Chapter 4

HOME RANGES AND HABITAT

Introduction

A home range consists of a more or less restricted area within which an animal moves when performing its normal activities (Harris *et al.*, 1990). Measuring home range size, shape, and pattern of utilisation is important for ecological studies concerned with population density, foraging behaviour, habitat selection, and spacing of individuals. In species that are cropped for meat production, collection will be most efficient and economical if animals are kept at or near an optimum population density. If animals are over-stocked there may be competition, resulting in the loss of condition in many and possibly the deaths of some. With the translocation of game becoming increasingly more common, it is important to know how many animals can be introduced to an area without exceeding the ecological carrying capacity. Even when animals are conserved for reasons other than meat production, it is pointless introducing them if the resultant competition will cause the loss of animals through emigration or death.

For grey rhebok, Oliver *et al.* (1978) recorded an average home range size of 76.7 ha for eight males (range 31 to 135.4 ha) at the Highmoor State Forest in Natal, while two females had home ranges of 43.1 and 117.1 ha. In the Free State, home ranges averaged 61 ha with a range of 46 to 187 ha (Ferreira, 1983). Ecological densities were 1/42 ha in Natal (Oliver *et al.*, 1978), 1/23 ha to 1/57 ha in the Drakensburg (Rowe-Rowe, 1994), and 1/15 ha in the Bontebok National Park (Beukes, 1984). The two social groups recorded were solitary males and family parties (Ferreira, 1983; Beukes, 1984). Family groups were small, numbering up to 12 individuals, and comprised an adult male with a harem of several females and young.

Mountain reedbuck males at Loskop had a mean territory size of 28 ha while females had a mean home range of 57 ha (Irby, 1976). Males occupied their territories throughout the year regardless of the presence of females. In Kenya, male territories were smaller and varied between 3.1 ha and 5.5 ha (Dunbar & Roberts, 1992). Ecological densities varied between 1/15 ha and 1/21 ha at Loskop (Irby, 1976), and 1/11 ha and 1/32 ha in the Drakensburg (Rowe-Rowe, 1994). Social organisation consisted of territorial males, non-territorial males, herds of females with young, and bachelor herds (Irby, 1976). Female herds were unstable and normally consisted of small groups of 3 - 8 individuals, with females and young moving from herd to herd and between territories of different males.

The two species utilise similar marginal habitats and are of a similar body size, yet have different social structures and eat different foods. Although their home ranges have been determined before, the present study allowed for a comparison between the two in an area in which they were sympatric, while the previous studies were not particularly rigorous in their assessments, nor did they use modern statistical methods of determining range use. As with many ungulates, grey rhebok and mountain reedbuck are often translocated between nature reserves and onto private land, so it is important to know the spatial limitations of new areas for re-introductions or artificial population increases. There were three aims to this component of the study:

1) To determine home range areas of grey rhebok and mountain reedbuck at Sterkfontein;
2) To compare and contrast range use between the two species;
3) To investigate habitat and other environmental variables that might influence range use within both species.

To accomplish these aims, the following questions were considered:

a. What are the home ranges of both species and how do they compare?
b. Within each home range, how is the space used (i.e. is the space used evenly or are there core areas)?
c. Are there any seasonal differences in home range use?
d. How much overlap is there within and between species?
e. What are the ecological densities of both species?
f. How do the food densities vary within the study site?
g. Within and between species, what are the causes of variation in home range size?

Methods

Study site and animals

The grey rhebok herds at Sterkfontein were found to be very stable for most of the year (see Chapter 3) and females accompanied males almost everywhere. As a result, home ranges were calculated for herds rather than individuals. Six harem herds were monitored within the main study area between February 2000 and April 2002. During this time there were two breaks of longer than two weeks in which no monitoring was done on any animals. These were 12 weeks between February and April 2001, and three weeks in August 2001. The herds were identified numerically as Groups 1 through to 6 and this was based on identification of harem males, certain females, group size and geographic position within the study area (because herds used exclusive home ranges). Five of these (Groups 1, 2, 3, 4 & 6) were monitored for the entire period, while Group 5 was only observed until September 2001. After this it ceased to exist. There were no other grey rhebok herds within the study area.

Mountain reedbuck herds were unstable and males did not maintain harems (Chapter 3), so males were treated individually in the calculation of home ranges. Ten territorial male mountain reedbuck were monitored within the main study area between February 2000 and April 2002, excluding the two periods mentioned above. Only one male was present for the entire period, while the others came and went at different times. The adults were identified as Males 1 through to 10 according to their horn shapes and geographic positions. There were other males present within the study area, but these were considered non-territorial and were difficult to identify. They were not included in the study. Female mountain reedbuck were not systematically monitored for home range analysis because it was difficult to identify them. However, three females were collared and were monitored to a limited extent.

Geographic positions

Geographic positions of grey rhebok herds were recorded in a discontinuous manner (Harris *et al.*, 1990) approximately four times a week. Their positions were only fixed once a day per group to ensure independence of data points and these were always recorded at the location of first sighting to avoid observer interference. This generally occurred at different times on different days because of variability in the order in which groups were located. Animals were located by sight and positions determined by triangulation using compass bearings from two known landmarks. These comprised telephone poles, large boulders, trees, etc., and the geographic positions of these were determined using a GPS (5 m estimated positional error). Groups 4, 5 and 6 occurred in hilly terrain and it often took longer to find them than Groups 1, 2 and 3. This meant that they were not always located if time was limited and the total number of positional fixes for them was, therefore, less.

Mountain reedbuck males were located discontinuously and their positions fixed in the same way as grey rhebok. They were located approximately three times a week, and the number of fixes varied between animals because of the different lengths of time over which they were in the study area and the degree of difficulty of location.

Triangulated bearings were transformed into Universal Transverse Mercator (UTM) coordinates using a mathematical equation written by the author, and these were entered into the software package CALHOME (U.S. Forest Service, Pacific Southwest Research Station) for home range estimation.

To assess the accuracy of the triangulation, coordinates of 20 positions were estimated from varying distances to landmarks, and these then compared with GPS coordinates of the same positions. Distances of 400 m between the animals and landmarks yielded errors of up to 30 m, while distances over 2 km were found to be unreliable, occasionally giving errors of 200 m. As a result, triangulation was carried out using the closest possible landmarks and these were never more than 400 m away. This meant that the maximum positional error of the coordinates used was 30 m. The 5 m GPS errors of landmarks were not taken into account because they were fixed for the entire study and did not vary every time a group of animals was located.

Home range estimation

Studies have suggested that because many home-range analytical techniques have a number of disadvantages, no one method is likely to be entirely satisfactory and at least two should be used in any study (Worton, 1989; Harris *et al.*, 1990). The two methods chosen for the present study were minimum convex polygon (MCP) and adaptive kernel (AK). The MCP method was selected because it has been frequently used by other studies and generally allows comparisons of results. Its faults include the tendency to incorporate areas that are not visited by the subject animals (Harris *et al.*, 1990) and an inability to indicate intensity of range use that can be used to visualise core areas (Gallerani-Lawson & Rodgers, 1997). While nothing can be done about the latter, the first problem can be reduced by using a 95 % MCP, whereby 5 % of positions that lie furthest from the centre of the home range are removed from the analysis (Harris *et al.*, 1990). However, when analyses are run with less than 100 % of the fixes, results between different software programmes are less comparable (Gallerani-Lawson & Rodgers, 1997).

The more recent AK method is being used more frequently in ecological studies (Harris *et al.*, 1990; Gallerani-Lawson & Rodgers, 1997) and is an elegant and powerful technique representing range configuration (Cresswell & Smith, 1992). It is an approach to home range analysis based on probability density estimations, so that the home range is described in terms of a probabilistic model. It is very useful for estimating the utilisation distribution density because there are no constraints placed on the form of the utilisation distribution (Worton, 1989). Due to the non-parametric statistical approach of its calculation, the method makes no assumptions about the distribution of the data (Gallerani-Lawson & Rodgers, 1997), although each point should be independent. Isopleths of 95 % and 50 % are generally used to estimate home-range areas and core areas respectively, and it was the intent to investigate the latter that motivated the use of this technique. During analyses, the number of grid cells was set at 30 cells x 30 cells, while the programme was set to select its own optimal bandwidth or "smoothing parameter" (Worton, 1989) using a least-squares cross validation (LSCV) score, which is a measure of how well the bandwidth fits the data

To ensure that enough positional fixes were collected to estimate home ranges reliably, accumulative home range areas were plotted against the number of positions fixed, and the point determined when an asymptote was reached. This was defined as the point after which additional locations resulted in a minimal increase in range size

(Harris *et al.*, 1990). After an asymptote is reached, additional positions still cause the home range area to fluctuate slightly above and below an average value (Harris *et al.*, 1990) and, because the number of positions differed between the groups, the home range area estimated for the final position may have been slightly above or below average, depending on whether it was increasing or decreasing at the time of the final fix. To reduce this problem an average home range area was calculated for each group using values from every 25th position after the asymptotic number was reached.

Vegetation surveys

Ten vegetation surveys were carried out between October 2001 and March 2002. Five surveys were done on steep slopes (>10°) while five were done on flat or gently sloping ground. They were done in pairs so that each steep slope had a corresponding flat area close by. Surveys were carried out using the step point method adapted from Barnes (1976), whereby observations were made every 1 m along transects of 200 m. At every point the nearest grass and nearest edible forb species were recorded and at every fourth point the distances to these plants were measured. Edible forbs were those that grey rhebok had fed on during the present study (pers. obs.). The aim of the surveys was to determine the plant species densities in different parts of the study area.

Investigating causes of variation in home range sizes

There are a number of ecological parameters that could influence home range size in antelope species. Those thought to be relevant to grey rhebok and mountain reedbuck in the present study were assessed and values assigned to them for each home range. These values were then incorporated into a Backward Stepwise Regression analysis with the aim of determining which parameters were the best predictors of home range size. The parameters selected differed between grey rhebok and mountain reedbuck because of their different social structures and ecological requirements.

For grey rhebok the variables selected were the following:

1) The average number of animals in each group, calculated from monthly counts;

2) The area of steep slope (>10°) within each home range, calculated using aerial photographs and knowledge of the terrain. Slope gradients were determined using a clinometer. This parameter was included because steep slopes are considered a standard requirement for grey rhebok habitat (Skinner & Smithers, 1990), and it appeared that herds with greater amounts of steep slope available had smaller home ranges;
3) The average distance to safety, defined as the distance that an animal had to move to get out of sight from a threat. This was calculated using aerial photographs and an overlay grid, whereby escape distances were estimated from 10 grid positions within each home range. This parameter was selected because grey rhebok do not hide when they feel threatened, but rather run out of sight or to a position far from the danger (Ferreira, 1983; pers. obs.). It was, therefore, thought to be a good measure of evasive behaviour.

There were other parameters that might influence home range sizes of grey rhebok in other geographical areas, but these were left out of this analysis because they were not thought to be relevant to the conditions of the present study. These parameters and the reasons for their exclusion are listed below.

The density of edible forbs is a direct measure of the amount of food available for grey rhebok within a given area, but was not included in the analysis because a two-way ANOVA (Table 11) found no evidence of a difference in densities between steep and flat areas. There was, therefore, no point in considering forb density as a predictor of home range size.

Veld age, measured as the time elapsed since the last fire, has been shown to influence habitat selection in grey rhebok (Beukes, 1984), but was not included in the analysis because it was the same throughout the study area. Rainfall was not included because variation in the study area was negligible, while distance to water was excluded because the home ranges of all grey rhebok herds adjoined sections of the dam and all had access. Aspect was not included because most steep slopes faced west over the dam.

An important factor in grey rhebok ecology is the concealment of lambs for about one month after birth. Observations indicated that grass over 40 cm in length was sufficient to conceal lambs (pers. obs.), and in December/January when lambs were born, almost all parts of the study area had a grass cover that was as long or longer than this. Because most areas were similar in this trait, this variable was excluded.

For mountain reedbuck the variables selected were the following:

1) The average number of attending females, estimated from counts of females either with territorial males or within their home ranges. This was included because the sign of a good territory for a mountain reedbuck male has been shown to be one which females regularly use (Dunbar & Roberts, 1992). Also, a good territory is often subject to more intensive competition and tends to be compressed (Dunbar & Roberts, 1992);
2) The amount of steep slope available, found to be important for females in Kenya (Dunbar & Roberts, 1992);
3) The area of cover for shelter and hiding, calculated using aerial maps and knowledge of the terrain. Mountain reedbuck tend to hide when threatened and use shelter more than grey rhebok. Cover in this sense indicates long grass (> 80 cm) or very rocky areas.

For mountain reedbuck, grass density can be considered a direct measure of the amount of food available, but was not included for the same reasons as given for forbs and grey rhebok. Veld age, rainfall, distance to water and aspect were also not included for the same reasons given for grey rhebok.

Statistical methods

Analyses of home range areas were carried out using the software package CALHOME. Differences between summer and winter home range areas were investigated using paired t-tests. Grass and forb densities on different slope gradients were compared using a two-way ANOVA. In an attempt to find factors that influence the use of home range area, Backward Stepwise Regression analyses were conducted using variables thought most likely to affect use of space.

Results

Accumulative home range area graphs

The approximate number of locations required for reliable home range analysis in grey rhebok herds varied between 80 and 180 positions (Appendix I). Group 5's home range reached an asymptote at 80 positions, but later the harem male died and was replaced by its neighbour. The home range subsequently increased again but did not level out. The number of locations required for mountain reedbuck varied between 50 and 120 positions (Appendix I). The graphs for Males 8 and 10 did not reach asymptotes.

Home ranges areas

The positions of the home ranges of grey rhebok herds did not perceptively change over the entire study period, so their geographic positions invariably indicated which herd they belonged to.

Ninety-five percent MCP home ranges of grey rhebok herds varied between 23.3 ha and 104.1 ha (Table 7), with an average of 57.9 ha, while 95 % AK home ranges varied between 30.7 ha and 113.5 ha. In all cases, the 95 % AK values were larger than their corresponding MCP values. Fifty percent AK areas varied between 7.5 ha and 29.1 ha, corresponding to 24 % and 29 % of their respective 95 % AK home ranges. The smallest ratio of 50 % to 95 % AK was 9 % for Group 1. Groups 4 and 5 were only located for 17 months (143 and 147 positions respectively) because Group 4 ceased to exist in September 2001, while the dynamics of Group 5 changed at the same time.

Table 7. Home ranges of six grey rhebok harem herds between February 2000 and April 2002. During analyses, the number of grid cells was set at 30 cells x 30 cells. MCP = minimum convex polygon, AK = adaptive kernel.

Group	Period observed (months)	Number of positions	Asymptotic number	Bandwidth (m)	MCP 95 % (ha)	AK 95 % (ha)	AK 50 % (ha)
1	24	287	150	244	73.7	108.5	9.7
2	24	327	180	185	76.8	100.1	29.1
3	24	395	150	219	104.1	113.5	22.4
4	17	143	100	172	39.7	63.3	7.8
5	17	147	80	131	23.3	30.7	7.5
6	24	205	80	140	29.9	37.8	9.4

Differences between summer and winter home range areas were investigated for Groups 1, 2, 3 and 6 (Table 8). Groups 4 and 5 were omitted because they had insufficient positional fixes for comparison. Summer months were October to March, while winter months were April to September. A paired t-test found no evidence of a seasonal difference in home range sizes ($t = -0.055$, $df = 3$, $p = 0.960$).

Table 8. Seasonal variation in home range areas of four grey rhebok herds.

Group	95 % MCP Summer	95 % MCP Winter
1	82.4	62.2
2	72.1	77.7
3	88.4	102.3
6	28.3	27.4

Male mountain reedbuck home ranges were smaller than grey rhebok herd home ranges (Table 9). Ninety-five percent MCP values for male mountain reedbuck varied between 7.1 ha and 21.4 ha, with an average of 14.8 ha, while 95 % AK values varied between 8.5 ha and 29.4 ha. Fifty percent AK home ranges varied between 1.8 ha and

4.1 ha, corresponding to 21 % and 14 % of their respective 95 % AK home ranges. The smallest ratio of 50 % to 95 % AK was 8 % for Male 1. Home ranges of Males 8 and 10 were probably underestimated because sufficient positions were not collected for accumulative area graphs to reach asymptotes (Appendix I).

Table 9. Home ranges of 10 territorial male mountain reedbuck between February 2000 and April 2002. During analyses, the number of grid cells was set at 30 cells x 30 cells. MCP = minimum convex polygon, AK = adaptive kernel, * = asymptote not achieved.

Male	Period observed (months)	Number of positions	Asymptotic number	Bandwidth (m)	MCP 95 % (ha)	AK 95 % (ha)	AK 50 % (ha)
1	17	101	70	98	16.3	23.2	1.9
2	24	127	90	108	21.4	29.4	4.1
3	17	143	50	76	9.3	13.8	2.1
4	16	135	120	114	17.0	26.0	3.0
5	19	157	90	92	14.7	22.5	3.9
6	22	118	50	102	17.9	27.8	3.7
7	18	120	80	80	7.1	8.5	1.8
8	15	99	*	90	16.8	21.3	3.1
9	20	114	80	86	14.5	21.9	3.3
10	12	74	*	94	13.3	17.5	3.7

Figure 10 shows the overall home range distributions and core areas of six grey rhebok herds in the main study area. The outermost boundaries used are from the 95 % MCP values because it was felt that they gave the best visual representation of the true extent of the home ranges, while the 95 % AK values projected a statistically estimated boundary that often exceeded the known borders of those same home ranges (pers. obs.). Core areas are, however, represented by 75 % and 50 % AK values because this method estimates utilisation distributions statistically, while the MCP method (50 %) can only determine the geographic centre of the range, which may have no bearing on the actual utilisation of space.

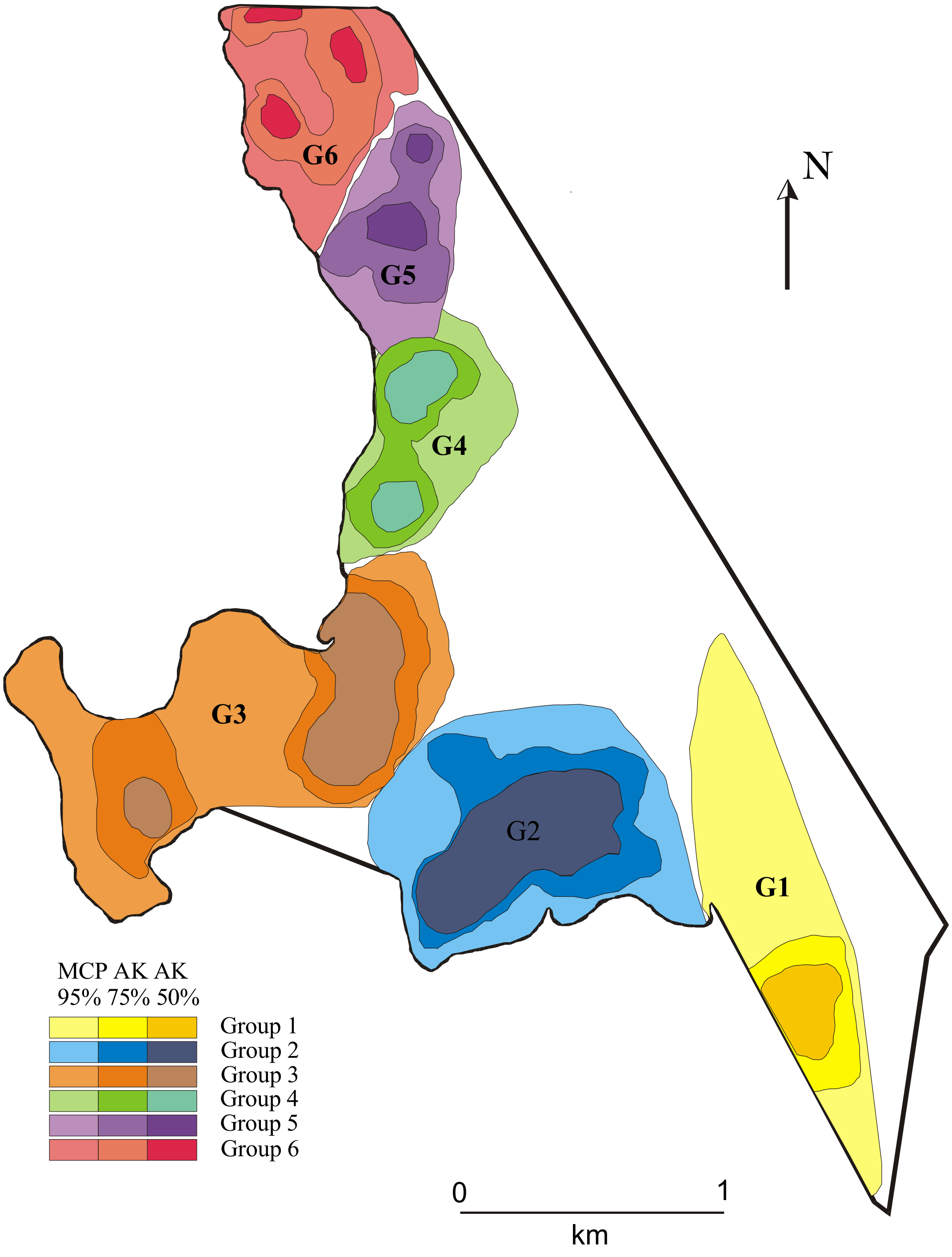

Figure 10. Home ranges of six harem herds of grey rhebok in the main study area of Sterkfontein between February 2000 and April 2002. External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 75 % and 50 % AK results.

All the herds occasionally strayed slightly into the home ranges of their neighbours, but these movements were temporary and usually only occurred after the initial position of the herd had been fixed for the day. Such positions were, therefore, not often recorded and this meant that there was very little overlap between neighbouring herds. The core areas of Groups 1 and 2 each comprised only one continuous area, while those of the remaining herds were split into two or three separate areas.

The home ranges of Groups 5 and 6 were predominantly within areas of steep slopes with gradients over 10° (Figure 11), while the home ranges of Groups 1, 2 and 3 were predominantly in flat or gently sloping areas with gradients of less than 10°. One third of the home range of Group 4 was on steep slopes.

Ninety five percent MCP home ranges of territorial male mountain reedbuck showed little overlap between individuals (Figure 12), while the core areas of most of these animals were single continuous patches. The home ranges of Males 7, 8, 9 and 10 were predominantly within areas of steep slopes while the home ranges of the other males were not. These remaining animals did, however, all have steep slopes within their home ranges and their cores areas overlapped to some extent with these steep slopes. No territorial males within the main study area had home ranges without any steep slopes. Most of the males had territories adjacent to or close to the dam, and all had access to permanent water without having to cross through another male's territory.

The home ranges used by three female mountain reedbuck are shown in Figure 13. These areas should not be compared statistically to the home ranges of males because they only comprised about 50 positional fixes for each animal. They are shown here to demonstrate the relatively large areas used by females in comparison to males and that the space use by the females overlaps with more than one territorial male. The red collar female appeared to have a larger home range than most other females, many of which spent the majority of their time on the steep slopes in the northern part of the study area. There was a very high degree of overlap between the home ranges of grey rhebok herds and male mountain reedbuck within the main study area (Figure 14).

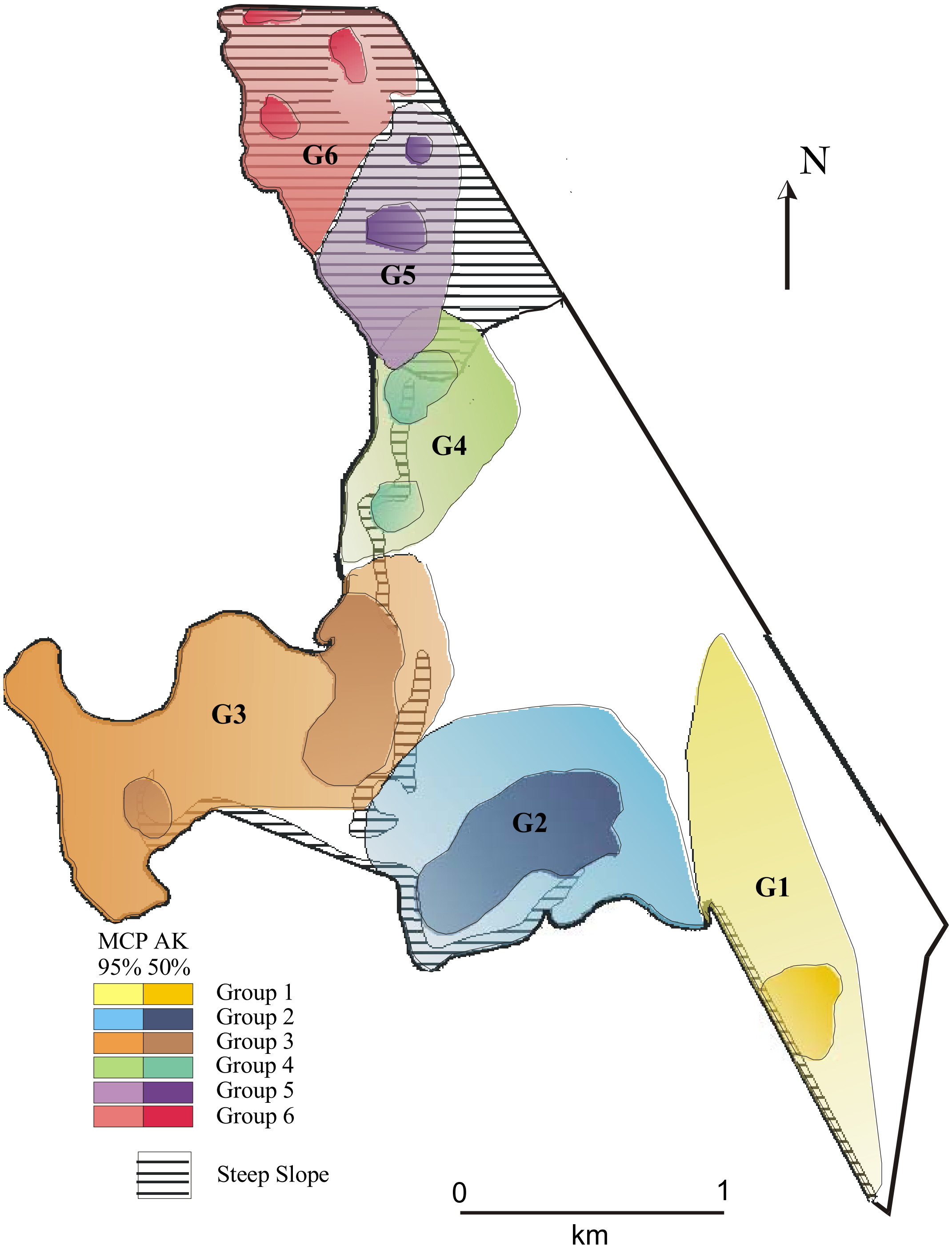

Figure 11. Grey rhebok home ranges and steep slopes (>10°) in the main study area at Sterkfontein. External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 50 % AK results.

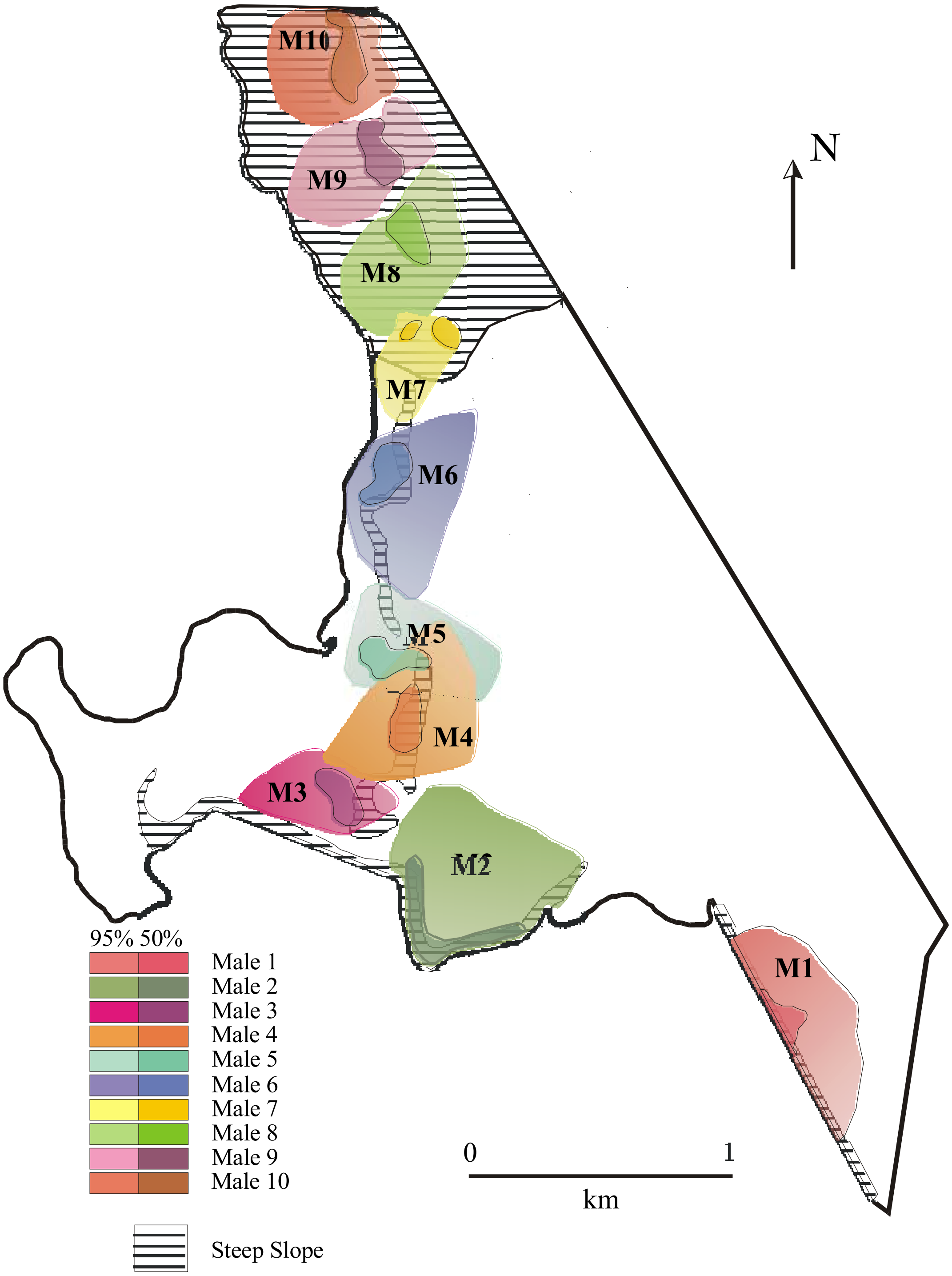

Figure 12. Home ranges of 10 territorial male mountain reedbuck in the main study area between February 2000 and April 2002, superimposed over steep slope (>10°). External boundaries of ranges are taken from 95 % MCP results, while core areas are taken from 50 % AK results.

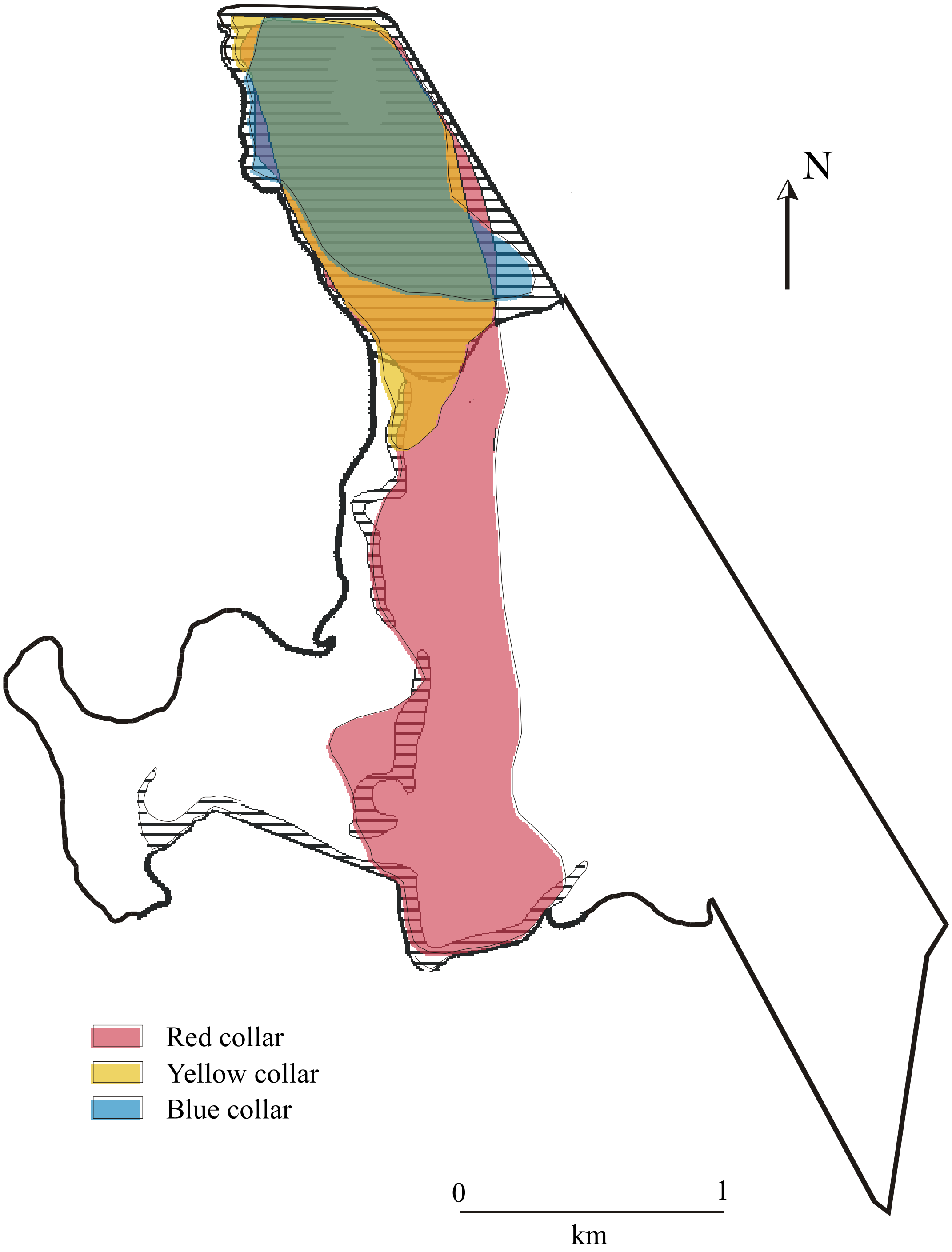

Figure 13. The space use of three mountain reedbuck females within the main study area.

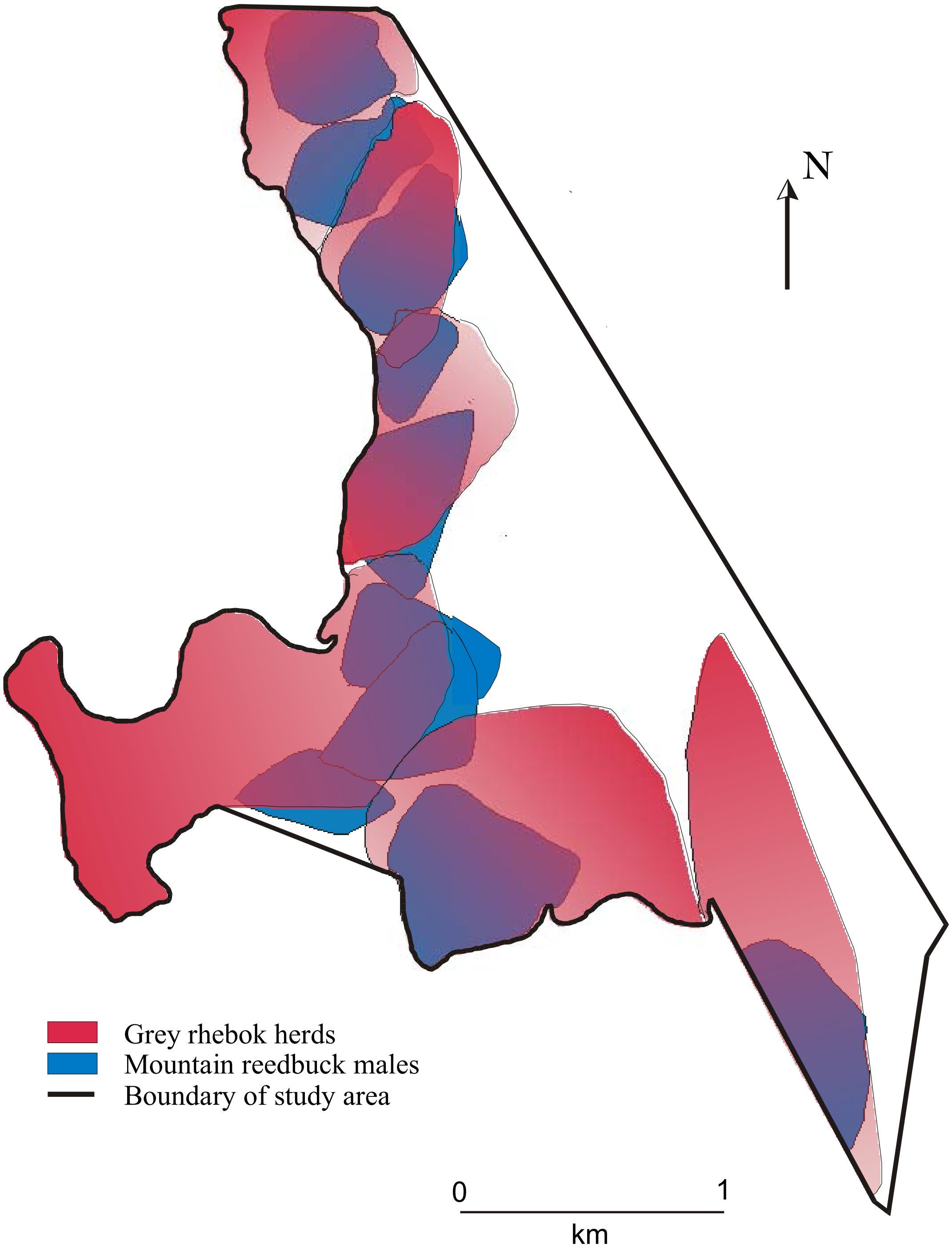

Figure 14. Home range overlap between grey rhebok herds and territorial male mountain reedbuck in the main study area between February 2000 and April 2002.

Ecological densities

The ecological density of grey rhebok in the main study area was 1/15.7 ha (taken from an average of 35 animals in 550 ha), while for mountain reedbuck before the snow it was 1/8.7 ha (at an average of 63 animals in 550 ha).

Vegetation surveys

Grass and forb densities are shown in Table 10. Overall, the average distance to the nearest grass was 29.5 mm, while the average distance to the nearest forb was 89.5 mm. A two-way ANOVA indicated a significant difference between plant types but no difference between flat and steep slopes, and no interaction (Table 11). All data points within a single transect were averaged and treated as one sample. Grass densities were higher than forb densities.

Table 10. Grass and forb densities on steep slopes and flat ground in five survey areas, given as the average distances to the nearest grasses and forbs. Standard deviations are in parentheses.

Gradient	Survey area	Average distance to nearest grass (mm).	Average distance to nearest forb (mm)
Flat	1	29 (31)	107 (78)
	2	20 (17)	64 (51)
	3	22 (19)	86 (59)
	4	31 (26)	86 (67)
	5	35 (26)	77 (60)
Steep	1	26 (26)	81 (63)
	2	30 (31)	89 (72)
	3	43 (32)	111 (72)
	4	29 (18)	77 (61)
	5	30 (21)	117 (121)

Table 11. Two-way ANOVA comparing grass and forb densities within steep and flat areas.

Source of variation	Df	SS	MS	F	P
Grass/forb	1	18000	18000	110.2	< 0.001
Slope	1	289	289	1.8	0.202
Grass/forb x slope	1	58	58	0.4	0.560
Residual	16	2612	163		
Total	19	20959	1103		

Causes of variation in home range size

The parameters included in the Backward Stepwise Regression of grey rhebok variables were the numbers of animals, area of steep slope and escape distance (Table 12). The dependent variable home range area can be predicted from a linear combination of the independent variables: area of steep slope ($p = 0.015$) and number of animals ($p = 0.098$). Using a Spearman Rank Correlation Coefficient there was a negative correlation (non-significant) between home range size and area of steep slope ($r = -0.714$, $p = 0.136$), but no correlation between home range size and number of animals per group ($r = 0.314$, $p = 0.564$). There was, however, a strong negative correlation between area of steep slope and escape distance ($r = -0.943$, $p = 0.017$). Groups with larger areas of steep slope available tended to have smaller home ranges, while in areas of steep slopes, the escape distance tended to be less.

The parameters included in the Backward Stepwise Regression of mountain reedbuck variables were the numbers of accompanying females, area of steep slope and area of cover (Table 13). All the variables were eliminated from the model so none were good predictors of home range size in mountain reedbuck. A Spearman Rank Correlation Coefficient found no evidence of correlations between home range size and average number of attending females ($r = 0.055$, $p = 0.865$), home range size and area of steep slope ($r = 0.006$, $p = 0.973$), or home range size and area of cover (r = -

0.188, p = 0.583). There was, however, a very strong positive correlation between the average number of attending females and area of steep slope (r = 0.818, p = 0.002).

Table 12. Parameters selected to test for predictor variables for home range areas for grey rhebok herds.

Group	MCP home range area (ha)	Average number of animals	Area of steep slope >10° (ha)	Average escape distance (m)
1	73.7	4.57	1.6	397
2	76.8	6.74	3.7	114
3	104.1	7.54	5.6	70
4	39.7	3.81	13.3	100
5	23.3	4.23	22.3	59
6	29.9	7.89	25.2	51

Table 13. Parameters selected to test for predictor variables for home range areas for territorial male mountain reedbuck.

Male	Home range (ha)	Average number of attending females	Area of steep slope >10° (ha)	Area of cover (ha)
1	16.3	0.67	1.6	0.5
2	21.4	0.68	3.5	2.0
3	9.3	0.27	0.9	4.1
4	17.0	0.22	2.6	5.5
5	14.7	0.08	1.1	4.4
6	17.9	0.78	4.5	1.9
7	7.10	0.57	6.0	1.4
8	16.8	2.96	14.0	2.6
9	14.5	8.44	13.1	7.8
10	13.3	8.18	9.0	9.2

Discussion

Home range areas

The geographic positions of the home ranges of the grey rhebok herds went virtually unchanged for the entire study period and there were no apparent seasonal variations. This was because the harem males retained their territories and harems for most of the period and this maintained the status quo (see Chapter 3). Their home range areas were similar to those found in Highmoor State Forest in Natal (Oliver *et al.*, 1978), where they varied between 31 and 135 ha (average 76.7) for eight males, and 43 ha and 117 ha for two females. Males and females were treated separately in that study, but the results should have been the same if herds had been used as the sampling unit instead of individuals. In the Free State, home ranges of herds averaged 61 ha with a range of 46 to 187 ha (Ferreira, 1983). Judging by the low average, the 187 ha value was probably a high outlier in the data set.

Fifty percent AK areas were small relative to their corresponding 95 % AK home ranges. In all six herds, these core areas comprised much less than 50 % of their territories, and in the case of Group 1 it was as low as 9 %. Also, all core areas either incorporated or were adjacent to steep slopes (Figure 11), even though for Group 1 the steep slope of the dam wall was not used very much. Grey rhebok, therefore, used some areas of their home ranges preferentially over others and they appeared to stay close to steep slopes on most occasions.

Ecological densities of grey rhebok at Sterkfontein were high compared to other areas. In Highmoor State Forest, ecological densities were 1/42 ha (Oliver *et al.*, 1978), while in the Drakensburg they ranged between 1/23 ha and 1/57 ha (Rowe-Rowe, 1994). Densities of 1/15 ha in the Bontebok National Park (Beukes, 1984) were very similar to those found in the present study, and in the former it was suggested that these values were high (Beukes, 1984). Although it was not proven in the present study, this must indicate a superior habitat for grey rhebok than other sites, which might result from the high number of forbs available at Sterkfontein compared to many other sites (pers. obs.).

There was very little overlap in home ranges between grey rhebok herds, and this fits with the highly territorial nature of the harem males (Ferreira, 1983; pers. obs.). Five antagonistic interactions were observed whereby one male strayed into another's territory when the resident male was present. In all cases, the intruding male was aggressively chased back to his territory. There was no toleration of trespasses and territories were almost entirely exclusive.

Grey rhebok herds used approximately 2/3 of the study area (estimated from 95 % MCP results), leaving only one gap large enough to incorporate an extra home range. That gap was between the straight north-eastern fence line and the home ranges of Groups 1, 2, 3 and 4 (Figure 10). At no time did any of the resident herds use this space, nor did any animals from within or outside the study area try to establish a new herd there. The reason for this was not established, but two plausible explanations were the lack of access to water and the lack of steep slopes. The only permanent free standing water was the Dam, but for an extra herd to get to this it would have had to pass through the home range of another group, running the gauntlet of interactions with other herds. Although grey rhebok previously have been considered independent of water (Skinner & Smithers, 1990), at Sterkfontein they were regularly observed drinking from the dam during the winter months between May and August (pers. obs.). They needed to do this because many of their food plants died during winter and must have provided very little moisture (pers. obs.). The animals were sometimes observed eating dead plant material that turned out, on examination, to be dry (pers. obs.). Within the gap there were also no steep slopes, and this may have been important. However, a near absence of steep slopes did not stop Group 1 from maintaining a long-term home range in an almost entirely flat area.

The fact that the number of territories and their positions within the study area hardly changed, and that no new herds were established for over two years, even with a large number of yearling males requiring territories at the end of every year, indicated that the area was probably saturated with herds. Introducing males into this area with the aim of increasing genetic variability would have been mostly unsuccessful because there was no space for an extra herd. It would have resulted in a territorial fight, with the most likely victor being the resident male.

Compared to mountain reedbuck at other sites, Sterkfontein males used smaller areas than males at Loskop Dam Nature Reserve (Loskop), where home ranges averaged 28 ha (Irby, 1976), but used larger areas than males in Kenya, where home ranges varied between 3.1 and 5.5 ha (Dunbar & Roberts, 1992). As found by Irby (1976) at Loskop, males at Sterkfontein occupied their territories throughout the year regardless of the presence of females.

Fifty percent AK home range core areas were small relative to their corresponding 95 % AK home ranges, indicating that mountain reedbuck males used certain areas within their home ranges preferentially over others. Core areas of all ten males included steep slopes (Figure 12). Ecological densities at Sterkfontein (1/9.2 ha) were higher than found previously in other areas. Loskop had densities of 1/15 ha to 1/21 ha (Irby, 1976), while in the Drakensburg densities varied from 1/11 ha to 1/32 ha (Rowe-Rowe, 1994). As expected from their territorial behaviour (Irby, 1976; pers. obs.), there was very little overlap in the home ranges of territorial males. There was, however, almost complete overlap between male mountain reedbuck and grey rhebok herds, indicating that they did not exclude each other.

Territorial male mountain reedbuck only used 27 % of the study area (estimated from 95 % MCP results), leaving areas large enough to incorporate many territories of similar size to those found during the present study. However, all male mountain reedbuck home ranges incorporated some steep areas and there were only two unused sites where steep slopes were available. These were on the west side of Male 3, and in the northern section near Males 7 and 8 (Figure 12). Also, all ten males had access to water from the dam. If males had held territories on the east side towards the fence, not only would they have had no access to steep slopes, but they would have had to pass through the territory of another male to get to the water. Mountain reedbuck are recorded as a water dependent species (Skinner & Smithers, 1990).

Vegetation surveys

Grass densities were higher than forb densities in all areas, but within in each plant type there were no differences between steep and flat areas and there was, therefore, no general pattern in relation to slope gradient. As a result, it is unlikely that grass and forb densities had any effect on home range size in mountain reedbuck or grey rhebok within the study area.

Although not tested statistically, there was further evidence for this. Within the home range of grey rhebok Group 3, between the two 75 % core areas (Figure 10), there was a site that had visibly high, although not quantified, densities of edible forbs available (pers. obs.). The herd was, however, rarely located in the area, and when they passed through it they generally did not remain for long. This high availability of food did not appear to influence their use of the site, and it may have been that some other factor affected the time they spent there. The position was very open and quite far from steep slopes.

Causes of variation in home range size

For grey rhebok, the best predictors of home range size were the area of steep slope available and the number of animals within each herd. As there was a negative correlation between home range size and area of steep slope, greater amounts of the latter apparently conveyed some advantage to herds. It either provided more of a certain resource that in turn made it possible for herds to survive in smaller areas, or caused increased competition between herds resulting in compression of territories (Dunbar & Roberts, 1992). There was, however, no correlation at all between numbers of animals in a herd and home range area when these were compared on their own but, when the amount of steep slope available was taken into account, the number of animals became a good predictor of home range size. This makes sense logically because more animals require more food, and because no pattern was found between forb densities and slope gradient, a higher food requirement translates to a larger area requirement.

The average escape distance was not found to be a good predictor of home range area, but it was strongly negatively correlated with area of steep slope. This is not surprising as the steep slopes provided lots of small hills and rocky outcrops that animals could run around to get out of sight. It is possible that escape distance was important to grey rhebok, but was not found to be a good predictor because the steep slope parameter was better.

For territorial male mountain reedbuck, none of the variables proved to be good predictors of home range size. This either indicates that there was no pattern to home range size, or that it was influenced by an untested parameter such as the strength of the dominance of the individual males. In this case, however, it is more likely that stronger males would have held territories with better access to females (Dunbar & Roberts, 1992), and this was not correlated to home range area.

There was a strong positive correlation between the average number of attending females and the area of steep slope. Females showed a strong preference for steep slopes, concurring with Dunbar & Roberts (1992), who found that there was a strong positive correlation between the female/male index and cliff height. It was hence suggested that female mountain reedbuck traded access to food resources against safety from predators and steeper terrain provided this safety. In the present study there were no apparent patterns to grass densities between the different sites tested, so females were not selecting steep slopes for greater food availability.

Interspecific comparison of home range size

The home ranges of territorial male mountain reedbuck in the present study were nearly four times smaller than the home ranges of the grey rhebok herds. The reason for this is most likely the different mating strategies of the two species. Female mountain reedbuck often concentrate on steep slopes for defensive purposes (Dunbar & Roberts, 1992), and the amount of food available within a male's territory is not a deciding factor for them. The mating system is resource defence polygyny but, rather than defending food resources, territorial males defend areas that offer protection to females, and successful males will hold territories where females congregate regularly. In such places males have regular, although not constant, access to females and the potential for mating is high. However, although territories do not have to contain enough food to satisfy a herd of females, they may have to have enough to sustain one territorial male. This is because territories/home ranges of different animals do not overlap and males rarely move out of their own areas into those of other males. They must, therefore, acquire most, if not all, of their food from within their own territory and this sets a lower limit for territory size.

Territorial male grey rhebok defend a harem of females all year, staying with them almost constantly and herding them around if necessary. This is female defence polygyny. The area defended by the male must, therefore, contain everything that female's need for survival and reproduction. This includes adequate food resources, adequate areas to evade predators, access to hiding places for newborn lambs and access to water. The fact that home range size was negatively correlated to the amount of steep slope available, but that there were no differences in forb density between steep areas and flat areas (i.e. smaller areas contain less food regardless of slope gradient), implies that the larger home ranges may have had food resources that exceeded requirements. This is corroborated by the observation that some areas within home ranges that were known to have a plentiful food supply were under-utilised (see above).

The higher overall densities of mountain reedbuck compared to grey rhebok suggests a larger food supply for the former. Grasses are certainly more abundant than forbs at Sterkfontein (Table 10), so the standing crop (biomass) is most likely bigger. This in itself, however, does not imply that there is more food available for mountain reedbuck because they are selective grazers, and large amounts of the standing crop of grass is unavailable to them. Moreover, the nutritional values of the grasses and forbs for the two antelope species were not known and greater quantities of grass may not equate to greater nutritional quality for feeding. Generally browse plants have higher levels of nitrogen than do grasses, but these can be bound to secondary compounds during mastication, making them less available for digestion (Robbins *et al.*, 1987a,b; Gordon, 2003).