be obtained. The height of incisor I_1 of all captured adult males was measured with calipers. The assumption was made that the degree of wear on I_1 would be relative to the age of the animal. A sample of 5 young males and 4 young females (all with deciduous teeth), aged 3-4 months (known age sample) was also captured and ear-tagged, with the ultimate aim of developing a field ageing technique based on degree of incisor wear. Two of these tagged females were subsequently recaptured, one at about 15 months and the other at about 20 months of age. Both had a mean newly erupted I_1 height of 13,7 mm, measured from gum to crown. In the sample of 15 captured adult males the youngest had a mean I_1 height of 12 mm whereas the mean I_1 height of the oldest male was only 4,5 mm. The I_1 heights of the other males were all between these extremes. It appeared, therefore, that the adult males in the sample covered a wide age range from young adult to old. It was interesting that the two males found dead in August 1974, nos. 0 and 4 (Table 1), were in fact the two oldest males, judging from incisor height (mean I_1 height 4,5 mm for male 4 and 5,7 mm for male 0) when captured. Using the ageing

TABLE 1

Minimum period spent on territory by marked males.

♂ collar number	Mean I height at capture (mm)	Date first seen on territory	Date last seen on territory	Period (months)	Fate
Blank	9,2	4.11.72	23.9.74	22½	
0	5,7	5.11.72	28.4.74	17½	Found dead Aug. 1974
3	6,3	4.11.72	30.4.74	18	
4	4,5	8.11.72	5.7.73	8	Found dead Aug. 1974
5	6,4	9.11.72	24.9.74	22½	
6	10,3	10.11.72	20.1.75	26	
7	10,8	6.12.72	24.9.74	21½	
8	10,8	8.12.72	23.9.74	21½	
10	11,6	20. 2.73	2.9.73	6½	
17	9,7	27. 9.72	4.9.73	11	
				17½ (mean)	

criteria of Rautenbach (1971), young males achieve a full set of permanent teeth and also maximum horn length at about 22 months. However, full physical maturity may not be attained until later, since Penzhorn (1974) presents evidence from 351 males shot in the Mountain Zebra National Park, which suggests that neither maximum mass nor maximum length may be attained before 3-3,5 years of age. It is not known how long after the attainment of physical maturity full behavioural maturity is attained, such that a male can challenge successfully for a territory. It seems unlikely that a male would reach this stage until 3-3,5 years old.

The ratio of bachelor : territorial males

An accurate figure for this ratio is impossible to obtain without a more intensive study than is presented here. A rough estimate can be derived from my census data.

I recorded an average total of 19 adult males per census which may have been territorial. There were on average 25 bachelors per census of which 26% were subadult - leaving about 19 adults. Thus the adult male population may have been divided about 50 : 50 into bachelor and territorial animals. This is in surprisingly close agreement with what I found for bontebok (David 1973) and what Leuthold (1966) reports for Uganda kob, *Kobus kob thomasi,* and Estes (1969) for wildebeest.

Quantitative study of daily activity of territorial males

Methods

The method used by Spinage (1968) during his study of the Uganda defassa waterbuck was adopted. The activities of springbok were divided into their most basic daily components as follows: grazing; ruminating; resting; walking and 'other', which included all other activities and comprised mostly sexual and agonistic behaviour (courtship and defence of territory, etc.). The balance was made up of miscellaneous activity. An activity sheet was used, having a column for each activity and detailed behaviour notes were made separately. A four-minute interval was used. Every four minutes a tick was entered in the appropriate activity column for the animal under observation. The activity occupying the major part of each four-minute interval was ticked and not necessarily the activity being performed at the end of each interval. Marked territorial males were chosen for study at different seasons of the year. They were watched if possible for 12 consecutive daylight hours, from 06h15 to 18h15, but in mid-winter the short days rendered 10,5 hours the maximum possible. Unfortunately, due to the fact that no male had a permanent harem of females with him, it proved impossible to watch individual females simultaneously. There were no marked females in the study area and limited time precluded the possibility of watching females separately.

All observations were made from a vehicle using binoculars. Observation distances varied from 20 to 400 m. The animals were accustomed to tourist traffic and care was taken not to disturb them.

Results (Table 2)

The time spent per day on each activity is expressed as a percentage. The activity pattern of any given animal could vary considerably from day to day, so that the amount of time spent per day in each activity was not constant, nor was the time of day when it was performed. The most important activity on a year-round basis was evidently grazing, with surprisingly little time, particularly in winter, spent ruminating. On most days the second most important activity was 'other', of which the most important components were courtship and herding of females, and defence of territory (any clash with another male was included here). The percentage time per day spent in these two activities has been listed separately in Table 2. Between them they comprise over 95% of 'other' activity. The balance is made up of miscellaneous other activity.

Male 0 was an active territorial male and usually (71% of 24 observations) had females on his territory. It is evident from Table 2 that his grazing time was least in February and showed a progressive rise through March and April. This corresponded with a peak of 'other' activity in February and a lower level (though still relatively high) during March and April. The mean value of Male 0's 'other' activity was 16,5% of the day for the seven observation days. He spent a mean of 7,4% of the day in sexual activities and 8,4% in defence of territory. These comprise 44,8% and 50,7% respectively of all other activity.

The time spent in sexual activity and defence of territory was greatest on the two February observation days which corresponds with the calculated peak of rutting. However, it is interesting that both activities remained fairly prominent right through to

TABLE 2

Analysis of daily activity of territorial males

Season	Date	Hrs. obs.	Male Collar number	% Graze	% Rumin-ate	% Rest	% Walking	Other activity: % Total	Other activity: % Defence of terr-itory	Other activity: % Sexual activity	No. of Flehmen displays	♀♀ Present
Rut	18. 2.73	12	0	31,5	15,45		16,0	37,0	27,6	9,4	5	Yes
	19. 2.73	12	0	37,8	30,0	1,1	8,9	22,2	8,33	13,33	2	Yes
	25. 3.73	9,5	0	53,1	25,2	4,9	7,7	9,1	1,4	4,9	3	Yes
Late Rut	7. 4.73	11,5	0	76,6	5,1	0	5,1	13,1	6,3	6,3	4	Yes
	8. 4.73	12	0	78,33	1,1	0	5,8	14,7	8,6	5,55	12	Yes
	21. 4.73	11,5	0	79,0	4,5	0	2,8	13,6	4,3	8,8	8	Yes
	22. 4.73	11,5	0	84,5	1,7	0	7,8	6,0	2,0	3,45	7	Yes
Winter non-rut	1. 6.73	9,5	17	67,33	10,4	1,4	6,25	14,6	0,7	9,0	5	Yes
	2. 6.73	10,5	17	76,4	8,1	2,5	6,8	6,2	2,5	1,9	3	Yes
Lamb-ing	3. 9.73	11,25	17	45,3	0	1,2	41,3	12,2	9,3	0	0	No
	4. 9.73	11,5	17	58,0	9,8	0	19,5	12,6	9,8	0	0	No
Pre-rut	5.12.73	12	10	75,0	21,66	0	2,2	1,1	0	0	0	No
	6.12.73	12	7	77,9	15,5	0	5,5	1,1	0	0	0	No

June (Table 2). This tends to bear out my supposition that courtship and mating may extend over a large part of the year, and observations showed that territories seemed to be defended throughout the year. It was unfortunately not possible to make observations with equal intensity at all seasons. The general level of activity is also reflected by the amount of walking done by the male (Table 2). This again was at a peak during February but remained at a fairly high level throughout. The mean value was 7,7% for the seven observation days. Although their territories are probably no larger than those of bontebok, it was noticeable that springbok did far more moving about. Territorial male bontebok tend to be rather sedentary. As suggested by Novellie (1975) this is probably due to the widely dispersed nature of food items preferred by springbok.

As mentioned, females are very transient on springbok territories. Males are nevertheless very active in herding females and much of their moving about is in response to females - either herding them or running to greet new arrivals on their territories. The degree to which a male attends to females was demonstrated by recording the amount of time he spent (a) with females, (b) alone and (c) with bachelor or rival males during the course of daily activity studies. Male 0, during 4 811 minutes (80 h) of observation, spent 56,7% of his time with females, 28,8% alone and 14,4% interacting with bachelor or rival males. This correlates fairly well with the result of casual observations. In 24 observations, Male 0 was 71% of the time with females and 25% alone. Thus it is clear that though territorial springbok males do not have permanent harems, some of them nevertheless spend a significant amount of time in the company of females.

It is interesting that Male 0 spent as little as 31,5% of the day grazing during the rut, whereas he spent as much as 84,5% of the day in the same activity at the end of April (Table 2). This increase in grazing time is mainly at the expense of ruminating and resting which drop to a low level, and partly due to a drop in other activity. How the male can maintain his condition and level of activity during the rut while spending a minimal amount of time grazing is not clear. According to Grobler & Marais (1967) 21% of the annual precipitation in the Swellendam area falls in December to February and 26% in March to May. There do not, therefore, appear to be *a priori* grounds for thinking that the quality of nutrition is higher during the summer (December-February). It is however possible that the increased time spent ruminating in summer is due to low forage quality. The grass in summer is often brown and dry and presumably contains a high proportion of fibrous stem. This would tend to make digestion slow and difficult, and more time for fermentation in the rumen would therefore be necessary to achieve breakdown of the cell walls. This may, therefore, partially account for the lower amount of time spent grazing in summer.

Louw (1969) presents data which show that most of the 'fynbos' grazing in the south-western Cape is deficient in protein and phosphorus at all seasons of the year. The southern renosterveld (which is probably closest to the type of vegetation occurring in the Bontebok Park), is deficient in protein and phosphorus but is only deficient in calcium and cobalt in the summer. In general, from Louw's Table 3 it would appear that there are greater mineral deficiencies in summer than in winter. This evidence tends to support my suggestion that forage quality is lower in summer.

Further examination of Table 2 lends support to this suggestion in that Male 17, observed during June and early September (winter and early spring) showed low percentages of ruminating. This being the season of highest rainfall one presumes forage quality to be high with greater proportions of easily digested leaf and shoot.

Males 10 and 7 showed a very low percentage of 'other' activity as both males were alone on the two days observed and neither interacted with females or other males. The exceptionally high proportion of walking and other activity shown by Male 17 on 3-4.9.73 was due to his being challenged and replaced by another territorial male. This will be further discussed below.

Courtship and mating

The courtship posture of the male ('nose-forward' posture), in which the head and neck are stretched forward with horns laid back and tail lifted has been described by Bigalke (1972) and Novellie (1975). In this posture it is usual for the male to run to greet any females appearing on his territory with loud grunting. Sometimes the male runs several hundred metres. As he approaches the females, the grunting may be prolonged to a roar with the nose sometimes raised well above the horizontal.

The male may stand in the nose-forward posture for minutes at a time in the midst of a group of females. He addresses the display to each in turn by pointing at or sniffing the perineal region of the female (Figure 1). This performance is a urination solicitation. Sometimes the female will urinate as soon as the male addresses the display to her (Figure 2). He then approaches and invariably licks the urine from the ground. He then performs *'Flehmen'* (Schneider 1934) (Figure 3) followed quite often by empty licking movements, licking of the lips and slight champing of the teeth. It was not unusual to see a male standing in display posture behind a female for several minutes if she did not urinate. He would take short steps forward with stiff forelegs while 'pointing' at her perineal region. This was frequently accompanied by a form of *'Laufschlag'* (Walther 1958) in which a stiff foreleg was raised and gently lowered behind the female without touching her (Figure 4). This would continue until the female urinated and the male would then perform *'Flehmen.'* If the female was unwilling she would continue grazing, ignoring the male completely, and moving slowly away all the time. If he was too persistent, she would sometimes turn through 180° and jump back past his rump. Several variations of *Laufschlag* in springbok were observed by Novellie (1975) who reported that though the male sometimes touched the female during *Laufschlag,* more usually he did not.

As already mentioned, territorial males spent much of their time in the company of females. Once a male had finished courtship activity he would usually settle down to grazing quietly with the females. Quite often he would leave the females, for example to chase bachelor males, and would return to them after an interval. Each time he returned he would normally commence with a bout of courtship activity.

An attempt was made to gauge the level of rutting activity by recording the number of times that the male performed *Flehmen* following urination by the female, during the course of daily activity studies. The results are recorded in the penultimate column of Table

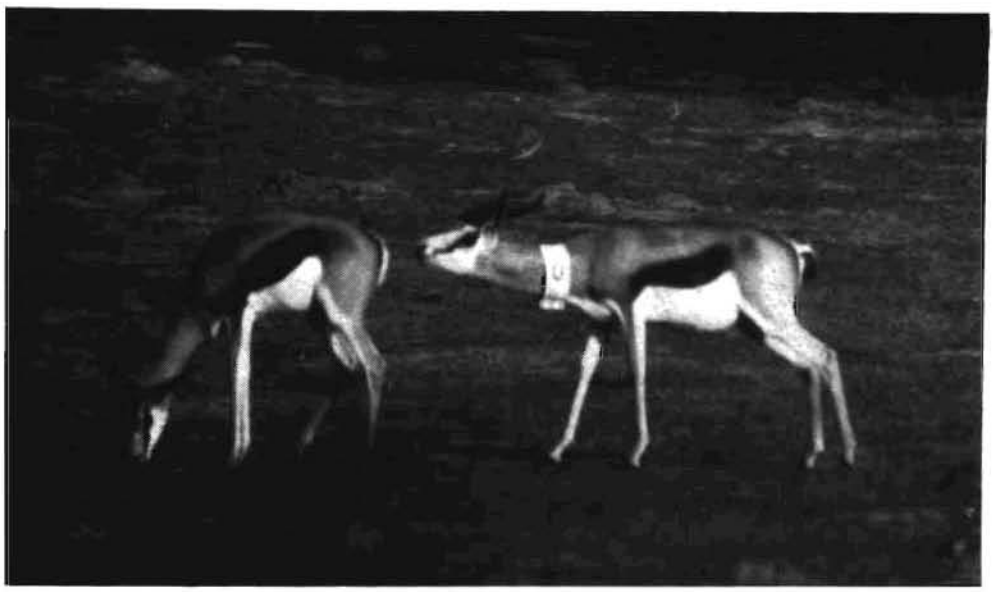

FIGURE 1 (Above)
Nose-forward posture. The male sniffs the perineal region of the female. This is a urination-solicitation.

FIGURE 2 (Below)
The female urinates in front of the male, who prepares to sniff the urine on the ground.

FIGURE 3 (Above)
'Flehmen', performed with open mouth by the male (right) after sampling the female's urine.

FIGURE 4 (Below)
'Laufschlag', by the male (left). He kicks forward with a stiff foreleg as he approaches the female. This is part of the urination-solicitation ceremony.

2. Males 17; 10 and 7 were alone in September and December 1973 and hence no *Flehmen* was observed. On every other occasion that a male with females was watched, there was a significant amount of sexual activity and up to 12 performances of *Flehmen* by the male. One can only conclude that the level of male interest in females remained high at least until early June. There did not appear to be any significant difference between the number of *Flehmen* performed in June and in February (peak of the rut). Male 17 performed *Flehmen* eight times on 1-2 June 1973, when accompanied by between 5 and 20 females; Male 0 seven times on 18-19 February 1973, when acccompanied by about 20 females.

Mating was seen three times, in late February and early March. It follows the typical gazelle pattern in which the female keeps walking constantly and the male is obliged to copulate while running bipedally behind her (Figure 5). Copulation thus consists of a single ejaculatory thrust.

Males were seen courting and herding females at most seasons of the year. Unfortunately, observations were not equally intensive throughout the year. It appeared that July was the low point in sexual activity. Male 17 was watched for eight hours on 4 July 1973. Although he was with females, there was minimal sexual activity. He did not sniff any females and no *Flehmen* was seen. It was particularly interesting to see conspicuous rutting activity ("false

FIGURE 5
Copulation. The male is obliged to mount while running bi-pedally behind the female, who continues to walk at a steady pace.

rut") in September 1972 and 1974, coinciding with the arrival of a crop of new lambs. Although no mating was seen, the possibility exists of a second small autumn lamb crop being produced following a spring rut, as reported by Bigalke (1970) for the Kimberley area and Kalahari Gemsbok Park. Evidence that this does happen at least in some years was obtained when four new lambs were seen on 6.3.76. Novellie (1975) observed the same phenomenon in the Transvaal.

A male would normally try to keep females on his territory by herding them. This consisted of walking behind them in nose-forward posture, shepherding them in the desired direction. Sometimes a female or group of females would suddenly dash off in some other direction. The male would then usually give chase at full speed and try and head them off. If he did not succeed in catching and herding them back to the middle of his territory within 100 m or so, he would usually give up the chase and let them go. After going to greet females moving on to his territory he would usually walk behind and chivvy them towards the centre of his territory.

Defence of territory

Some males were very active in defence of their territories and although it was not possible to make observations in every month, yet defence of territory was seen on every visit to the study area. This fact coupled with the observed tenure of the same territory by the same male for two years or more made it clear that territories were defended throughout the year. Active defence takes the form of chasing strange males away from the area. Reference has already been made to the amount of time spent per day in this activity by some territorial males. It is clearly an activity of considerable importance.

Territorial males were seen many times running to where one or a group of males had appeared on the edge of their territories, sometimes as much as 400 m away. The territory holder chased interlopers at any speed from a walk, through a canter to a furious gallop, and usually gave vent to grunting similar to the courtship grunt. When chasing bachelors the pace was usually a gentle canter, interspersed with spurts of galloping over short distances of 20-30 m. The bachelors often ran just out of the way or in a circle and then continued grazing as before. Sometimes the male would chase the bachelors for several hundred metres right off his territory. Bachelor males were always docile in these situations. They retreated immediately before the territory owner and were never seen to challenge or fight him. Conversely, a territorial male never caught up with a bachelor while chasing him and was never seen to inflict any injury. Bachelors would often retreat when the territory owner was still far off. Cases were seen where a trespassing male would run away when the approaching territory holder was as much as 250 m from him. Ritualization in chasing was evident in that a territory owner would never press home his attack on a bachelor but always allowed the latter to escape.

Sometimes it happened that two neighbouring territory holders would meet while chasing bachelors on their common border. In this situation they usually ignored each other but each would keep more or less to his own side of the boundary. If a territorial male overstepped the boundary on to his neighbour's property, the owner would come across to

see him off, but usually at a walk. The first male would then retreat to his own territory, also at a walk, with the other following and then they might graze only 20-30 m apart for a while, before moving off.

The most serious chasing seen occurred on Male 0's territory on 18-19 February 1973 (rutting peak). This involved a single (unmarked) adult male which ran into the middle of a group of females on Male 0's territory at full speed, scattering them in all directions. This precipitated a furious chase by Male 0. The intruding male ran in circles at high speed coming back to the females at every opportunity and running through them. Eventually Male 0 succeeded in chasing the intruder out and then followed behind him at a walk for several hundred metres to the boundary of his territory. As this point the two males grazed close together and several brief horn battles ensued. In between the fights the males grazed agonistically - facing each other about 30 cm apart and frequently feinting to engage horns (Figure 6). This continued for about half an hour until Male 0 turned and walked back to his own territory. The other male remained where he was. This whole process was repeated several times on the same and the following day. It seemed evident that the interloper was not an ordinary bachelor but either a neighbouring territory holder or an unpropertied, but challenging, male aspiring to hold his own territory. In this case the challenge was unsuccessful since Male 0 continued to hold the same territory for at least the next 14 months (Table 1). Very similar behaviour was witnessed between neighbouring bontebok territorial males (David 1973).

Replacement of a territorial male

A most interesting case of a successful challenge was witnessed on 3-4 September 1973. Male 17 had been seen on the same territory for the previous year and was with females in 20 out of 30 observations.

Male 17 was located at 07h05 on 3.9.73 grazing alone on his territory. At 08h00 he walked about 300 m to the south where another adult male was grazing alone close to the southern border of Male 17's territory. Male 17 stopped to perform linked urination-defaecation about 20 m from the other male, who groomed himself vigorously. The males then grazed very close together. They both performed 'champing' - with heads up they made biting movements of the incisors accompanied by pronounced jerking up-and-down movements of the chin (Figure 7). Champing is clearly aggressive (threatening) in function. They continued to graze close together, facing each other (agonistic grazing) and both performed displacement grooming. In between grazing the males engaged horns in brief clashes lasting 1-15 seconds each. There were at least 15 such clashes, and in between the males would stand with heads up looking around, or one would 'walk' the other backwards with heads lowered in combat position, but horns not engaged.

The main fight began at 08h20. This consisted of 15 minutes of continuous hard wrestling with horns interlocked. Eventually at 08h35 Male 17 broke away and ran off pursued by the other for about 100 m. The males then separated. However, when Male 17 started to walk back to the heart of his territory the rival male followed close behind him at a walk. Male 17 was then harassed almost continuously by the other male for the remainder of the day and

for much of the following day. The rival established himself in the heart of Male 17's territory and every time Male 17 approached he would run out and chase him away. Male 17 always gave ground and retreated when the other came near. The rival would then follow behind Male 17 at a walk often for several hundred metres until they were right off the territory. The challenger would then walk back to the heart of the territory and Male 17 after a while would follow, until the challenger turned and chased him away again. They continued back and forth in this see-saw fashion many times. There were several more hard fights during the course of this and the next day, but none as prolonged as the first one, and it appeared that the battle was in fact lost and won during that first encounter.

The effect of this challenge on Male 17's daily activity can be clearly seen from Table 2. On 3 September he spent only 45% of the day grazing and over 41% walking due to constant harassment by the challenger. The time spent in direct interactions with the other male is shown under defence of territory. The total 'other' activity was high on both 3 and 4 September mainly due to involvement with the challenger.

On subsequent visits to the study area the challenger was seen still holding Male 17's territory on 23.12.73 and 24.9.74. He was identified by the shape of his horns and of the brown forehead blaze. Male 17 was seen for the last time with a group of bachelors on 4.12.73.

Springbok males were seen fighting vigorously on at least eight days between March 1972 and September 1974, not including playful sparring commonly seen among bachelors. The points of springbok horns are turned inward so that their use as stabbing weapons is precluded and injuries seldom occur. It appears that fighting for the right to hold a territory may be the normal way of settling territorial disputes among springbok. It has not become ritualized.

Territorial advertising

Living in open country and being brightly coloured springbok are fairly conspicuous animals. It seems probable (as suggested by Bigalke 1972) that solitary territorial males advertise their status just by being there and by their greater activity both in courting females and in chasing out trespassing males. Schenkel (1966) points out that manifestations of presence are important in maintenance of territory. Certainly territorial springbok are very alert and spend time looking around. They are quick to spot either intruders or approaching females, and by displaying the appropriate aggression or courtship they advertise their presence.

As noted by Bigalke (1972) the springbok preorbital gland does not secrete and they do not use glandular scent marks as a form of advertising. However, another form of scent marking is by means of dung and urine, which is regarded by Estes (1969) as the oldest form of territory demarcation. Springbok males use a linked urination-defaecation sequence (Bigalke 1972; David 1973) in which urination is performed in a wide 'rocking-horse' stance and followed at once by defaecation in a deep crouch on the same spot (Figures 8 & 9). This conspicuous behaviour serves as a ritualized display advertising the status of the male. Springbok may paw the spot two or three times with either forefoot

FIGURE 6 (Above)

A pause during a fight between a territorial male (with collar) and a challenger. The males face each other, about 30 cm apart and feint to engage horns.

FIGURE 7 (Below)

A territorial male (with collar) being challenged by another male. The males threaten each other by standing close together with heads up and performing pronounced jerking up-and-down movements of the chin. The territory holder, in this instance, was defeated by the other male in the ensuing fight and lost his territory.

FIGURES 8 & 9
Linked urination-defaecation by a territorial male on a dung-site. This behaviour is related to marking of territory.

before urinating. Pawing occurred in 39 out of 65 observations (60%) of linked urination-defaecation.

There are fairly conspicuous dung-sites scattered all over the territories, situated on bare earth or where the grass is very short. Territorial males usually use these dung-sites and in 107 observations of linked urination-defaecation they used a dung-site in 83 cases (78%). This seems to indicate that the dung-sites are of some significance to the animals and may serve as markers of territory (Bigalke 1972). Their precise function, however, is hard to ascertain. Bachelor males were also seen performing linked urination-defaecation on a dung-site from time to time. Mason (1976) states that territorial springbok did not use dung-sites in the Jack Scott Reserve, Transvaal.

It was interesting to see that territorial springbok and bontebok often used the same dung-sites. Close inspection showed that there were normally distinct piles of bontebok and springbok dung lying side by side on the same site. It was noticeable that the male usually chose a pile of springbok dung on which to drop fresh dung.

Like Thomson's gazelle (Walther 1964), springbok males quite often perform conspicuous bush-horning in which a low bush or clump of grass is vigorously thrashed with the horns. Less often the horns are rubbed in the soil. Bigalke (1972 citing Walther 1968), who calls it 'sweeping', considers this to be a display making males more conspicuous and should therefore be regarded as a form of 'dynamic-optic' marking.

The number of bush-hornings performed by territorial males was observed during the course of daily activity studies. During the 13 days of observation, males horned low bushes or shrubs 55 times and horned the ground 8 times. This gives a mean of 5, with a range from 0 to 13, times per day. It was noticeable that Males 10 and 7 who were alone on the two days of activity analysis, performed only one horning between them in two days of observations. This was in contrast to Male 17 who performed 13 hornings on 3.9.73 when strongly challenged by a rival male, and Male 0 who performed 8 and 10 hornings during two observations days in February at the peak of the rut.

The longest time that a male spent horning a shrub was about 120 seconds and the shortest about 5 seconds. Some hornings were performed in the presence of a rival or bachelors and were undoubtedly redirected aggression. Others were performed in the presence of females or while the animal was alone. Females have not been seen to horn shrubs or the ground. From observation it seems clear that bush- or ground-horning is aggressive and is a display characteristic of territorial males. I would prefer to call it demonstration-threat.

DISCUSSION

The behaviour and social organization of springbok resemble those of other territorial antelope species which have been described. The finding of year-round territoriality in a seasonal breeder is interesting and corresponds to what was found by Estes (1969) for wildebeest in the Ngorongoro Crater, and myself for bontebok in the present study area

(David 1973). A prerequisite for year-round territoriality is an adequate supply of forage at all seasons. Despite the dry summers this appears to be available at Swellendam.

Springbok behaviour seems to resemble that of the gazelles fairly closely. Springbok males are rather active in defence of their land and though they may sometimes allow bachelors on to their territory they will not allow them to court females. In this respect they resemble Thomson's gazelle *(Gazella thomsonii),* which is apparently more actively territorial than Grant's gazelle *(G. granti)* (Estes 1967). As already mentioned, it is not unusual to see springbok males fighting in defence of territory. In this respect they more closely resemble *thomsonii,* rather than *granti* which largely replaces fighting with a neck display (Estes 1967). However, it would seem that Thomson's bucks fight even more frequently than springbok, since Estes remarks: "Yet most encounters between territorial males end, or begin with, fighting." In style of fighting, it would appear from Estes's description that, springbok resemble Grant's rather than Thomson's gazelle. *Granti* males engage horns firmly with foreheads almost flat to the ground and then wrestle, as do springbok. Whereas, "instead of engaging horns, *thomsonii* bucks spring at each other, bang horns and leap back, . . ." (Estes 1967).

With regard to marking behaviour, springbok resemble Grant's gazelle which, unlike Thomson bucks (Brooks 1961; Walther 1964), do not mark with the pre-orbital gland but rely solely on the linked urination-defaecation display (Walther 1965; Estes 1967).

The courtship display of springbok has similarities with that of Thomson's and Grant's gazelles, as described by Walther (1964, 1965). Springbok raise the tail, like *granti* bucks, when displaying, but often the nose-forward posture is not very pronounced and the carriage of the head tends to be more erect than in either of the gazelles.

ACKNOWLEDGEMENTS

Thanks are due to the National Parks Board of Trustees for permission to work in the Bontebok National Park and for supplying immobilizing drugs. The helpful co-operation of Mr L van Zyl, Conservator of the Park during the time of the study, was much appreciated. I would like to thank Prof. R C Bigalke, University of Stellenbosch, Cape; Prof. P A Jewell, formerly of Royal Holloway College, Surrey; and Prof. W R Siegfried, University of Cape Town, for constructive criticism of the manuscript. The University of Cape Town supplied a grant in aid of publication.

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