

Behavioural ecology and communication in the Cape grysbok

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The behaviour of the Cape grysbok, a small antelope inhabiting the fynbos vegetation of the southern and western Cape, is described. Three wild grysbok males, fitted with radio transmitters, were observed to remain within well-defined ranges which averaged 2,5 ha in area. These ranges were evidently defended territories, but no incidences of active territorial defence were observed. Wild grysbok spent an average of 50% of the day active and 50% inactive during winter. Fighting between captive males tended to escalate rapidly to damaging levels, and threat displays were relatively unimportant. In courtship behaviour tactile and olfactory communication were prominent, but visual displays were poorly developed. Scent marking with the preorbital glands was frequent in males but rare in females. Marking was associated with agonistic encounters between males, and also tended to occur in response to novel environments. Dominant males marked more frequently than subordinates. The frequency of preorbital marking and courtship behaviour in males varied seasonally, reaching a peak in the main conception period. The distribution of births in captivity showed a peak in spring.

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Die gedrag van die Kaapse grysbok, 'n klein wildsboksoort wat die fynbos van die Suid- en Weskaap bewoon, word beskryf. Drie grysbokramme, wat met radiosenders toegerus was, het hul aktiwiteite tot spesifieke gebiede van sowat 2,5 ha beperk. Hierdie gebiede was waarskynlik verdedigde territoriums, alhoewel geen territoriale verdedigingsvoorvalle waargeneem is nie. Gedurende die winter was grysbokke in die natuur gemiddeld 50% van die dag aktief en 50% onaktief. In gevangenskap het die intensiteit van gevegte tussen ramme vinnig toegeneem tot 'n skadelike vlak, terwyl aggressiewe vertoningsgedrag relatief onontwikkel is. Tas- en olfaktoriese kommunikasie was belangrik tydens paringsgedrag, terwyl visuele vertonings swak ontwikkel was. Ramme het gereeld met hul preorbitale kliere gemerk, hoewel die verskynsel selde by ooie waargeneem is. Merkkativiteite het tydens antagonistiese gedrag tussen ramme voorgekom, en nuwe omgewings het ook hierdie gedrag ontlok. Dominante ramme het meer gereeld as ondergeskikte ramme gemerk. Die intensiteit van preorbitale merkgedrag en hofmaakgedrag by ramme het seisoenaal gevarieer, met 'n maksimum in die paarseisoen. In gevangenskap het geboortes hoofsaaklik in die lente voorgekom.

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Jarman's (1974) study of the relationships between the behaviour of African antelope and their ecology revealed the distinctive position of the small antelope (members of the tribes Neotragini and Cephalophini). With some exceptions they favour closed habitats, often dense forest or thicket. Virtually all small antelope species are solitary or associate in pairs, rather than in groups as do most larger antelope. The evidence accumulated so far indicates that all species exhibit territorial behaviour. Males occupy permanent territories which, Jarman (1974) suggested, function not only to ensure mating opportunities but also to defend their relatively scarce, sparsely distributed food supply. This is in contrast to many of the open-country, gregarious antelope, where male territories are often only maintained in the mating season and which usually function only as a means of ensuring access to females.

The secretiveness of most small antelope makes them difficult to study and thus, except for the relatively conspicuous klipspringer (*Oreotragus oreotragus*) and dik-dik (*Madoqua (Rhynchotragus) kirkii*) (see Hendrichs 1975; Dunbar & Dunbar 1980; Norton 1980), understanding of the social organization and communication of the small antelope has lagged behind that of other bovids. Yet, the Cape grysbok is one of the few antelope that can survive in relatively small patches of indigenous vegetation surrounded by cultivated lands, and it can become a problem animal in vineyards, orchards and plantations (Manson 1974). It is largely confined to the coastal regions and mountain ranges of the south-western, southern and eastern Cape Province. Although it occurs in other vegetation types, it is essentially an animal of the Cape fynbos, both in the winter and non-seasonal rainfall belts (Bigalke 1979).

The main objective of the present study was to describe the social organization of the Cape grysbok (*Raphicerus melanotis*). More specifically the study was designed to ascertain whether or not grysbok exhibit territorial behaviour, and also whether they are monogamous, like some small antelope species (Hendrichs 1975; Dunbar & Dunbar 1980), or whether they have other mating habits. Owing to their relatively densely vegetated habitat, and their largely nocturnal habits, the behaviour of free-ranging grysbok could not be watched. This made it difficult to determine their social organization, particularly to establish whether or not they are territorial.

Space-related dominance is the criterion whereby territoriality may be diagnosed (Leuthold 1977); a territorial male dominates all other males within his territory, but in a neighbouring territory he is subordinate to the territorial owner. To help resolve the question, agonistic encounters between captive grysbok males were arranged so as to determine whether dominance

depended on where the encounter occurred. If grysbok are in fact territorial it might be expected that a male in a familiar environment would dominate intruders, but would be subordinate to other males encountered in an unfamiliar environment. In addition the behaviour which occurred during agonistic encounters was recorded so as to evaluate Geist's (1966, 1974) hypothesis that combat in small ungulates is less ritualized and more damaging than that of larger ungulates.

The question of seasonal variation in behaviour was also examined. Many ungulates breed seasonally, and in males seasonal breeding is associated with changes in testes size and testosterone secretion. Seasonal changes in androgen secretion are in turn accompanied by changes in aggressiveness and sexual behaviour (Lincoln & Short 1980). The activity of scent glands and the intensity of scent-marking behaviour are also known to vary under the influence of androgens (Thiessen, Friend & Lindzey 1968; Johnson 1973). The frequency of sexual and scent-marking behaviour in grysbok was therefore recorded over one seasonal cycle to establish whether this varies seasonally.

Methods

Observations on free-ranging grysbok

The use of space and daily variation in activity

Two grysbok males, an adult and a juvenile, were captured in the Jonkershoek Valley, 11 km south-east of Stellenbosch. They were fitted with radio transmitters mounted on neck collars and released near the point of capture. Another animal, a female which had been kept for about a year in captivity, was also fitted with a transmitter, and released in the same area as the two males. An additional transmitter was fitted on a male at the De Mond Forest Reserve near Bredasdorp, southern Cape. Two double Yagi antennas were used to determine the exact position of the animal by triangulation. The movements of the grysbok at Jonkershoek were monitored from 17 June to 15 August 1973, and the male at De Mond was tracked for one week during March 1974.

The signals were affected by movement of the transmitter — a signal from a moving animal could be distinguished from one from a stationary animal, and this allowed study of activity patterns. According to the signal the animal could be classified as 'active' (which indicated any behaviour involving movement of the head or neck such as feeding, walking, running or grooming), or as 'inactive' (either lying down or standing motionless).

Recording of activity patterns was done only for the three animals at Jonkershoek. Signals were received every hour. However, some signals were either inaudible or too weak to distinguish between activity and inactivity, so it was impossible to monitor activity uninterruptedly over 24-h periods. In total 247 signals, 67 from the adult male, 102 from the adult female and 78 from the juvenile male were usable. Signals from each hour of the 24-h cycle were pooled and the percentage active as opposed to inactive was calculated.

Estimates of the sizes of the areas occupied by each grysbok at Jonkershoek were also based on 247 readings, distributed between the three individuals as given above. The area occupied by the male at De Mond was estimated from 128 readings.

Observations on captive animals

Wild grysbok were caught on the Cape Flats and kept either in walled enclosures (dimensions 5 × 20m or 6 × 4 m), or in fenced camps of about 60 × 70 m. They quickly became tame and bred readily, so that a captive colony was soon

established. Observation procedures are described below.

Communication by scent

Seasonal variation in the intensity of marking by three captive males was investigated by counting the number of preorbital scent marks deposited each day in their pens. Each male was kept alone in a pen. First, all preorbital marks present in the pen were removed. Sufficient cut branches of the alien tree *Acacia cyclops* were placed in the pens to ensure that the number of marks deposited was not limited by the number of suitable marking points. Twenty-four hours later the number of preorbital marks was counted. The procedure was repeated 1–5 times each month from March 1979 to July 1980. The mean number of marks deposited daily was compared between the three individual males and between the months of the study period by means of two-factor analysis of variance (Snedecor & Cochran 1967).

Courtship behaviour

Observations involved a pair of grysbok kept in separate pens, the male alone and the female with another female. Encounters between the pair were arranged by introducing the female into the male's pen. Interactions between the pair were recorded during 10-min observation periods. Descriptions of all action sequences were spoken into a tape recorder or written down. From one to five 10-min periods were completed each month from October 1979 to July 1980, the total number amounting to 37. The mean rates at which the various courtship actions were performed were calculated for each month of the study period. The monthly means were compared to assess whether they showed a tendency to increase during the peak conception period (autumn — see below). These data did not meet the requirements for parametric statistical analysis (normal distribution with homogeneity of variance) and therefore the significance of differences between months was tested by means of the non-parametric Kruskal-Wallis analysis by ranks (Siegel 1956).

Interactions between males

Four males were available for study, each housed in one of a battery of 6 × 4 m walled pens. Wire mesh gates, covered with plastic sheeting, allowed access from one pen to another. Encounters between the males were arranged by herding one ram, termed the visiting ram, into the pen of the other, termed the home ram. The actions of each ram were recorded until one of them retreated from the other, whereupon the encounter was terminated and the visitor returned to his home pen. A total of 40 such encounters was observed over two years. For each pair of rams 50% of the encounters took place in the pen of one, and 50% in the pen of the other. The encounters were alternated so that if a ram took the role of visitor in one encounter he remained in his home pen for the next. This procedure was designed to determine whether the outcome of an encounter depended on the pen in which it occurred. To prevent injuries the horn tips of each animal were sawn off and a 70–100 mm length of rubber tubing pushed over each horn.

Results

Social groups and the use of space

During the course of field observations at Jonkershoek and De Mond records were kept of the age and sex composition of all grysbok groups that were sighted. These observations indicated that grysbok are generally solitary — males and females were seldom seen together. Of a total of 40 sightings

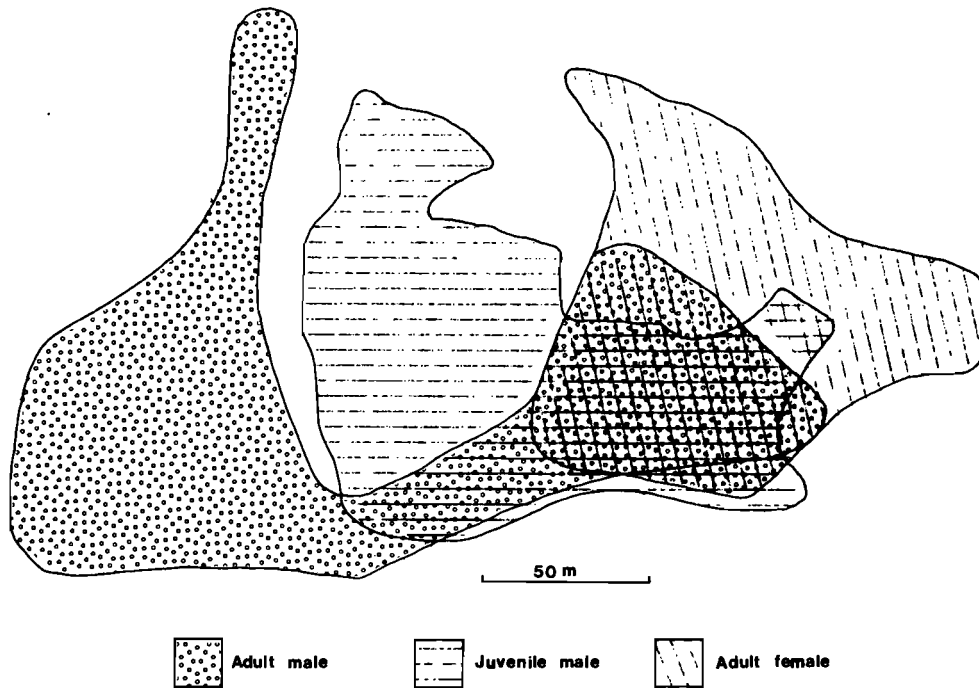


Figure 1 Areas occupied by three grysbok observed in the Jonkershoek Valley between 17 June and 15 August 1973. The areas were estimated from 247 radio telemetric readings; 67 from the adult male, 78 from the juvenile male and 102 from the female.

38 were single animals, one was a female with her dependent lamb, and only one was a male and female in association.

The area used by the three animals tracked at Jonkershoek is shown in Figure 1. Each grysbok remained within a specific area during the observation period. The range of the adult male did not overlap those of the other two except during a three-day period when he entered the female's area. The signals received showed that the pair were together at this time. The juvenile male's range extended over 1,26 ha, overlapping the female's area but not the adult male's. The female occupied 1,06 ha, and the adult male 1,53 ha. The male tracked at the De Mond Reserve occupied a larger area, about 4,84 ha.

Daily variation in activity

Variation in the proportion of radio telemetric signals recorded as 'active' over the 24-h cycle is shown in Figure 2. The results indicate that grysbok tend to be relatively more active at night than during the day. For the daylight hours (Figure 2) an

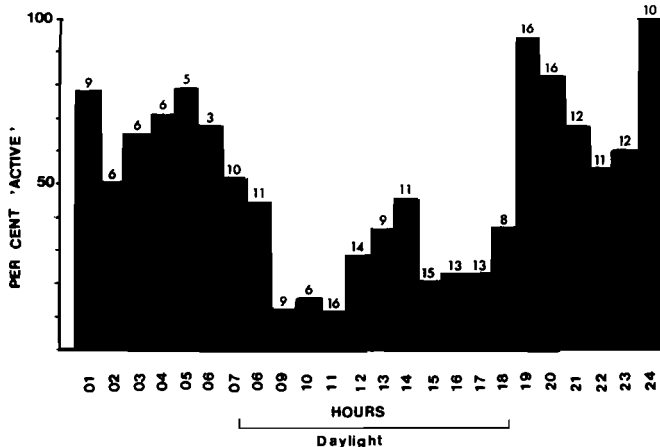


Figure 2 Daily variation in the percentage of radio telemetric signals recorded as 'active' for three grysbok observed in the Jonkershoek Valley between 17 June and 15 August 1973. The sample sizes (number of signals) are shown above each bar of the histogram.

average of 26% of signals was scored as active and 74% as inactive. By comparison an average of 70% of signals was recorded as active at night, and 30% as inactive. The values for each hour are based on small sample sizes (see Figure 2), and represent pooled data from only three grysbok. Nevertheless the pattern in Figure 2 is representative of all three grysbok considered individually; all tended to be more active at night. For the daylight hours the average proportion of signals recorded as active was 22% for the adult female and 29% for each of the males. At night averages of 74%, 76% and 63% of signals were recorded as active for the female, the juvenile male and the adult male respectively.

The estimated proportion of the whole 24-h day spent being active was 50% for the female, 47% for the adult male and 54% for the juvenile male. The average for the three animals is 50% of the day active and 50% inactive.

Scent marking with dung, urine and glandular secretions

Deposition of scent marks is one of the most common actions performed by grysbok males and since it occurs during the course of social interactions the scent-marking actions are described first.

Accumulations of dung are widespread among mammals and it is often speculated that these play a role in communication, particularly as territorial markers (Ralls 1971). We found the dung heaps of wild Cape grysbok to be roughly circular, usually about 1 m in diameter and 100 mm deep, resulting from regular deposition of faeces over long periods. In captivity all grysbok — males and females, adults and juveniles — used dung heaps, and they defaecated and urinated only on the heap. In small enclosures only one heap was normally used, and all individuals in the enclosure used the same heap. The number of heaps used by wild grysbok could not, however, be definitely established. The grysbok performed a stereotyped urination — defaecation sequence on the heap, first urinating and then defaecating. In adult males the urination — defaecation sequence was occasionally preceded by sniffing and paw-

ing at the heap. The urination posture was similar in both sexes except that males placed their hindlegs further back and did not squat so deeply as females. In defaecation females simply raised their hindquarters slightly, whereas males moved their hindquarters forward so the faeces were deposited at the same spot as the urine.

Both sexes have paired preorbital glands which secrete a black, sticky substance. However, normally only adult males used the glands to deposit scent marks; we only twice observed deposition of preorbital secretion in captive females. The preorbital glands of females are smaller than those of males and they secrete less actively (Manson 1974). Juveniles of either sex were never observed using their preorbital glands.

The actions involved in depositing preorbital secretion onto dried stalks or grass stems resemble those described for other antelope species (Walther 1968; Gosling 1972). Grysbok males usually sniffed a marking post before scent deposition, and sometimes also licked the mark or bit off the tip of the stem before marking. Most preorbital marking occurred at night; in four days of observation one captive male marked 119 times of which 19 occurred during daylight.

Figure 3 shows the mean number of preorbital marks deposited daily by three captive males during each month of the observation period. The analysis of variance showed significant differences between the individual males ($F = 65,96$; $df = 2\ 111$; $P < 0,01$), male A depositing more marks than the others virtually throughout the observation period (Figure 3). Male A consistently dominated the others in agonistic encounters (see below). This result is in accord with the frequently reported observation that dominant animals mark more frequently than subordinates (Ralls 1971).

The difference between the monthly means was also significant ($F = 6,73$; $df = 16\ 111$; $P < 0,01$). All three males showed peaks in the mean number of marks deposited in March 1979, September 1979 and March–April 1980. Thus high frequencies of marking were recorded in both autumns (March–April) of the observation period, and also in the spring of 1979 (September). As discussed below the autumn peaks coincide with the peak conception period in the captive grysbok.

Interactions between male and female

Captive grysbok were observed copulating a total of six times. The pattern of precopulatory interactions between male and female, and the actual copulation was similar in all observed cases. The receptive female would walk steadily around the pen

usually with her tail raised to the horizontal position. The male would follow closely, intensively licking the female's perineal region and rump. At intervals the male would mount. In mounting the male's forelegs did not touch the female but hung free on either side of the body. The female normally moved forward as the male mounted and he would keep up for a few paces by moving on his hindlegs. Most mounts were unsuccessful in achieving intromission and the male would then continue following and licking the female. He would frequently utter bleating sounds, often while licking or just before mounting. Eventually the male would mount successfully and, after an ejaculatory thrust, would pay no further attention to the female. The Laufs Schlag, or mating kick (Walther 1974), common in the courtship of many antelope, was never observed in grysbok.

Of the 37 planned encounters between the captive male and female two led to copulation, one on 3 April and the other on 6 June. However, elements of the precopulatory procedure described above occurred in all encounters. The frequencies with which some of these actions were performed varied over the observation period (Figure 4a & b). Licking of the female, mounting and bleating by the male were all relatively infrequent from October to February, but increased in frequency during March to June. Frequencies were particularly high during the months when mating occurred (April and June). The Kruskal-Wallis test showed the variation between months to be significant for both licking of the female ($H = 17,41$; $df = 9$; $P < 0,05$) and bleating by the male ($H = 17,0$; $df = 9$; $P < 0,05$). For mounting, however, the difference between months was not quite significant at $P < 0,05$ ($H = 15,25$; $df = 9$; $0,05 < P < 0,10$). The high frequencies of these actions over March to June suggest an autumn increase in the intensity of male courtship responses.

The female sometimes responded to the male's approach by kicking backwards at him with her hock, a response which was not seen during the precopulatory sequences. The frequency of kicking was high between October and February and lower between March and July (Figure 4a), in other words, negatively correlated with the frequencies of mounting, licking and bleating. The difference between months in the mean frequency of kicking by the female was significant ($H = 22,54$; $df = 9$; $P < 0,01$).

The male sometimes showed the characteristic *Flehmen* or 'lip-curl', an action performed by the males of many bovid species in response to the odour of female urine. Unlike other male courtship actions the frequency of *Flehmen* did not in-

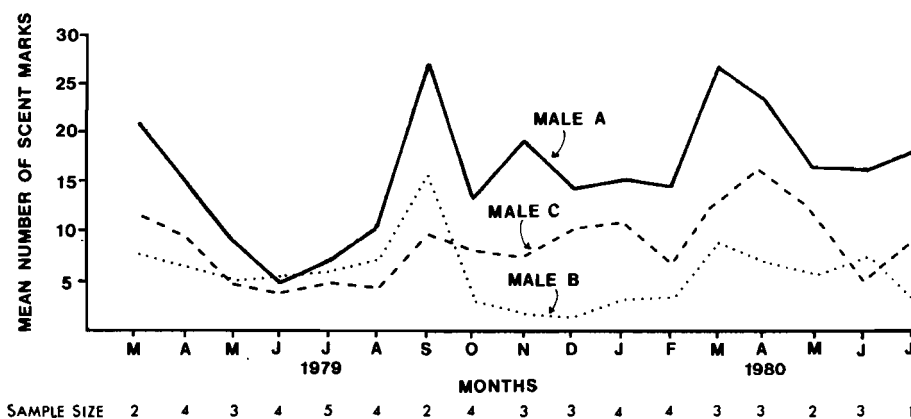


Figure 3 Changes in the mean number of preorbital gland scent marks deposited per day by three captive grysbok males between March 1979 and July 1980. The sample sizes for each month (the number of days on which scent marks were counted) are shown.

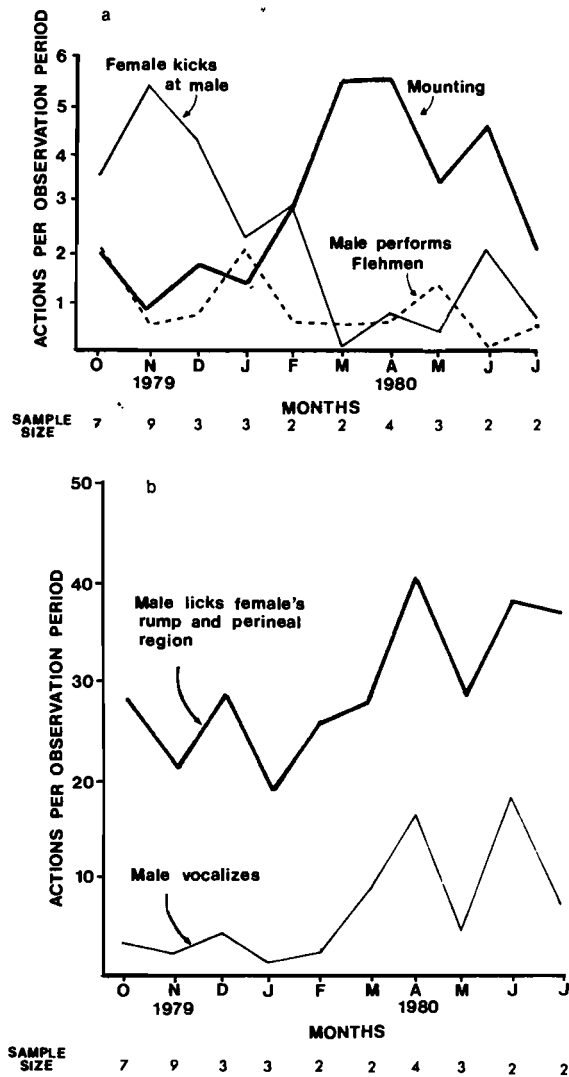


Figure 4 Changes in the frequency of some actions associated with the courtship behaviour of a pair of grysbok observed between October 1979 and July 1980. The frequency is expressed as the mean number of actions observed in each 10-min observation period. The sample sizes for each month (number of observation periods) are shown. (a) Mounting and *Flehmen* performed by the male, and kicking by the female. (b) Licking of the female and vocalization by the male.

crease during the autumn (Figure 4a), and the difference between the monthly means was not significant. During the two planned encounters when copulation was observed the male did not perform *Flehmen* at all but proceeded with licking and mounting immediately the female entered his pen. This suggests that *Flehmen* is not essential for the detection of oestrus — the tendency of the receptive female to raise her tail presumably providing the male with a visual cue. Another male action of possible significance in courtship is rubbing the underside of the muzzle on the female's head, neck or back. In the 10-min encounters between male and female, chin rubbing was confined to the first two months of the study period and it did not occur in the precopulatory sequences.

During chin rubbing the male's preorbital glands occasionally made brief contact with the female, but no sign of the black secretion was observed to adhere to her. Females were never observed rubbing their chins on adult males.

The female also bleated during encounters with the male but this occurred less frequently than the male vocalization. Averaged over the whole observation period (October to July) the female vocalized 1.2 times in each 10-min period compared with the male's average of 6.3 times. The female bleated

in situations where she was apparently threatened by the male. She would bleat and cringe submissively if approached rapidly by the male when she first entered his pen, and also if followed too persistently by the male when she was unreceptive. Unlike the male the female did not bleat during the precopulatory interactions, and the frequency of the female's bleat showed no indication of seasonal differences.

Interactions between males

Adult grysbok males are intolerant of each other and it proved impossible to keep more than one in the same enclosure. When it happened that two captive males came into contact with one another one or both usually suffered serious horn wounds.

The 40 planned encounters between the captive males all ended with the flight of one, usually but not always pursued by the other. For any pair of males it was always the same individual that retreated, irrespective of whether the encounter took place in his own pen or in his opponent's pen. The retreating male is referred to as the subordinate and the other as the dominant. The dominant-subordinate relationship between individual males remained consistent during the two years over which observations were made.

Table 1 lists the various actions observed during agonistic encounters between grysbok males, and shows the percentage of the 40 planned encounters in which each action was recorded. In most encounters the subordinate either fled or behaved submissively (see below) immediately he saw the dominant, but in some he threatened or actually attacked the dominant. In all cases, however, the dominant affirmed his status by counter-attacking and causing the subordinate to flee. Actual fighting occurred in only two of the 40 encounters. In these the rams faced one another, each going down on his metacarpals, with hindlegs braced and horns angled forward. They lunged repeatedly at one another and made head-to-head contact, each attempting to push the other aside. Both males were frequently jabbed in the head, neck and body, and were it not

Table 1 Actions recorded in 40 agonistic encounters between captive grysbok males, showing the percentage of encounters in which each action occurred

Action	Percentage of encounters	
	Performed by dominant male	Performed by subordinate male
Fighting	5	5
Horning of opponent (apart from during fights)	35	2,5
Horn presentation	40	22,5
Chasing opponent	70	0
Submissive lying (head and neck extended)	0	30
Submissive cringing	0	25
Sniffing of opponent	22,5	17,5
Grunting	47,5	7,5
Horning of objects	5	0
Preorbital markings	42,5	15
Sniffing of dung heap	15	2,5
Pawing of dung heap	2,5	0
Linked urination — defaecation on a dung heap	10	0
Feeding	7,5	5
Grooming	5	0

for the rubber horn guards both combatants would have been injured.

Apart from the two that involved fighting, horning of the subordinate by the dominant occurred in 14 of the 40 encounters. In one encounter the subordinate lunged and jabbed the approaching dominant. Males were also observed approaching their opponents with their horns angled forward (see horn presentation, Table 1). This action resembled the horn presentation threat display (Walther 1974) which is common among bovids.

The subordinate male sometimes responded to the approach of the dominant either by lying down with his head and neck outstretched or by 'cringing', that is by lowering his head and neck and flexing his legs slightly (see submissive lying and submissive cringing — Table 1). During both lying and cringing the subordinate remained rigidly motionless. These postures are similar to the submissive postures described in other ungulates (Walther 1974). The dominant would approach the lying or cringing subordinate slowly with nose extended forward. This was usually followed by sniffing of the subordinate, at which the subordinate would often sniff in return. Sniffing was normally directed at either the anal or the head region although once the dominant sniffed extensively at the subordinate's preorbital glands.

Although the dominant male tended to approach the lying or cringing subordinate slowly, and at times appeared reluctant to horn him, these submissive postures were not successful in preventing attack. Of the 12 encounters in which the subordinate adopted the submissive lying posture he was horned and chased in seven. In the remainder the subordinate broke away and fled before the dominant reached him.

During chases the dominant male frequently uttered an abrupt grunt repeated at short intervals. This vocalization was also heard during the two observed fights. In two encounters the dominants horned the vegetation in the pens (Table 1) an action that has frequently been recorded in bovid agonistic behaviour (Walther 1974).

Deposition of preorbital scent was performed by both dominants and subordinates but more frequently by the former (Table 1). However, the location of the encounter appeared to be more important in determining whether a male would mark than the dominant-subordinate relationships; visiting males tended to mark more than home males. Dominant males marked in only five of the 20 encounters in their home pens but in 12 of the 20 encounters in their opponents' pens. Similarly the subordinates marked in 6 of the 20 encounters in strange pens but in none of those in their home pens. The null hypothesis of independence between the occurrence of marking and the location of the encounter is rejected at the 5% level (2×2 contingency tests, $\chi^2 = 5,01$ for dominant males and 4,9 for subordinates).

The location of the encounter therefore needs to be considered when comparing the frequency of preorbital marking by dominants with that of subordinates. Although dominants marked more frequently than subordinates in both strange and home pens the difference is not statistically significant at the 5% level ($\chi^2 = 3,64$ in strange pens and 3,66 in home pens). The linked urination-defaecation sequence was performed only by dominant males. These occurred in four encounters, one in the home pen and three in the subordinates' pens.

Interaction between females

Female grysbok tolerate one another more readily than the males and two or more females can remain within the same

enclosure permanently. In one enclosure inhabited by several females one was clearly the dominant; she would chase other females, attempting to butt them with her head. Since females have no horns, this caused no serious injury. Submissive females would sometimes lie down when approached by the dominant in the same way as described for the males. However, such obvious dominant-subordinate relationships did not always develop between females; two raised together as lambs shared a pen as adults without any sign of agonistic interactions.

The seasonal distribution of grysbok births in captivity

The females in the captive colony gave birth to a total of 18 lambs. Although lambs were born in most months of the year there was clearly a birth peak in the spring and early summer (September to December, Figure 5).

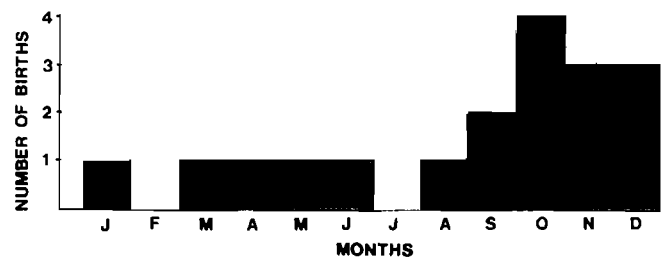


Figure 5 Variation between months in the number of grysbok births recorded in captivity.

Discussion

In all adequately studied small antelope, adult males have been observed to defend their territories by actively intercepting and chasing intruders (Hendrichs 1975; Dunbar & Dunbar 1979, 1980; Norton 1980). The wild grysbok males observed in the present study occupied well-defined ranges but we could not establish definitely whether these ranges were defended territories. We could not watch interactions between free-ranging grysbok and therefore saw no incidences of active territorial defence. It was also uncertain how many unmarked grysbok shared the study areas with the radio-collared animals. Nevertheless the marked intolerance of one another shown by captive males supports the idea that the ranges of wild males are in fact defended territories.

On the other hand, the outcomes of the planned agonistic encounters between the captive grysbok males seem inconsistent with territoriality. In a territorial species a male in his home environment would be expected to dominate visitors, whereas in fact the dominant-subordinate relationships between the captive males remained unchanged irrespective of where the encounters took place. This result may have been due to the unnatural conditions in captivity. The males were known to one another before observations began and the dominant-subordinate relationships may have already been established. Although each male remained in one particular pen throughout the two years observation on agonistic behaviour, there had been several rearrangements of accommodation three months before observations began and, as a result, the males were familiar with one another's pens. The pens were also very much smaller (4 × 6 m) than the areas that would normally be occupied by free-ranging males. These conditions may have accounted for the observed lack of relationship between dominance and the location at which the encounter occurred.

The average range size of the three grysbok males tracked

in this study was about 2,5 ha, which is smaller than that reported for other small antelope species. Dunbar & Dunbar (1974) report an average size of 8 ha for klipspringer territories in Ethiopia; Norton (1980) estimates an average of 15 ha for klipspringers in the southern Cape and 49 ha in the north-western Cape. Hendricks (1975) gives an average of 7–8 ha for dik-dik territories. Territory size in small antelope can vary greatly depending on habitat quality (Norton 1980), and the sample size of ranges obtained in the present study is inadequate to give a reliable average size. Nevertheless it is noteworthy that the grysbok female remained within an area of only 1,1 ha. The ability to survive in small patches of natural vegetation surrounded by disturbed land probably accounts for the grysbok's success in relatively heavily populated areas.

The encounters between the captive grysbok males quickly escalated to the point where the horns were used to stab the opponent; horning of at least one of the combatants occurred in 17 of the 40 planned agonistic encounters. This is unusual in the Bovidae (Walther 1974), where in most species the horns have evolved primarily to catch the opponents' blows and bind the heads together during pushing duels. As pointed out by Keast (1963) all the small antelope have straight stabbing horns that are not adapted for interlocking with an opponent's horns.

In ungulates with horns capable of piercing the opponent the tendency to strike is often inhibited, and threat displays predominate in agonistic encounters (Geist 1966). In the grysbok, however, threat displays seemed poorly developed. Ritualized presentation of the horns is a widespread threat display in African antelope which is probably derived from an intention movement to attack. In some species horn presentation is associated with exaggerated postures that presumably enhance the signal value of the display, and the animals may rigidly maintain the postures for up to several minutes (Walther 1974). However, the posture in which the grysbok presented horns was not exaggerated (the horns were angled slightly forward and the head carried at the same level as the body), nor was the posture held for more than one or two seconds. Moreover horn presentation was normally followed by direct attack on the opponent. Horn presentation in grysbok may therefore be merely an intention movement to attack with little signal content. At any rate it did not seem to be an important display acting as a substitute for direct aggression. Horning of the ground or vegetation has been interpreted as a threat display in ungulates (Estes 1969; Walther 1974) but in grysbok it was infrequent and thus seemed to be of limited importance as a threat signal.

The apparent unimportance of visual threat displays in grysbok may be related to the closed nature of their habitat and their nocturnal habits, situations in which visual displays would not be so effective. One might then expect a relatively greater development of non-visual threat displays in compensation. The grunting vocalization was common in agonistic encounters but was heard mostly during the course of fights and vigorous chases. It therefore apparently does not play a prominent role as a substitute for direct attack.

The agonistic behaviour of grysbok is in accord with Geist's (1966, 1974) hypothesis that small ungulates have less ritualized and more dangerous forms of combat than larger species. Various arguments in favour of the hypothesis are outlined below.

Maynard Smith & Price (1973) showed that ritualized or 'conventional' fighting could evolve through individual selection provided the penalty for retreating uninjured was lower than that of serious injury. If the reverse is true then damaging

combat could be evolutionarily stable. Thus if small antelope have evolved a tendency towards unritualized combats one would expect that (i) the consequences of combat injuries are less serious for small antelope than large ones; and (ii) that the penalty for retreating uninjured (e.g. after a ritualized encounter) is relatively more serious for small antelope than large ones. There are arguments in favour of both these predictions.

First Geist (1966) pointed out that the severity of horn wounds depends on body size. Larger animals inflict more serious injuries because of the greater energy they can put into the blow, and the greater resistance of the heavier body adds to the severity of the injury. A second point is that small antelope rely on their inconspicuousness to avoid predators, their size and dense habitats preadapting them to a hiding strategy. Larger antelope tend to rely on their speed to escape predators (Jarman 1974). Temporary disablement as a result of fighting would reduce the fitness of runners to a greater extent than hidiers.

Because of the differences in food requirements and social organization it seems likely that the penalty for retreating uninjured from a combat over territorial ownership would be relatively higher for a small antelope than for a large one. Small antelope feed more selectively than large ones and therefore a comparatively small proportion of the vegetation constitutes food for small antelope (Jarman 1974). Small antelope occupy permanent territories that include their entire home range (Leuthold 1977) and, as noted above, Jarman (1974) suggested that their territories serve to defend their food supply as well as mating rights.

In contrast the territory in many large antelope species forms only part of the male's total range, and in some species it is defended consistently only in the rutting season (e.g. Estes 1969; Leuthold 1977). A large antelope male that fails to hold a territory may join a bachelor herd and compete again for a territory the following breeding season. Bachelor herds are normally restricted to marginal habitat, although if territoriality is seasonal this may only be for the duration of the rutting season (Leuthold 1977).

Because of the greater degree of competition for food among small antelope it seems unlikely that they could so readily maintain themselves in marginal habitat if this had to be shared with other non-territorial males. Thus if a small antelope male retreated from an agonistic encounter, and consequently lost his territory, he would not only sacrifice mating opportunities but, if alternative territories were occupied, he would be excluded from an adequate food supply. This situation is likely to favour damaging rather than ritualized combat for territorial ownership.

Another aspect of possible importance is that in gregarious antelope the group offers protection against predators. For a gregarious antelope it may be more adaptive to tolerate subordinates, rather than to injure or chase them and so disrupt group cohesion. This may have favoured ritualized threat signals in larger antelope.

Geist (1974) reasoned that populations of small ungulates have a faster turnover rate than populations of large ungulates because of their shorter life-span, and in consequence there is greater selection for non-damaging intraspecific fighting in large species than in small ones. He argued that as the number of breeding seasons in which a male breeds becomes reduced, a greater risk of death from combat becomes acceptable. This reasoning is, however, open to question. If damaging combat tends to reduce reproductive output when compared with non-

damaging combat, it will not be favoured by natural selection, irrespective of the number of opportunities for reproduction a male may have during his lifetime. The critical factor determining whether damaging combat would be favoured by natural selection is, as indicated above, the cost of injury relative to the cost of retreating uninjured.

The fighting behaviour of another small antelope, Maxwell's duiker (*Cephalophus maxwelli*), is similar to that of grysbok in that it readily escalates to potentially damaging levels (Ralls 1975). On the other hand, Hendrichs (1975) describes the fights between neighbouring territorial dik-dik males as being ritualized. It is possibly important that both our study and that of Ralls (1975) concerned captive animals. Under confined conditions retreat is restricted and fights may more readily escalate. More detailed studies of combat behaviour in free-ranging small antelope are required to fully evaluate the arguments presented above.

In view of the intolerance of grysbok males of one another the occurrence of stereotyped submissive postures in encounters between males was unexpected. However, these submissive postures were clearly ineffective in the sense that they did not appease the dominant animal; the submissive subordinate was never allowed to remain in the dominant's pen. Submissive postures are generally more frequent in captive ungulates, where the subordinate has less chance of escape, than in wild ones (Walther 1974). It therefore seems doubtful that submissive displays play a prominent role in the agonistic behaviour of adult grysbok males in their natural environment. Walther (1974) observed very frequent submissive displays on the part of a wild young dik-dik male when approached by its father. Young dik-dik are expelled from their parents' territory once they reach a certain age and Walther suggests that the function of the submissive display may be to appease parental aggression and allow the juvenile to remain longer in its parents' territory. This may be the most important context in which the submissive display occurs in grysbok.

The fact that male and female grysbok are seldom seen together, as well as the limited overlap between the ranges of the adult male and female at Jonkershoek (Figure 1), suggests that pairs do not share a joint territory as do klipspringer and dik-dik (Hendrichs 1975; Dunbar & Dunbar 1980; Norton 1980).

In steenbok and grey duiker individuals of both sexes generally remain alone in discrete home ranges (Dunbar & Dunbar 1979; M. Cohen pers. comm. 1982). There is limited overlap between individuals of the same sex but male ranges may overlap those of two or more females and *vice versa*. The information on grysbok suggests that their mating system is similar to that of the grey duiker and steenbok, but further study is required for definite conclusions.

In contrast to the larger social antelope, where display postures are common in male courtship behaviour, obvious visual displays were absent in grysbok. In particular there was no sign of the horizontal head and neck extension (the low stretch) which is widespread in bovid courtship behaviour (Walther 1974). This posture occurs in the courtship of dik-dik males where it is accompanied by raising of the forehead tuft (Tinley 1969; Walther 1974). On the other hand tactile communication between male and female, particularly licking of the female's ano-genital region and rump, seems more pronounced in grysbok than in most large antelope (Walther 1974). Vocalizations were also common in grysbok courtship behaviour. As indicated above the closed habitat and nocturnal habits of grysbok would favour auditory and tactile com-

munication rather than visual displays.

In common with small antelope in general (Jarman 1974), marking with preorbital secretion is well developed in grysbok. Their scent-marking behaviour shows certain features that have been observed in a variety of other mammals. Firstly dominant animals mark more frequently than subordinates, a phenomenon that has been recorded in marsupials, lagomorphs and rodents as well as artiodactyls (see Ralls 1971). Secondly marking is associated with agonistic encounters. Ralls (1971) observed that marking often occurs in situations where an animal is motivated to aggression, and this appears true not only of grysbok but also of many other ungulates (Walther 1978). Grysbok males also marked more frequently in unfamiliar pens than in their home pens. This reflects the general tendency of grysbok males to mark frequently when in a new environment (Manson 1974). The tendency to scent mark in novel situations or on unfamiliar objects is also widespread, and Kleiman (1966) suggested that scent marking in many mammals evolved from autonomic responses to unfamiliar stimuli.

The functions of scent marking in African antelope are not entirely clear. Two hypotheses that have frequently been advanced are:

- (i) The marks signal territorial occupancy, deterring potential competitors.
- (ii) Marking is a means of labelling habitat for the animal's own use, rather than a signal to conspecifics (see Johnson 1973; Leuthold 1977; Walther 1978).

However, as pointed out by Leuthold (1977), there is as yet no experimental evidence to support either hypothesis.

Chin rubbing in grysbok may simply represent grooming of the female by the male, but it is possible that the action deposits glandular secretion on the female. Gerneke & Cohen (1978) describe an intermandibular glandular region in the steenbok which secretes an off-white flaky substance. Steenbok males rub the intermandibular area on objects in the environment and also on females during courtship interactions. A flaky substance was observed on the intermandibular area of grysbok which resembled that described in steenbok by Gerneke & Cohen (1978), and possibly this is transferred to the female during chin-rubbing. Deposition of scent on conspecifics occurs in a number of mammals, including bovids (Ralls 1971; Johnson 1973) but its function is not clearly understood.

The spring – early summer birth peak we observed in captive grysbok has also been reported in klipspringer in the western Cape by Norton (1980). The phenology of the vegetation in the winter and non-seasonal rainfall belts of the Cape Province is complex; growing seasons differ between the various plant life forms, and in species rich communities at least some growth can occur at any time of the year (Bond 1980; Kruger 1981). However, observations suggest that on the whole spring is the season of most active plant growth (Kruger 1981), so it is possible that the grysbok birth peak coincides with the period of maximum food availability. However, information is required on the diet composition of grysbok, and on the phenology of the vegetation components that are most important in their diet, before definite conclusions can be drawn.

From observations on captive grysbok the gestation period is estimated at about 180 days. The birth peak from September to December should therefore be preceded by a peak conception period from March to June. The expected peak conception period coincides approximately with the February to June peak in the frequencies of preorbital marking and courtship activity. It is possible that the seasonal variation in the intensity of male

courtship and marking behaviour reflects seasonal variation in testosterone secretion (Lincoln & Short 1980).

It would be adaptive for grysbok males to increase courtship behaviour at the time of the year when females are most likely to be receptive. The increase in the frequency of marking in the mating period indicates that its function is related to reproductive behaviour, signalling to potentially competing males or possibly also to prospective mates.

In some ungulates there are two birth seasons and two conception periods annually, one in spring and the other in autumn. Kellas (1955) reports that this is so in the dik-dik, in which males show two peaks in testes weight, corresponding with the two mating peaks. Figure 5 suggests only a spring lambing peak for grysbok. However, there was a marked increase in pre-ovulatory marking by males in spring (September, Figure 3) which could indicate a tendency towards spring mating. A larger sample of grysbok births may reveal an autumn peak.

Conclusions

The social behaviour of grysbok is similar to that described by Jarman (1974) for small antelope in general. Their fighting behaviour is in accord with the hypothesis that small antelope tend to have dangerous rather than ritualized combats. Their courtship behaviour conforms to expectations for a nocturnal animal of closed habitats in that visual displays are poorly developed while olfactory, auditory and tactile communication are more prominent. Pre-ovulatory secretion evidently plays an important role in communication, and experimental work is required to determine its function.

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