

Chapter 5

ACTIVITY PATTERNS, FORAGING BEHAVIOUR AND SOCIAL BEHAVIOUR

Introduction

Although grey rhebok and mountain reedbuck share similar habitat, they differ significantly in their feeding and social behaviour. As described in earlier chapters, grey rhebok are browsers (Ferreira, 1983; Beukes, 1984) and live in harems where a single adult male defends a small group of females and young on a permanent basis (Esser, 1973; Beukes, 1984). Mountain reedbuck are grazers (Irby, 1976), and although males are territorial, they only defend an area that female herds move in and out of temporarily (Irby, 1976). Female herds are transitory, with animals breaking up into small groups and reforming larger groups on a regular basis (Irby, 1976).

Foraging behaviour should differ between the two species as a result of the differences in growth habit of the food they eat. Grass plants grew at higher densities than forbs at Sterkfontein (see Chapter 4) indicating that the food supply of mountain reedbuck was generally closer together than that of grey rhebok. Although small, these differences in densities should influence the average distances that the two species need to move between food sources, thus affecting foraging behaviour with a knock-on effect to other behaviours. Additionally, nutritional differences between forbs and grasses might influence the quantities of food required which would influence the time spent feeding.

Klein & Fairall (1986) compared foraging behaviour and associated energetics of two antelope species with different feeding requirements (impala and blesbok) and found that the grazer (blesbok) had a shorter daily feeding time than the mixed feeder (impala). This was thought to be associated with the blesboks' efficiency as a bulk feeder and the longer time required for digestion of its coarser diet. In the present study, due to the similarity in size of grey rhebok and mountain reedbuck, and similar

use of marginal habitat, a comparative behavioural study of the two species, similar to that of Klein & Fairall (1986), was expected to find that grey rhebok fed for longer but spent less time digesting food than mountain reedbuck due to their contrasting feeding requirements.

The differing group structures should result in contrasting male reproductive behaviour due to the disparate access to females. Harem male grey rhebok have access to their females at all times with no competition from other males (apart from rare challenges from intruding males: see Chapter 3), and are, therefore, always aware of the reproductive status of these females. In contrast, male mountain reedbuck are often solitary and have sporadic access to females. To increase their chances of detecting oestrus in females and thus mating, they might be expected to test females whenever they get the opportunity. Moreover, mountain reedbuck are relatively aseasonal when compared with grey rhebok (Irby, 1979; Esser, 1973; Skinner & Smithers, 1990), and should test females over longer periods of the year. There were two aims to this component of the study:

- 1) To quantify behaviour and estimate activity budgets and patterns for both species;
- 2) To compare differences in behaviour between the two species in relation to ecological differences such as foraging and social behaviour.

To accomplish these aims, the following questions were considered:

- a. How much time overall is spent performing different behaviours during the day and how do the two species compare? (i.e. what are the activity budgets)?
- b. How do the two species spread these different behaviours throughout the day (activity patterns)?
- c. Are they more active or inactive at certain times of day?
- d. Is there any seasonal variation in activity (resting and feeding behaviour)?
- e. How active are the two species at night?
- f. When, and how often, does reproductive behaviour take place?
- g. How do males demarcate their territories?

Methods

Study site and animals

This component of the study was conducted within the main study site at Sterkfontein in an area of approximately 550 ha (see Chapter 2). Behavioural observations were made over a one-year period between May 2001 and April 2002. These were carried out primarily in daylight between 06h00 and 18h00, and at varying times of the day in an attempt to represent different periods equally. Three harem herds of grey rhebok were monitored (Groups 2, 3 and 4), while the remaining herds were difficult to observe either because of rough terrain (Group 6) or because of skittish behaviour (Group 1). Group 5 ceased to exist in September 2001 and was excluded from the study. Six adult male mountain reedbeek were monitored and observations were made whether or not females accompanied them. Due to female movement patterns, three of these males were predominantly solitary. Female mountain reedbeek were observed in differing group sizes without differentiating between individuals.

Behaviour

Behaviour was measured predominantly by scan observations (Martin & Bateson, 1993). Normally only one herd was observed at a time, but when grey rhebok and mountain reedbeek were close together behaviour of both species was recorded simultaneously, so long as all animals could be observed clearly. Solitary animals were also observed. Observations were carried out either from a vehicle, or on foot from a hidden position, so that the subjects' behaviour was not affected by the presence of the observer. If the animals were disturbed, behavioural recording was delayed until they appeared to pay no attention to the observer. Animals were watched with binoculars from distances varying between 50 and 300 m.

Observation periods lasted a minimum of 1 hour, unless the subjects moved out of sight or were disturbed, while 2- and 3-hour periods were also regularly monitored. These longer observations often allowed an entire period of behaviour to be recorded. For example, if the animals were feeding when observations started, but then became inactive, data collection sometimes continued into the next active period. For

purposes of estimating activity budgets and patterns, these longer observation periods were split into separate hourly periods. In total, 295 one-hour observation periods were conducted on grey rhebok herds. Of these, harem males were observed for only 247 hours because on 48 occasions they were either not present or were only present for a short period. For mountain reedbuck, 141 one-hour observation periods were conducted on males and 109 on female herds.

Every 2 minutes the whole group of subjects were rapidly scanned and the behaviour of each animal recorded at that instant. Within grey rhebok herds, male behaviour was differentiated from that of females and young over the age of five months, while the behaviour of lambs under five months old was also differentiated. After five months they were considered fully weaned and males between the ages of five- and eleven months were grouped with the females because they remained sub-ordinate to the harem male and showed no signs of sexual maturity. It was also difficult to differentiate between them from a long distance in a short space of time. Females within the same herd, as well as young over five months age were treated as one “individual”, with their data being pooled. At about the age of eleven months, young males were evicted from their natal groups by the harem males and disappeared.

In mountain reedbuck, male behaviour was also differentiated from that of females, but the behaviour of lambs younger than six months age was not recorded due to the difficulty of observing them. Again, female behaviour was recorded without differentiating between individuals and their data were pooled.

Although Jarman & Jarman (1973) found that a 4 minute recording interval was adequate when studying the activity of impala in the Serengeti, and that compared with a 1- or 2 minute interval, 4 minutes did not substantially increase the error in recording major activities, it was decided in the present study that a 2 minute interval was manageable. Apart from increasing the data set, it reduced the time wasted between recordings.

During observations, behaviour was split into the following categories:

- Feeding (grazing/browsing)
- Standing head up (not feeding)
- Standing alert (vigilant)
- Standing grooming
- Walking/running
- Defecating/urinating
- Territorial marking (adult males only)
- Ruminating
- Lying inactive
- Lying grooming
- Sexual behaviour (adult males only): Urine sniffing, vulva sniffing, flehmen, licking lips, laufs Schlag, & mounting.

When observations were made from distances greater than 100 m, and on animals that were either lying inactive or standing but not feeding, it was difficult to determine whether they were ruminating. At these times ruminating was excluded and behaviour was only recorded as lying inactive or standing head up (not feeding). Quantification of ruminating behaviour was, therefore, restricted to observations from less than 100 m.

Scan sampling allowed the recording of behaviour from more than one individual at the same time, so it was unnecessary to watch individuals continuously. However, certain uncommon or short duration behaviours were watched for continuously and recorded whenever they occurred, regardless of whether they occurred at the 2-minute interval. These behaviours were territorial marking by males (grey rhebok: see below), sexual behaviour (normally initiated by males), submissive behaviour (young males submitting to adult males), and drinking. Alert behaviour was recorded but was unusual because there were virtually no natural predators and the only threat came from humans.

In addition to diurnal observations, nocturnal behaviour was recorded for both species over a number of separate six-hour periods. Grey rhebok were observed at night on

eight occasions, while mountain reedbuck were observed on four occasions. Due to the difficulties of viewing at night, behavioural categories were restricted to active or inactive (lying), and the scanning frequency was reduced to five-minute intervals. Due to the low number of observation periods, only averages were determined and no statistical analyses were attempted.

Activity budgets and activity patterns

Activity budgets are used here to indicate the overall average percentage of time spent engaged in various behavioural activities during the day. Behaviours were placed in the following categories: feeding, standing (not feeding but sometimes ruminating), walking (including running), grooming (both standing grooming and lying grooming), resting (including lying inactive and lying ruminating) and other (including defecating, marking, standing alert and sexual behaviour). Ruminating was excluded as an independent activity. Budgets were estimated for males and females of both antelope species, using overall averages calculated from hourly averages (i.e. all times of the day were equally represented). No seasonal patterns were considered.

Activity patterns indicate the percentage of time spent engaged in various behaviours at different times of the day and in two seasons, summer and winter. Behaviours were categorised as for budgets, but for each gender of each species, summer (November to February) and winter (May to August) were differentiated, and days were split into periods of two-hours (06h00 - 07h59, 08h00 - 09h59, 10h00 - 11h59, etc.).

Territorial marking

Male grey rhebok performed territorial marking by frequently defecating small amounts of faeces within their home ranges. Whereas females and young males defecated once every 1 – 2 hours, harem males defecated much more often, sometimes more than 20 times per hour. This was often done at visible markers such as grass tufts, bushes, termite mounds or telephone poles, while females appeared to defecate randomly.

The frequency of territorial marking was investigated in three harem male grey rhebok from groups 2, 3 & 4 between May 2001 and April 2002. During scan observations for general behaviour (see above), the males could be individually monitored for marking behaviour because it was easy to detect when they lifted their white tails to defecate. To standardise the results, the number of marks made during the males' active periods were divided by the time of observation, and the number of marks per hour derived from this (periods of inactivity were excluded).

Although male mountain reedbeek were territorial, they did not perform the same marking behaviour and were, therefore, not monitored for it.

Statistical methods

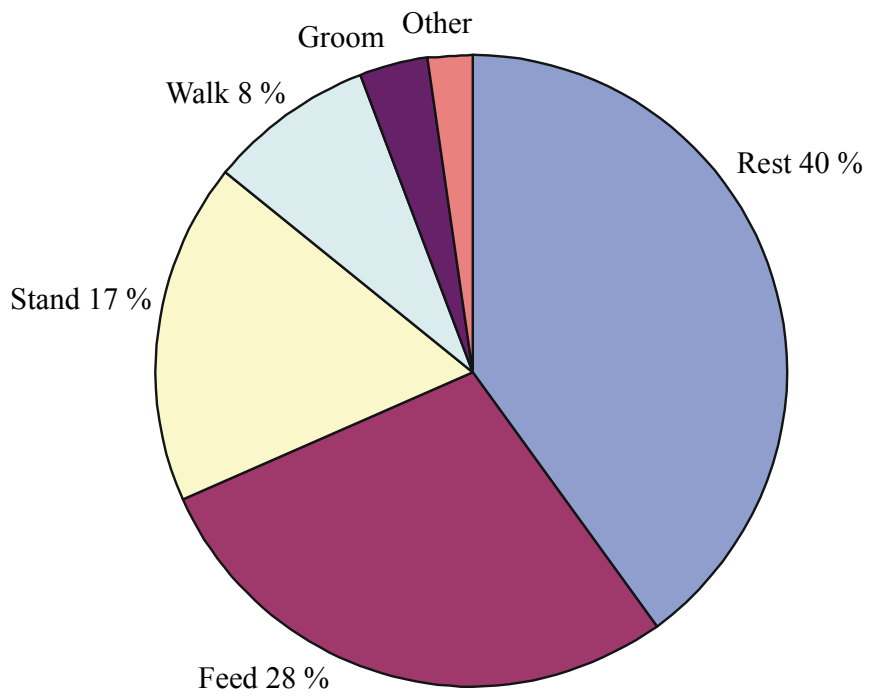
Seasonal differences in time spent resting and feeding were investigated using paired t-tests, and then analyses of variance were used to make comparisons between genders, species, and times of day. Times of day were split into 1-hour periods (unlike the activity pattern graphs below which were split into 2-hour periods) starting at 07h00 and finishing at 18h00. Seasonal differences in marking frequencies between three territorial male grey rhebok were tested for using a two-way ANOVA, as were submissive behaviour of young male grey rhebok from three herds.

Results

Diurnal activity budgets

Male grey rhebok rested for 40 % of daylight hours, compared to 44 % by female grey rhebok (Figure 15). Male mountain reedbeek rested for 57 % of daylight hours, compared to 54 % by females (Figure 16). In contrast, the percentage of time spent feeding was more similar between the two species, with male and female grey rhebok feeding for 28 % and 33 % of daylight hours respectively, and male and female mountain reedbeek feeding for 28 % and 31 % respectively.

(a) Males



(b) Females

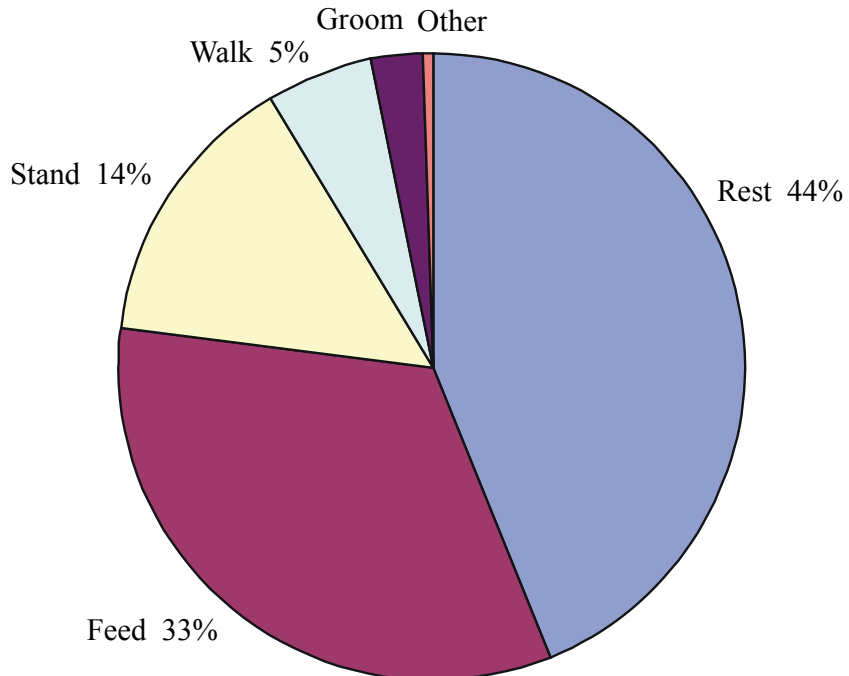
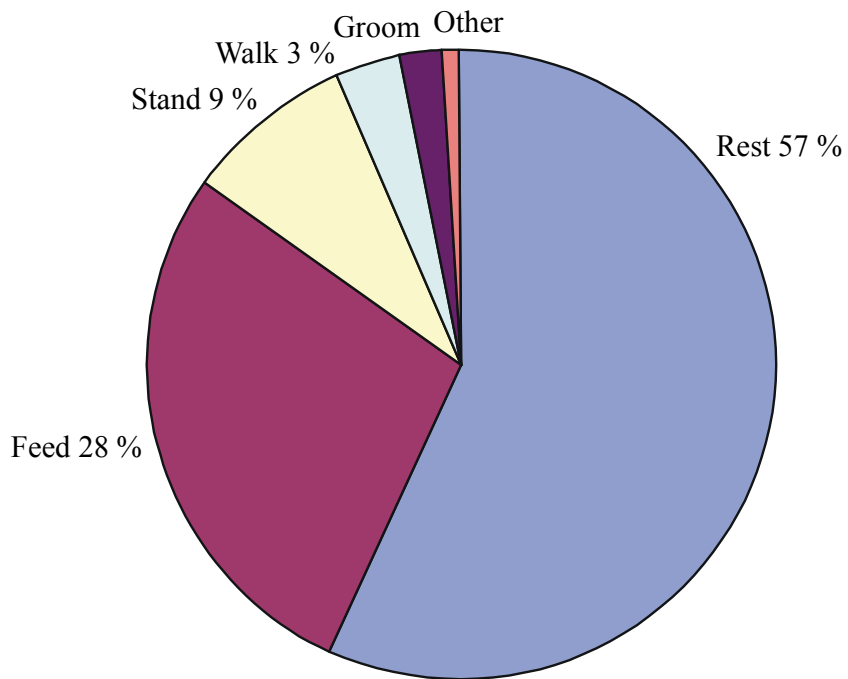


Figure 15. Activity budgets of grey rhebok at Sterkfontein: (a) males; (b) females.

(a) Males



(b) Females

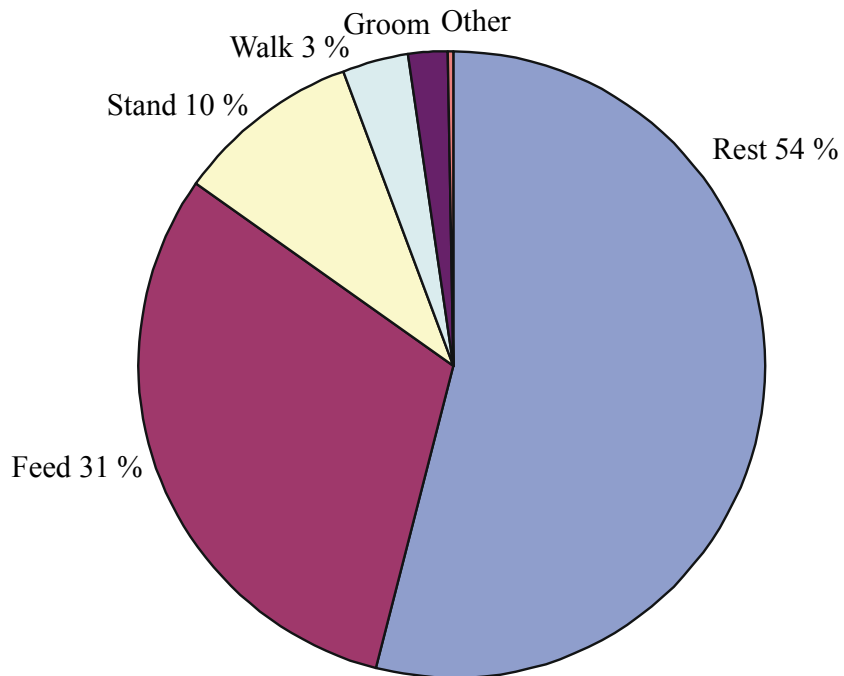
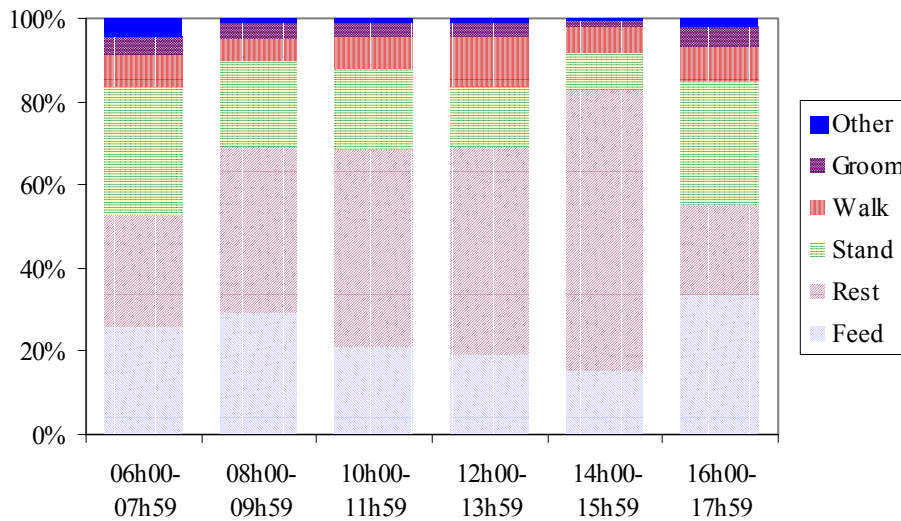


Figure 16. Activity budgets of mountain reedback at Sterkfontein: (a) males; (b) females.

Diurnal activity patterns

Male grey rhebok had similar feeding patterns in both summer and winter, whereby they fed most during the periods 08h00-09h59 and 16h00-17h59, and least during the periods 12h00-13h59 and 14h00-15h59 (Figure 17). In both seasons they were most active (i.e. they rested the least) during the periods 06h00-07h59 and 16h00-17h59.

(a)



(b)

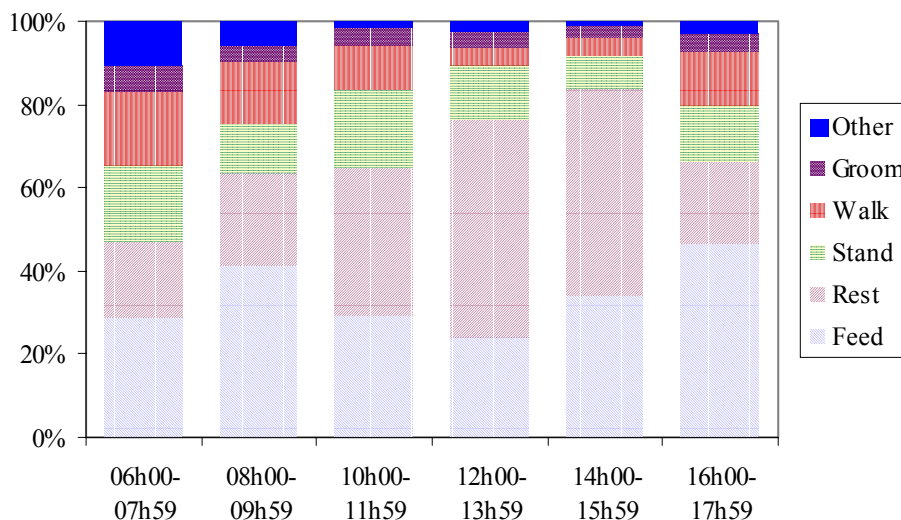
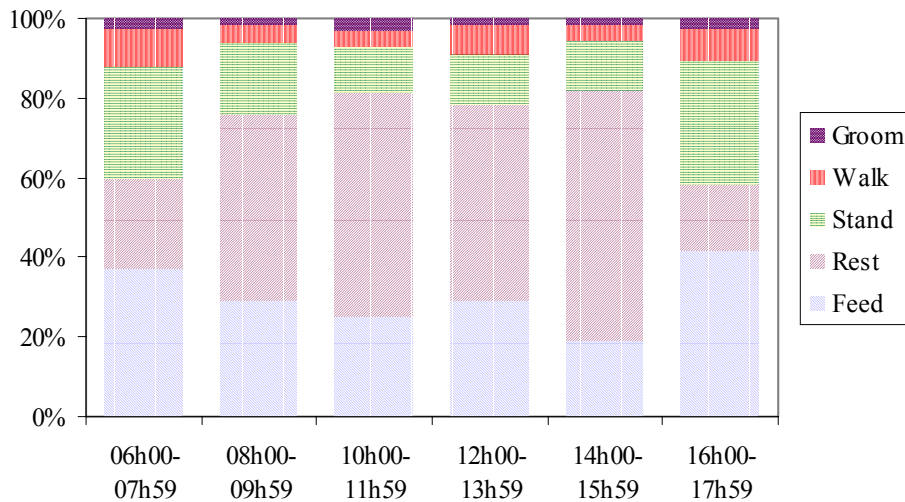


Figure 17. The diurnal activity patterns of male grey rhebok: (a) November to February; (b) May to August.

In summer, female grey rhebok fed most and were most active during the periods 06h00-07h59 and 16h00-17h59, while in winter they fed most and were most active during the periods 08h00-09h59 and 16h00-17h59 (Figure 18). In general, the activities of male and female grey rhebok overlapped so that they were normally active at the same times and inactive (resting) at the same times.

(a)



(b)

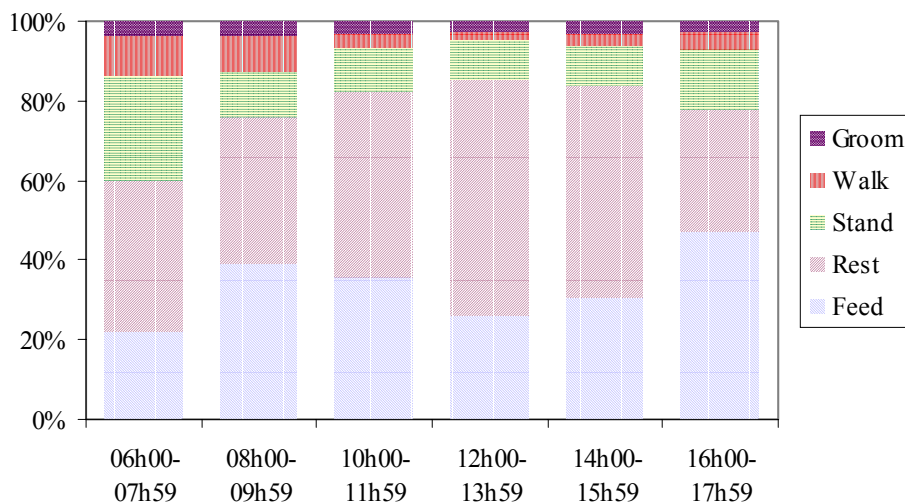
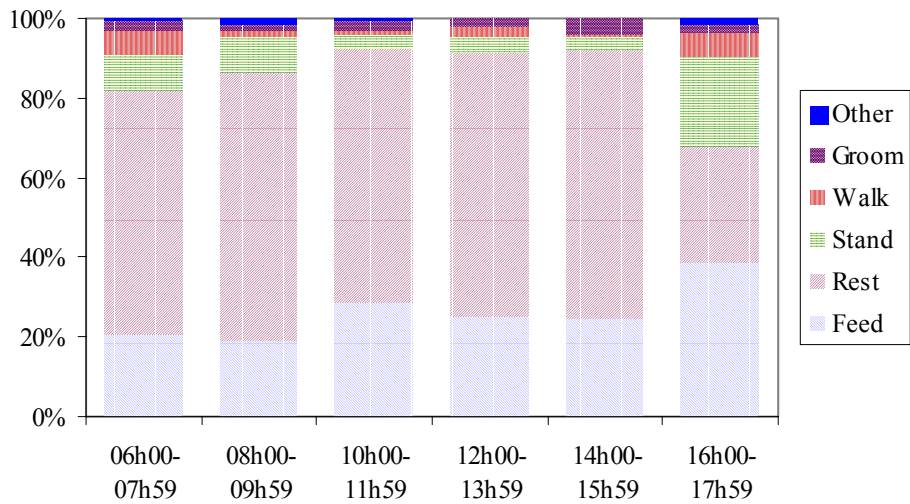


Figure 18. The diurnal activity patterns of female grey rhebok: (a) November to February; (b) May to August.

Male mountain reedbeek fed most during the period 16h00-17h59 in both seasons (Figure 19). In summer they rested to a similar degree in all time periods, except 16h00-17h59, when they rested much less, while in winter they rested more during the periods 12h00-13h59 and 14h00-15h59, and least during 16h00-17h59.

(a)



(b)

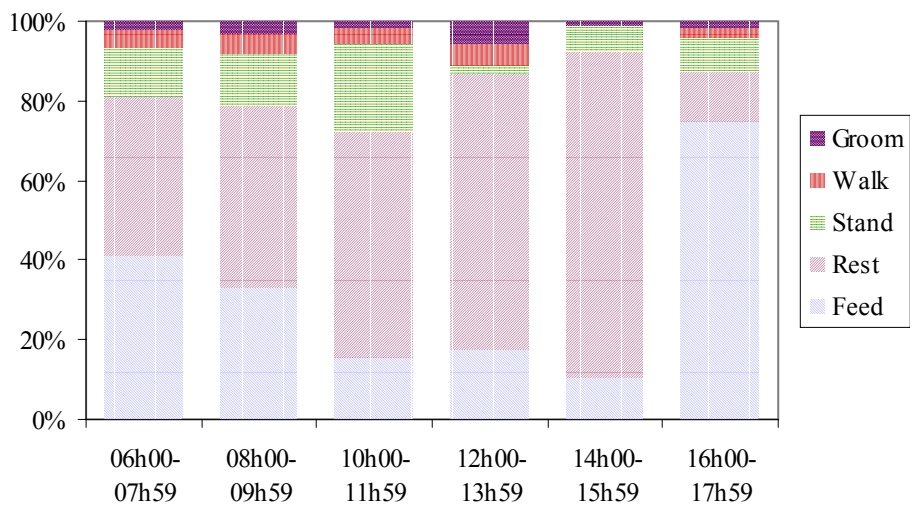
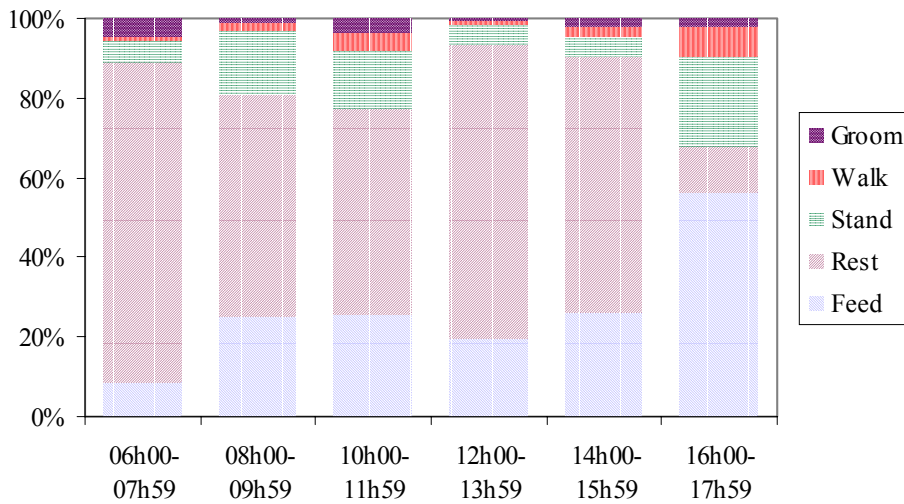


Figure 19. The diurnal activity patterns of male mountain reedbeek: (a) November to February; (b) May to August.

Female mountain reedbeek fed most during the time period 16h00-17h59 in both seasons (Figure 20). In summer they rested more during the periods 06h00-07h59 and 12h00-13h59, while in winter they rested by far the most during the period 10h00-11h59.

(a)



(b)

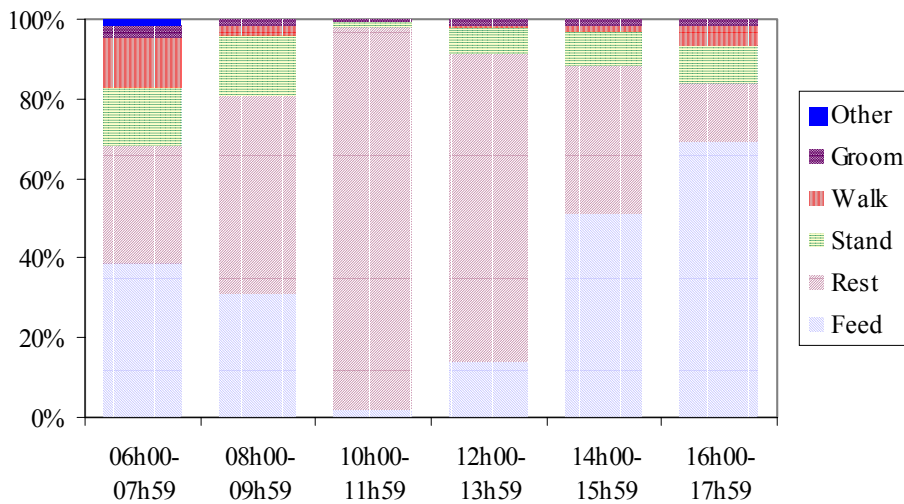


Figure 20. The diurnal activity patterns of female mountain reedbeek: (a) November to February; (b) May to August.

To investigate seasonal variation in resting behaviour of male and female grey rhebok, and male and female mountain reedbuck, four separate paired t-tests were conducted using summer (Nov – Jan) and winter (May - Jul) data. Overall averages from 11 one-hour time periods were included for each season within a species (e.g. 6h00-06h59, 07h00-07h59, etc.). There were no seasonal differences found (Male grey rhebok: $t = 1.404$, $df = 10$, $p = 0.191$; Female grey rhebok: $t = -0.154$, $df = 10$, $p = 0.881$; Male mountain reedbuck: $t = 0.523$, $df = 10$, $p = 0.612$; Female mountain reedbuck: $t = 0.295$, $df = 10$, $p = 0.774$). Seasonal data were, therefore, pooled for the rest of the analysis.

A two-way ANOVA was used to investigate variation in resting behaviour between different times of the day for both genders of both species (Table 14). Highly significant differences were found between species categories, between times of day, and there was also an interaction. Multiple pairwise comparisons using the Tukey test indicated that both male and female grey rhebok spent less time resting than male and female mountain reedbuck, but that male and female grey rhebok did not differ from each other, and male and female mountain reedbuck did not differ from each other. Between time periods, male grey rhebok were less active from 12h00-14h59 than from 06h00-08-59 and 17h00-17h59, while female grey rhebok were less active during the period 12h00-12h59 than 17h00-17h59. Both male and female mountain reedbuck were more active during the period 16h00-17h59 than at any other time of day. The interaction term indicated that the differences found in activity levels between different times of the day depended on which species or gender was considered (i.e. it differed between grey rhebok and mountain reedbuck).

Table 14. Two-way ANOVA comparing the differences between grey rhebok and mountain reedbuck (of both genders) and between periods of the day in the time spent resting. Species category refers to male grey rhebok, female grey rhebok, male mountain reedbuck, and female mountain reedbuck.

Source of variation	DF	SS	MS	F	P
Species category	3	11961	3987	16.4	< 0.001
Time	10	32327	3233	13.3	< 0.001
Species x time	30	12243	408	1.7	0.033
Residual	88	21395	243		
Total	131	77925	595		

Although time spent resting was used as an indication of levels of activity (because lying/resting was defined as inactive), periods of activity (defined as not lying down) did not necessarily mean feeding. As a result, variation in feeding behaviour was also tested using a two-way ANOVA (Table 15). No differences were found between species categories (although the result was marginal), but there was a strong difference between times of day. There was no interaction, although again this was marginal. Multiple pairwise comparisons using the Tukey test indicated that all animals fed more during the period 16h00-17h59 than at any other time of day.

Table 15. Two-way ANOVA comparing the differences between grey rhebok and mountain reedbuck (of both genders) and between periods of the day in the time spent feeding. Species category refers to male grey rhebok, female grey rhebok, male mountain reedbuck, and female mountain reedbuck.

Source of variation	DF	SS	MS	F	P
Species category	3	0.080	0.027	2.249	0.088
Time	10	1.186	0.119	10.011	< 0.001
Species x time	30	0.520	0.017	1.462	0.088
Residual	88	1.043	0.012		
Total	131	0.022	0.022		

Because territorial male mountain reedbuck did not have full time access to females, it was thought that when they did have access, they might spend more time testing females for oestrus and less time feeding. Time spent feeding by solitary males was, therefore, compared with time spent feeding by males with attending females (using hourly averages). No differences were found ($t = 0.497$, $df = 20$, $p = 0.625$).

Patterns of activity and inactivity

A typical day for grey rhebok involved foraging for between one and two hours, followed by a rest period of similar length. This was then followed by more activity for one to two hours, and then more resting. Although grey rhebok were on average less active during the middle of the day than early morning and late afternoon (see above), the times when animals were active varied from day to day and were often determined by the timing of previous activities. For example, on one day a herd might have been active at 08h00 and inactive at 12h00, while on the next day the same herd could have been inactive at 08h00 but active at 12h00, even in hot weather.

Mountain reedbuck activity periods were generally more fixed, with early morning (06h00 – 09h00) being a period of activity, and midday being a period of inactivity. Following this, late afternoon was normally an active time, while the night included alternating periods of activity and inactivity. These patterns were not rigidly fixed, however, and animals were sometimes active at midday.

Nocturnal activity patterns

At night, grey rhebok were active for 57 % of the time, while mountain reedbuck were active for 72 % of the time (Figure 21). No comparative statistical analyses were attempted. Both species were active on and off throughout the night during both summer and winter.

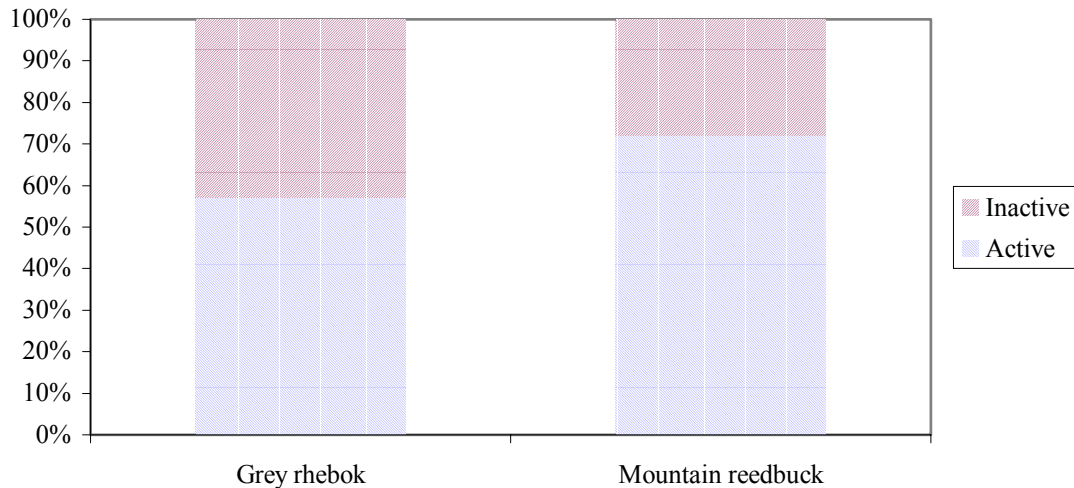


Figure 21. The nocturnal activity budgets of grey rhebok and mountain reedbuck at Sterkfontein.

Ruminating and drinking

Due to the difficulties in observing ruminating behaviour clearly, especially in mountain reedbuck, the number of observation periods in which it was quantified was small and unevenly spread between times of day. This meant that no statistical analysis was possible to compare differences between the two species. No attempt was made to quantify ruminating behaviour at night.

Grey rhebok generally ruminated while lying down, although they occasionally did so while standing. During periods of resting they spent an average of 33 % of the time ruminating, and this gave an overall time spent ruminating of 14 %. Similarly, mountain reedbuck ruminated mostly while lying down, and they spent an average of 40 % of the time ruminating during these periods. This gave an overall time spent ruminating of 22 %.

Grey rhebok groups were seen drinking on 58 separate occasions during diurnal observations in 2000 and 2001 (Figure 22). Most observations occurred between June and September, while none occurred between November and February. No drinking occurred during scan observations. Mountain reedbuck were never seen drinking

during the study period, although there were occasions when they were found very close to the dam, and were thought to have been drinking before being found.

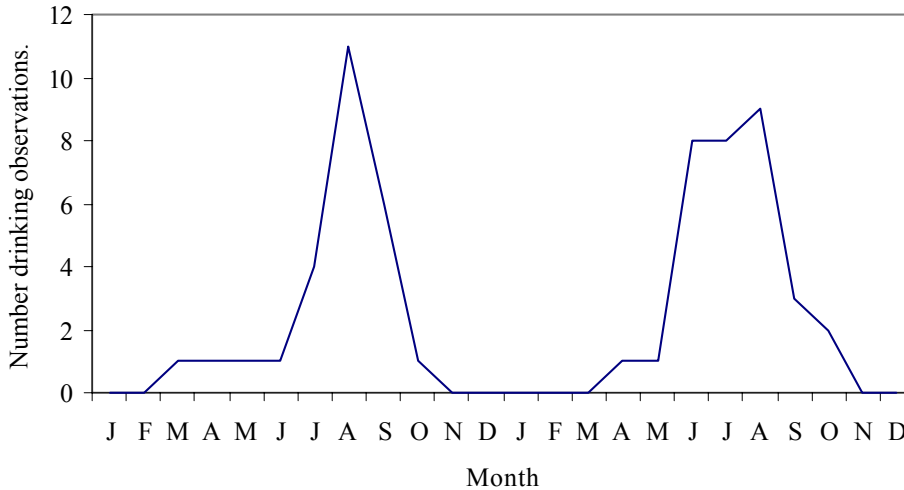


Figure 22. Number of drinking observations made on grey rhebok between January 2000 and December 2001.

Male reproductive behaviour

Harem male grey rhebok were often seen smelling female urine and faeces on the ground, apparently testing for signs of oestrus. This appeared to be opportunistic, however, and was only carried out when males noticed females urinating or defecating nearby. In most cases the males followed this up by marking with their own faeces at the same site. Unlike mountain reedbuck (see below), male grey rhebok did not often test female reproductive condition by sniffing at their rump areas.

Mating behaviour was only seen six times in grey rhebok during the entire study period, and harem males always initiated it. Mating occurred in January (once), March (twice), April (once), May (once), and November (once). The January and November observations were from the same male and female, both of which resulted in successful lambing, and both of which resulted in two of only three lambs born out of season during the study period (see Chapter 3).

A characteristic posture of a sexually aroused male from the beginning of a mating sequence was to stand with his neck at a vertical angle, ears pinned back horizontally, while at the same time licking his muzzle continuously (this was also seen in males responding to females returning to the group after being separated for a short time). The males' black penis was generally visible at these times as well. In all observed mating sequences the male followed the female around continuously, keeping his nose close to her rump, while repeatedly licking his muzzle and sniffing and licking around her tail and vaginal area. He often rested his head on the females' rump or back, and raised his front legs underneath her in a stiff gait (laufschlag). This sometimes continued for a few minutes while the female foraged and flicked her tail. Several mounting attempts then followed, generally with the behaviour described above taking place between consecutive mounts. Ejaculation was marked by a convulsive thrust, after which the male immediately stopped following the female, groomed, and then moved away to feed or lie down.

In all six mating observations, males mated (i.e. ejaculated) more than once with the same female, and often many times in one day. Males also stayed with females between mating episodes and, therefore, performed mate guarding. The time interval between first signs of sexual behaviour and the first mount varied between three and ten minutes, while time intervals between ejaculations of separate copulations varied between five and 45 minutes. On one occasion, the harem male from Group 3 mated with the same female 10 times in a five-hour period between 12h00 and 17h00, after which observations ceased. He was then seen mating with the same female the following morning, albeit for a shorter time period. The receptive period (oestrus) of female grey rhebok was, therefore, at least 24 hours.

Mountain reedbuck males were observed sniffing the rumps of females in all months of the year except August, but in most cases no further sexual behaviour occurred. The average number of tail sniffs recorded for males that were accompanied by more than one female (observations of solitary males and males with only one accompanying female were excluded) was 3.7 times per hour ($n = 33$). Males sometimes showed no interest in females during an observation period, even if females were present, while the most active male sniffed the rump of 28 females in one hour after a large group of females had entered his territory.

Occasionally males followed females for a short period after testing, but extended sexual and mating behaviour was only seen on two occasions (once in June 2001, and once in December 2001). This behaviour was well described by Irby (1976). Males initiated mating sequences by smelling the vaginal area of a female, and continued by following her closely, while smelling and licking around her vaginal area. At these times some females continued feeding, others assumed a tense head down posture, while others ran off. Males then performed the high, stiff legged gait (laufschlag). Multiple mounting attempts were then made, with the final one ending in a convulsive thrust signifying ejaculation. After this males stood quietly for a few seconds and then began grooming. The males were not seen to mate with the same female again the same day, implying that the female receptive period was very short and ended after the first mating. Males were not seen guarding females after mating.

Territorial marking and territory patrols

Harem male grey rhebok marked within their territories using faeces and urine in every month of the year. Marking could be clearly differentiated from the standard defecation behaviour of females and young animals because of the difference in frequency and volume of faeces produced. Whereas the average hourly frequency of defecation by harem males varied between five and sixteen deposits per hour (Table 16), females and young animals only defecated once every one or two hours (pers. obs.). The average wet mass of a single deposit of faeces produced by harem males was 4.9 g (S.D. = 2.4, 3 separate males, n = 54), compared to 36.8 g for females (S.D. = 8.2, 5 females, n = 47). Also, harem males generally defecated at visible markers, such as large tufts of grass, bushes, or termite mounds, while females and young animals often deposited faeces where there were no apparent markers. The markers used by the males often had old faeces around them, although these were not easily seen because they were normally underneath vegetation. It was known that these older faeces predominantly originated from the same males because they were often seen marking at the same places and because territories did not overlap (except to a very small degree at the edges; see Chapter 4). Occasionally, however, males patrolling the edges of their territories located middens that had been deposited by a neighbouring male (pers. obs.). When this occurred, the male being observed invariably sniffed at the site and then marked over the other male's faeces. In addition to the standard

marking behaviour, harem males also marked over the fresh urine and faeces of females if the male was close by when the females defecated.

Table 16 shows the average hourly frequency of territorial marking by three harem males over three different time periods. December to February represented summer, May to August represented winter, and October/November represented the period when yearling males were evicted from their natal groups. This latter period was included to test whether harem males marked more during this relatively “aggressive” time.

Table 16. Average hourly frequency of territorial marking by three harem male grey rhebok over three time periods.

	Male 2		Male 3		Male 4	
	mean	std.dev.	mean	std.dev.	mean	std.dev.
December-February	8.273	4.221	8.842	5.419	8.417	6.215
May-August	12.071	5.929	11.667	7.062	5.167	2.787
October-November	15.917	6.807	13.235	7.155	11.625	6.116

The variation in marking frequency was tested using a two-way ANOVA, comparing the three males and three time periods (Table 17). Data were \log_{10} transformed. There was evidence of a difference between males and strong evidence of a difference between time periods, but no evidence of an interaction. The differences between seasons were not dependent on which males were considered. Multiple pairwise comparisons using the Tukey test indicated that the differences between the males occurred between males 2 & 4 in winter, at which time the marking frequency by male 4 was lower. At other times of the year there were no differences between males. All three males marked their territories more frequently during October/November (the “aggressive” period) than during other months.

Table 17. Two way ANOVA comparing the frequency of territorial marking by three harem male grey rhebok over three time periods. Data were \log_{10} transformed.

Source of variation	Df	SS	MS	F	P
Male	2	0.468	0.234	4.003	0.021
Time period	2	1.138	0.569	9.731	<0.001
Male x time period	4	0.404	0.101	1.729	0.148
Residual	114	6.666	0.059		
Total	122	8.856	0.073		

Harem male grey rhebok were occasionally found away from their herds and appeared to be patrolling the boundaries of their territories and marking these with faeces. Patrolling was most common between November and January, and least common between March and August (Figure 23). Because territorial male mountain reedbuck were often solitary as a consequence of females moving in and out of their territories, and because they did not perform marking behaviour in the same way as grey rhebok, they were not monitored for territory patrols.

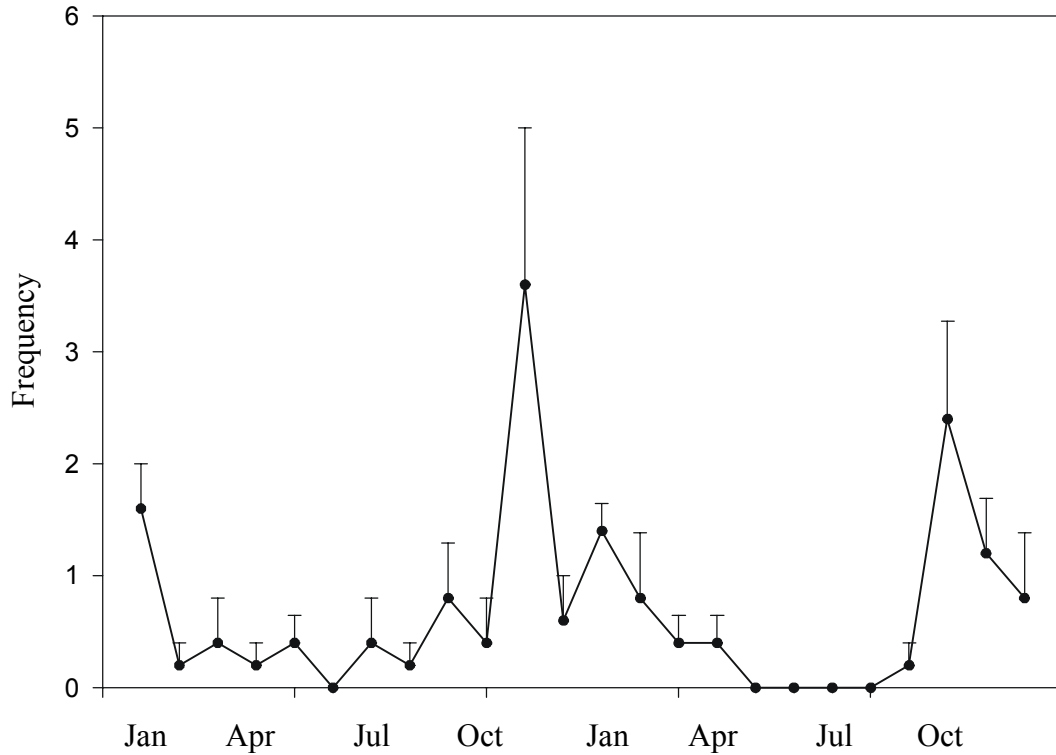


Figure 23. Average monthly frequency of territory patrols by harem male grey rhebok at Sterkfontein. N = 5 males. Error bars represent standard error.

Juvenile submission

In grey rhebok, submissive behaviour of young males reacting to the presence of harem males was first observed at the age of two months. At that stage it was not strongly pronounced, and was characterised by a slight lowering and shaking of the head so that the ears could be seen moving. As the lambs got older, the submissive behaviour became more exaggerated, with the head and body being lowered closer to the ground, and the head shaken more strongly. When they reached the age of nine months the submissive posturing sometimes became more extreme, particularly when the harem male was close, and they lowered their whole bodies to the ground. Between this age and the period of eviction, the young males often approached the harem male with the apparent intent to show submission. Such submissive posturing

was not seen in female grey rhebok lambs, nor was it seen in mountain reedbeek lambs.

There was a significant increase in the frequency of submissive behaviour from the age of two months through to 11 months in male grey rhebok lambs (Figure 24 & Table 18). There was also a highly significant difference between Groups but no interaction. Multiple pairwise comparisons using the Tukey test indicated that young males from Group 3 submitted more frequently to their harem male than those from Groups 2 and 4, while in all Groups young males submitted to harem males more frequently during the period 8 – 11 months age than during the period 2 – 5 months age.

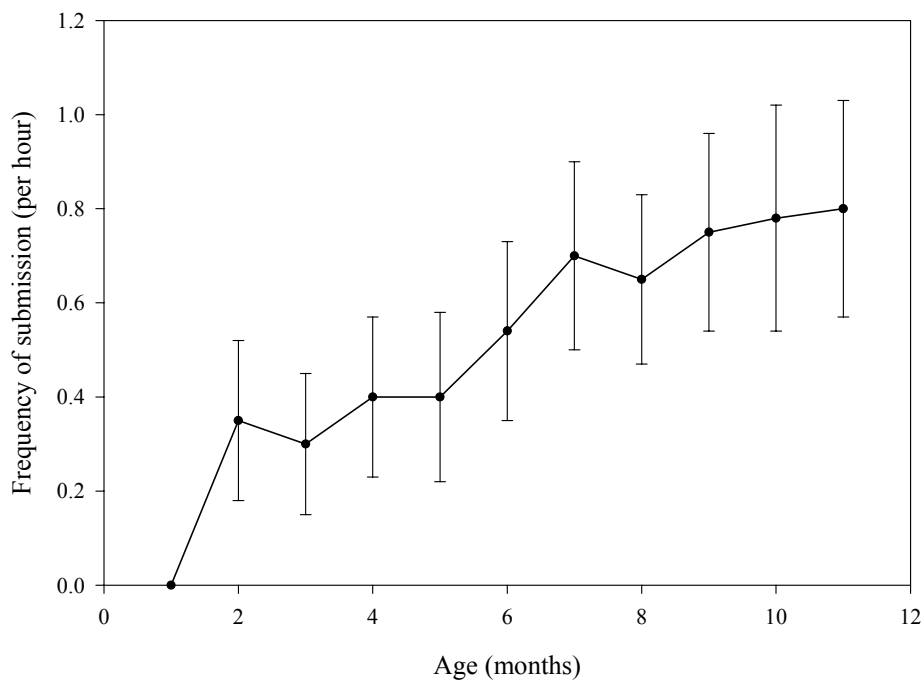


Figure 24. Variation in the frequency of submission in male grey rhebok lambs with increasing age. Error bars represent standard error.

Table 18. Two-way ANOVA comparing the differences in frequency of submissive behaviour between three groups and three age categories (2 – 5 months, 5 – 8 months, 8 – 11 months) of male grey rhebok lambs.

Source of variation	Df	SS	MS	F	P
Group	2	12.012	6.006	6.939	0.001
Age	2	5.485	2.743	3.169	0.045
Group x age	4	0.129	0.032	0.037	0.997
Residual	162	140.211	0.865		
Total	170	157.836	0.928		

Eviction of juveniles

All juvenile male grey rhebok were evicted from their natal groups at the age of about 11 months (Table 19). The actual eviction event was observed twice, while for those events not seen, the eviction date was estimated indirectly as the day after which they no longer mixed with the group.

Table 19. Eviction dates for 13 juvenile male grey rhebok.

Group	2000		2001	
	Eviction date	Eviction age	Eviction date	Eviction age
1	November 29	11 months	Died before	-
2	October 28 & 31	11 months	December 18	12 months
3	November 1 & 3	11 months	December 18	13 months
4	October 25 & 26	11 months	Died before	-
5	November 24	11 months	November 10	11 months
6	November 6	11 months	October 15	11 months

One such eviction event proceeded as follows. The harem male approached the juvenile male, who in turn submitted. Instead of moving away, as was the custom on previous occasions, the adult kept moving towards the juvenile in a threatening

manor, with head lowered trying to butt him. The juvenile tried to move away, but the adult kept following, initially at a walking pace. The more the juvenile moved away, the more the adult followed with increasing pace. The whole herd became disrupted and eventually the juvenile tried to hide behind adult females. The young male eventually got separated and the adult chased him at full running speed in circles and then out of sight. The juvenile male could often be heard making bleating sounds. A few minutes later the adult male returned but the juvenile did not. The latter was never aloud to rejoin the herd again.

For about two months after juvenile males were evicted, the harem males were often found on their own in areas peripheral to their territories, where the young males were known to reside. The harem males appeared to search for the juveniles to reinforce their dominance and chase them away again. One young male was cornered by a harem male and was repeatedly butted and prodded by the latter, but the accidental interference of the observer probably prevented serious injury to the juvenile. Another young male was chased along a fence into the dam and had to swim around the fence, which protruded 25 m into the water, to escape. The adult remained at the water line to make sure the young animal did not return, so if the fence had not been there, the yearling would have drowned.

In addition to the juvenile males, the harem males evicted four young female grey rhebok between eight and 12 months age. One such event was seen, with the harem male aggressively chasing the female around until she moved away from the herd. Two of the females evicted were allowed to return to their herds after about two months, but before being allowed back they remained on the peripheries of their home ranges and avoided contact with their natal groups.

Eviction was not so well defined in mountain reedbuck because juvenile males did not live in harems. Rather, when they reached the stage of being a potential threat to territorial males, they were chased away from their mothers into another male's territory, from where they would be chased again. Territorial male mountain reedbuck were seen chasing juveniles of 6 to 12 months age on five occasions. These chases occurred in April (x 3), September and November, and generally continued for 2-300 m with the young males being forced out of the adult's territory. However, because

the females and young animals were not identifiable, it was not possible to tell whether these young males were able to return to their mothers.

Discussion

Activity budgets

Activity budgets of grey rhebok are not well described by other authors. Beukes (1984) found that foraging was the dominant activity during the day, taking up an average of 56 % of daylight hours. Assuming foraging in this case meant being active, this was very similar to the results of the present study, where grey rhebok males were active for 60 % and females for 56 % of daylight hours.

According to Beukes (1984), this percentage time foraging was higher than expected, because of a positive correlation found by Owen-Smith & Novellie (1982) between body mass and the proportion of time spent foraging in different ungulate species. According to this theory, an antelope the size of grey rhebok (22 kg) should spend only 35 % of the day feeding. Beukes (1984) suggested that grey rhebok might have spent less time feeding at night, which would have compensated for the excess in the day, and that the amount of leaf and branch material that they made use of was relatively small in proportion to the total vegetation available, and this would have increased the time necessary for foraging. However, Beukes' (1984) value of 56 % was for foraging, not feeding, and in the present study grey rhebok spent 28 % (males) and 33 % (females) of daylight hours feeding. This was closer to the predicted value determined using the correlation found by Owen-Smith & Novellie (1982). Moreover, grey rhebok were found to be active at night to the same degree as during the day at Sterkfontein, so this could not have compensated for any excess feeding during the day.

Activity budgets of mountain reedbuck are also not previously well described, with Irby (1981, 1982) only giving a break down of periods of activity and inactivity. Southern mountain reedbuck at Loskop showed an average diurnal activity frequency of 47 % (Irby, 1981). Of this, feeding comprised 62 % and, therefore, made up an average of 29 % of the daily activity budget. Results from Chanler's mountain

reedbuck in Kenya were very similar (Irby, 1982). This compares favourably with the present study, although in the previous examples, standing was considered “inactive”. Roberts & Dunbar (1991) provide the only break down of activity budgets into other behaviours including feeding, resting, standing, moving and other infrequent behaviour. Chanler’s mountain reedbuck at Eburru Cliffs, Kenya, spent 39 % of diurnal observations feeding (males and females were similar) (Roberts & Dunbar, 1991). There were no inter-sexual differences in time budgets across months for feeding, moving and standing, although females lay down more than males.

Klein & Fairall (1986) compared the foraging behaviour of a grazing antelope, the blesbok, with that of a mixed feeder, the impala. They found that the grazer spent less time feeding and more time resting than the mixed feeder, and the reasons for this were thought to be associated with the formers efficiency as a bulk feeder, as well as the longer time required for digestion of its coarser diet. In a similar way during the present study, the grazing mountain reedbuck spent more time resting during the day than the browsing grey rhebok.

Unlike with the blesbok and impala (Klein & Fairall, 1986), however, the present study did not find a difference in the time spent feeding between grey rhebok and mountain reedbuck. This may be partially because mountain reedbuck were selective grazers (Irby, 1976), unlike blesbok, and would have taken longer to select food items than bulk grazers. In addition, although grey rhebok probably required lower quantities of food than mountain reedbuck (an assumption made because they have a slightly lower body mass, and are browsers), their food was more spread out and smaller in size per item (pers. obs.). It is possible, therefore, that the differences in food quantities required (greater for mountain reedbuck) and gathering times (less for mountain reedbuck) of the two species cancelled each other out, but this remains to be tested.

Diurnal activity patterns

There was a common trend to the diurnal activity patterns of both grey rhebok and mountain reedbuck at Sterkfontein, and this was that animals generally rested more in

the middle of the day, and fed more in the early morning and late afternoon. The pattern was more accentuated in mountain reedbuck, which were especially active in late afternoon. Moreover, mountain reedbuck tended to rest more than grey rhebok in all periods. Additionally, there were no obvious seasonal differences, with both species following similar patterns in both summer and winter.

There was, however, a difference in the general sequential pattern of behaviour through the course of a day. Grey rhebok tended to be active for up to two hours, then inactive for a similar period, then active again. They showed no periods of extended activity or inactivity, and continued the pattern throughout the day and night. Mountain reedbuck had more fixed periods of activity and inactivity whereby they were generally active in the early morning and late afternoon, and inactive during midday.

Esser (1973) found a pattern of increased foraging activity in the late afternoon in grey rhebok, which was similar to the present study with the addition that grey rhebok were more active in the morning as well as late afternoon relative to the middle of the day. Beukes (1984) indicated that the activity patterns of the male and females within a harem herd alternated, so that when the male was active, the females were not, and vice versa. This was suggested to result from the advantage conveyed by always having some animals vigilant. In contrast, the present study found that during most observation periods males and females were generally active or inactive at the same time, although there were short periods during which some animals were active while others were inactive. It was a common occurrence that once one animal within a herd lay down, the rest followed suit within a few minutes.

Beukes (1984) found that grey rhebok spent more time feeding in winter (June) than summer (December), although there was no seasonal influence on the overall activity budget. The feeding differences were thought to result from changes in the availability of young plant material (leaves and branches) and protein content caused by changes in rainfall. There were no seasonal differences in the feeding behaviour of grey rhebok at Sterkfontein, which was perhaps surprising considering the degree to which forbs dried up or died at Sterkfontein towards the end of winter (pers. obs.).

The activity patterns of mountain reedbuck in the present study were similar to those found by Irby (1981, 1982) at Loskop, and in the Rift Valley, Kenya, as well as by Roberts & Dunbar (1991) at Eburru Cliffs. The two Kenyan studies were conducted on Chanler's mountain reedbuck, a subspecies of the southern mountain reedbuck found in South Africa. These studies found that mountain reedbuck had well defined diurnal cycles of activity, with distinct resting periods around midday. The activity cycles of males and females were closely correlated, with temperature being an important determinant of activity. In dry months, animals were more active between 06h00 and 09h00 than in wet months, but less active between 14h00 and 16h00. In the present study no statistical seasonal differences were found in activity levels, although descriptively mountain reedbuck were more active between 06h00 and 09h00 in the dry months relative to the wet months. The diurnal cycles found by Irby (1981, 1982) and Roberts & Dunbar (1991) were more extreme than was the case at Sterkfontein, with the earlier studies finding that mountain reedbuck became almost totally inactive in the middle of the day. One factor that could have been responsible for this difference was the temperature at midday. Maximum diurnal temperatures at Eburru Cliffs were 35° C in summer (Roberts & Dunbar, 1991), while at Loskop they were 32° C (Irby, 1981). Maximum diurnal temperatures at Sterkfontein were only 25° C in summer, and this may have allowed animals to remain active occasionally at the warmest time of day.

Roberts & Dunbar (1991) also found that activity and feeding levels of mountain reedbuck, as well as the proportion of time spent ruminating, were lower in the wet season when forage quality and availability were higher. No such seasonal differences were found in activity habits of mountain reedbuck during the present study where activity levels were compared between summer and winter. Patterns of rumination were not compared between seasons.

All previous studies found that mountain reedbuck exhibited a consistent diurnal movement pattern, wherein animals habitually descended slowly in the morning from the upper slopes of the hills they inhabited, remained on low ground during the early afternoon, and returned up slope in the late afternoon. Temperature was considered the most likely proximate factor regulating this movement pattern. Similar diurnal

movement patterns in mountain reedbuck at Sterkfontein did not occur. This was probably because the hillsides on which they were observed were not as high as occurred in the previous studies, and the subsequent temperature differences between different heights on slopes were not as extreme. Mountain reedbuck did often descend to lower slopes or to the water at night, but the reasons for this were not tested. Temperatures at night, especially in winter, would be coldest at the bottom of the slopes near the dam, so it is unlikely that the movement down slope at night was temperature driven. It may have been related to human activities.

Nocturnal activity patterns

Grey rhebok were active at night to a similar degree (57 % mixed gender) as they were during the day (60 % males, 56 % females). No previous studies have monitored activity at night, although Beukes (1984) suggested that they might be less active at night. Clearly this is not the case, with grey rhebok conducting the same activities at night as they do during the day.

Mountain reedbuck were more active at night (72 % mixed sex) compared with the day (43 % males, 46 % females). This agreed with Roberts & Dunbar (1991), who found that Chanler's mountain reedbuck in Kenya were also active throughout the night, with periodic peaks and troughs in feeding and resting. Activity levels tended to be higher at night than during daylight, with less pronounced resting periods.

In contrast, some other antelope species including impala (Jarman & Jarman, 1973) and blesbok (Du Plessis, 1968) are reported to be less active at night.

Ruminating and drinking

Both species in the present study ruminated primarily while lying down. This was similar to blesbok (Klein & Fairall, 1986), but different from impala (Klein & Fairall, 1986; Oliver, 2002), with the latter ruminating while standing. Grey rhebok ruminated for 14 % of daylight hours compared to 22 % by mountain reedbuck. This fairly small difference was probably the result of differing digestibility of their food plants.

Grey rhebok at Sterkfontein regularly drank during the dry period at the end of winter when their food plants were low in moisture (pers. obs.). On some occasions animals were seen eating dead plant material that was almost completely lacking any water content (pers. obs.). Grey rhebok were previously recorded as being water independent (Skinner & Smithers, 1990) but it is possible that at the end of winter there was not enough moisture in their food to provide for all their needs. It was not tested whether drinking was obligatory during the present study, but the regularity of this behaviour at the relevant time during both 2000 and 2001 indicates that it might have been. Also, all six herds of grey rhebok that lived within the study area (see Chapter 4) had access to water (the dam), and although there was sufficient space left within the study site to hold another herd, this did not happen. The potential site would have had no access to the dam, and it is possible that the lack of water access excluded the possibility of another herd being founded. This was not tested, however.

Mountain reedbuck were never seen drinking during the study period, although they are recorded as water dependent (Skinner & Smithers, 1990). It was unusual for them to be on the lower slopes during the day, hence the lack of drinking observations, but they were sometimes found very close to the dam at night, and this was probably the time when they did most of their drinking. Additionally, there was a small area on the main hillside that almost always had a small amount of freestanding water that originated from a spring. Mountain reedbuck were often seen in the vicinity of this area, although they could never be observed closely enough to determine whether they were drinking.

Irby (1976) observed mountain reedbuck drinking during daylight hours in all seasons at Loskop, but at such low frequencies that no seasonal comparisons could be made. No drinking observations occurred at other sites (Irby, 1976), although as occurred during the present study, animals were seen near water in Ohrigstad, Giant's Castle, and the Cole Ranch (Kenya).

Male reproductive behaviour

An important difference in the reproductive behaviour of grey rhebok and mountain reedbuck was that grey rhebok harem males rarely sniffed the vulva region of their

herd females (although they did sometimes test urine on the ground), while mountain reedbuck did this in almost every month of the year, apparently at every chance they had. There were two probable reasons for this difference. The first, and most important, was that grey rhebok males defended females, and had access to them at any time they wanted, and at all times of the year. They were only separated from these females for short periods when they patrolled their territories, and they very rarely had competition from other males. In contrast, territorial male mountain reedbuck only had temporary access to females because they defended resources that females selected preferentially (steep slopes). Males, therefore, needed to test the females every time they roamed into their territories to check for signs of oestrus. They had regular competition from other males because every time the females moved out of one territory, they consequently moved into another one, whereupon a different male investigated them. The second reason was that grey rhebok are seasonal in their breeding behaviour (with the exception of rare out of season births, see Chapter 3; also Skinner & Smithers, 1990), while mountain reedbuck are generally more aseasonal (although in the present study, material obtained from culled animals showed that mountain reedbuck were fairly seasonal, see Chapter 3; also Irby, 1979). Breeding males from aseasonal species should test females for signs of oestrus for more extended periods of the year relative to seasonal species.

A second difference between grey rhebok and mountain reedbuck occurred in the mating behaviour. Although both species showed similar behaviour leading up to and including ejaculation (including multiple mounting attempts before ejaculation), they differed in the number of times males mated with the same female (i.e. number of ejaculations), the time period over which mating took place (i.e. the length of oestrus), and mate guarding. Harem male grey rhebok mated with a specific female in oestrus many times in one day, and over the period of several hours. Sometimes it continued into a second day. After the final mount and ejaculation of one mating, there was a transitory period when normal activities resumed before the male started showing interest in the female again. Mate guarding, and the virtual permanent defence of females, meant that harem males were almost guaranteed to be the fathers of all the offspring in their herd.

Territorial male mountain reedbuck, however, only mated once with a certain female, and after ejaculation there were no more attempts. Irby (1979) did not establish the duration of female receptivity. As with the present study, males normally only mated once with females, but one observation was recorded where a male copulated with a female at least three times during one 12-hour period. This is in contrast to the findings of the present study, but implies that oestrus lasts a short time in mountain reedbuck, which is more in line with mating behaviour of other antelope species. Males did not perform mate guarding, and this may have been partly because females can move between the territories of different males whenever they chose. As a result, a male that does guard a female during her receptive period would be wasting his time if that female moves into a separate territory while still in oestrus and mates with another male.

Mating events were not seen very often, so cannot be used as a measure of seasonality. The observations of grey rhebok lambs and foetuses of culled mountain reedbuck are a better guide for seasonality (see Chapter 3).

Territorial marking and territory patrols

Harem male grey rhebok performed distinct marking behaviour within their territories during all months of the year using faeces and urine, while territorial male mountain reedbuck did not. Although both species were territorial and prohibited other males from using their areas, the differences in social structure of the two may be the reason for the difference in marking. Grey rhebok males maintained a harem of females year-round, while mountain reedbuck males did not; they only maintained a territory from which females came and went. Also, grey rhebok home ranges, which were the same areas as the territories (see Chapter 4), were larger than those of male mountain reedbuck, and it was uncommon for two grey rhebok herds to be in sight of each other, so visual cues between harem males, such as posturing, were not often used. In contrast, territorial male mountain reedbuck were more often within view of each other, so visual cues between them were used regularly (pers. obs.), possibly reducing the need for odour cues.

Many species demarcate their territories using faeces, because faeces are a good substrate for glandular secretions, can be used as visual signposts, and have a low energetic cost to produce (Gosling, 1985). Marking is most commonly carried out by males that have established dominance over their peers in contests and is almost universally linked to agonistic behaviour, forming a central part of many ritualised contests between males (Gosling, 1990). However, marking does not often repel intruders, and in some species non-territorial males carry it out as well. At Sterkfontein, juvenile male grey rhebok that still belonged to their natal harem herds never performed marking behaviour, but one intruding male (from outside the study area) did mark within another male's territory before being chased out.

Other southern African antelope species that use faeces include, amongst others, black wildebeest, springbok, klipspringer, oribi, and steenbok (Skinner & Smithers, 1990). These species have differing social structures, and none have the same harem structure of grey rhebok. There seems, therefore, to be no specific type of social structure that results in territorial marking using faeces. Unlike some of the abovementioned species, such as the oribi, the middens produced by grey rhebok are small in scale and cannot be used as a visual signpost because they are generally hidden under vegetation. They may, however, be used as olfactory cues, and indeed males were occasionally seen sniffing middens on the edges of their territories that had been deposited by a neighbouring male (pers. obs.). When this occurred, the male being observed invariably marked over the other male's faeces.

Harem male grey rhebok marked their territories in all months of the year, but the frequency of marking was highest at the time when juvenile males were evicted from their natal groups. For most of the year, harem males had few competitors to contend with, and during the present study only three intruding males were seen within the study site (only one of these challenged for a territory) (see Chapter 3). During the period when juvenile males were evicted, however, there were many young males roaming around searching for new areas to live in and territories to start. This would have resulted in an increase in the number of interactions between intruding males and harem males, and this may have caused the increase in frequency of territorial marking by harem males to strengthen the odour signals that indicate their presence (Gosling, 1990). It was at this time as well that harem males moved away from their

herds more frequently to patrol their territories, and this fits with the increased marking rate.

The use of faeces in marking is constrained by production, and their availability may limit the marking rate in species that use them to advertise territorial boundaries (Komers, 1996), or mark over the faeces and urine of females (Moodie & Byers, 1989). Animals should then regulate the volume of each mark and prioritise the placement of marks to areas where their value as an advertisement is greatest (Brashares & Arcese, 1999). Harem male grey rhebok marked more frequently and with smaller volumes of faeces than juvenile males and females, so they were apparently constrained by production. However, they did regularly mark well within their boundaries, not just on the edges (pers. obs.).

In contrast, territorial male mountain reedbuck did not clearly mark areas with faeces or urine, even though they were territorial and defended their areas from other males. Irby (1976) also found that mountain reedbuck males did not utilise obvious advertisement devices such as prominent glandular secretions or defecation along territorial boundaries. Instead they used optic marking displays comprising a head up, alert posture with stiff legged jumping gait in conjunction with short whistles. The use of whistles as a territorial marker could not be differentiated from their use as warning signals.

Juvenile submission

As juvenile male grey rhebok got older they became more submissive to harem males, and were most submissive in the last three months before being evicted. This makes sense because the harem males would have been expected to become more aggressive towards these young males as they approached sexual maturity and become more of a threat to the dominance of the adults.

Submissive behaviour was not observed in juvenile male mountain reedbuck during the present study, and the only related behaviour was territorial males chasing young males around occasionally. Irby (1976) did not record any submissive behaviour amongst mountain reedbuck either.

Eviction of juveniles

All juvenile male grey rhebok were evicted from their natal herds at the similar age of 11 months. This generally occurred between October and November, shortly before new lambs were born (see Chapter 3). The main reason for the evictions was probably that the young males were approaching sexual maturity and would have become a threat to the mating rights of the harem males. Additional benefits arising from their expulsion would have been incest avoidance and reduction in intra-specific competition for feeding resources just before group sizes increased with new lambs. The reason for eviction of juvenile female grey rhebok was less clear when it is considered that some of these females were allowed back into their natal herds. Incest avoidance would be a likely cause of their removal, but one such female was mated by her father after returning to the herd and successfully produced a lamb.

Juvenile male mountain reedbuck were expelled from the territories of adult males sometime after the age of nine months. Irby (1979) found that most males left or were forced from their groups with which their mothers were associated between the ages of nine and 15 months. Separation was described as a slow process characterised by aggressive behaviour initiated by the adult male followed by long periods when the immature male was ignored. Tolerance of immature males within groups varied between individual adult males and between populations.