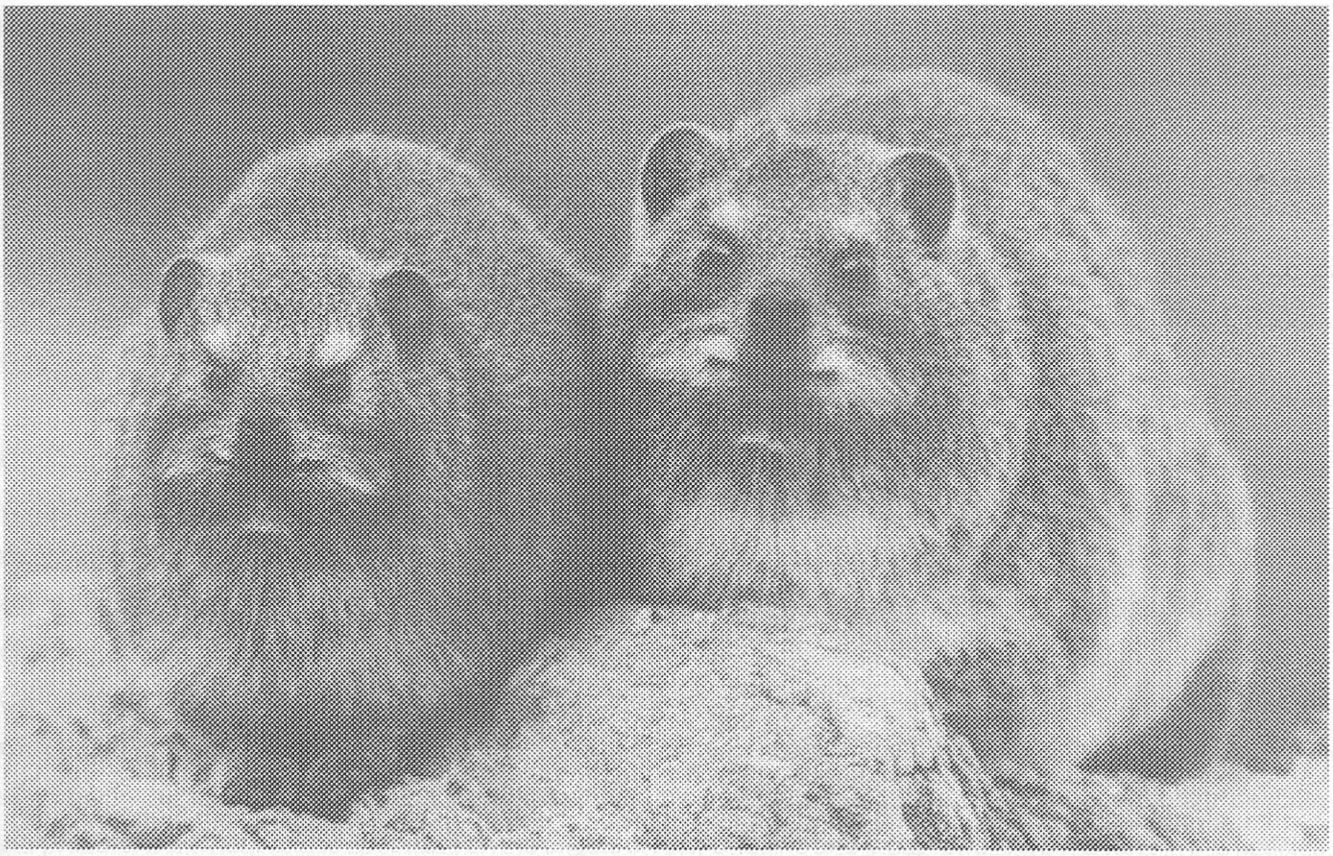
THE PREY BASE



CHAPTER 4

ROCK HYRAX DEMOGRAPHY AND BEHAVIOUR

INTRODUCTION

Rock hyrax are diurnal and social herbivores (weighing up to 4kg), and occur in the rocky habitats of Africa (Chapter 1). They are well able to cope with very arid regimes (Louw *et al.* 1972) such as the Karoo. Their association with rocky habitats has been described (see page 36) but seldom evaluated quantitatively. They are gregarious with a wide vocal repertoire (Fourie 1977). The social organisation of rock hyrax is common to many mammals (Clark 1978), where groups each consist of a matriline of up to 17 adult females monopolised by a single territorial male, with young of both sexes (Coe 1962; Hoeck, Klein & Hoeck 1982; Fourie & Perrin 1987b). Dispersal is usually more obligatory for immature male hyrax than immature females. However, this social organisation is known to be somewhat flexible (Hoeck *et al.* 1982). Rock hyrax can be prolific breeders and this aspect of their biology has attracted considerable scientific attention because of the agricultural importance of population irruptions (see page 2). In the Karoo, this breeding is distinctly seasonal (Millar 1971; Fourie 1983). *Procavia* species will graze and browse, but smaller species from the *Heterohyrax* genus (found further north in Africa) are predominantly browsers (Sale 1965; Turner & Watson 1965; Fourie 1983).

A thorough investigation of the influence of predation by black eagles and other predators on rock hyrax demography probably requires more knowledge of the prey base than of the predator guild. For the purposes of this study it was essential to obtain accurate estimates of hyrax population sizes in black eagle territories within the KRNP. The first part of this chapter outlines how this was done by close examination of the relationship between rock hyrax and their refuge resources which were described in the last chapter. Two methods of population estimation are considered. Knowledge of the distribution patterns of hyrax within these habitats and their behaviour was also needed to interpret black eagle foraging behaviour in Chapter 6. Presentation of behavioural data in this chapter is mainly limited to behaviour which is relevant to the hyrax population model evolved in Chapter 12, but I take the opportunity to describe anti-predator behaviour and to speculate on the origins of rock-dwelling and group-dwelling behaviour in this species. Prey defence behaviour is often over-looked in predator-prey studies (Malcom 1992). Besides abundance of rock hyrax, it was necessary to gain a comprehensive understanding of the structure and processes of this prey population. This chapter considers factors other than predation, particularly climate, which may cause or influence the loss or addition of individuals to the hyrax population.

METHODS

Annual censuses at hyrax colonies

Rock hyrax are known to be thermally labile and must raise their body temperature each morning before feeding, usually by sunbathing (page 26). This affords the best opportunity of getting an accurate total count of a particular group. Most hyrax groups consistently overnight in certain outcrops but some move between locations (see later). I use the term group when referring to the social unit and colony when referring to a regularly-used outcrop.

I counted hyrax groups from distances ranging from 50-150m using a pair of Swift Satellite 20*80 binoculars mounted on a tripod. Before the sun reached the colony, I positioned myself with an unobstructed view of its east-facing aspect and remained there for approximately 90 min. or until I had obtained a satisfactory count. I made regular sweeps of the study group until I obtained a consistent tally for each of three identifiable age classes (Figure 20). At first, the hyrax line up side by side immediately outside their crevices allowing close comparison of body size.

Initial doubts about the accuracy of these counts were largely dispelled by conducting sample counts immediately prior to intensive behavioural observations (see later) of specific groups. Confident estimates of group size are obtained during such detailed observations, and the sample counts were in close agreement with these. However the counts did prove to be weather-dependent. On cold, still, sunny mornings hyrax sit on top of rocks and an accurate count can be obtained within 30 min. of the sun reaching the colony. But hyrax sunbathe in sheltered (concealed) nooks in windy conditions; their sunbathing is brief on warm mornings and may not be synchronised; and their emergence

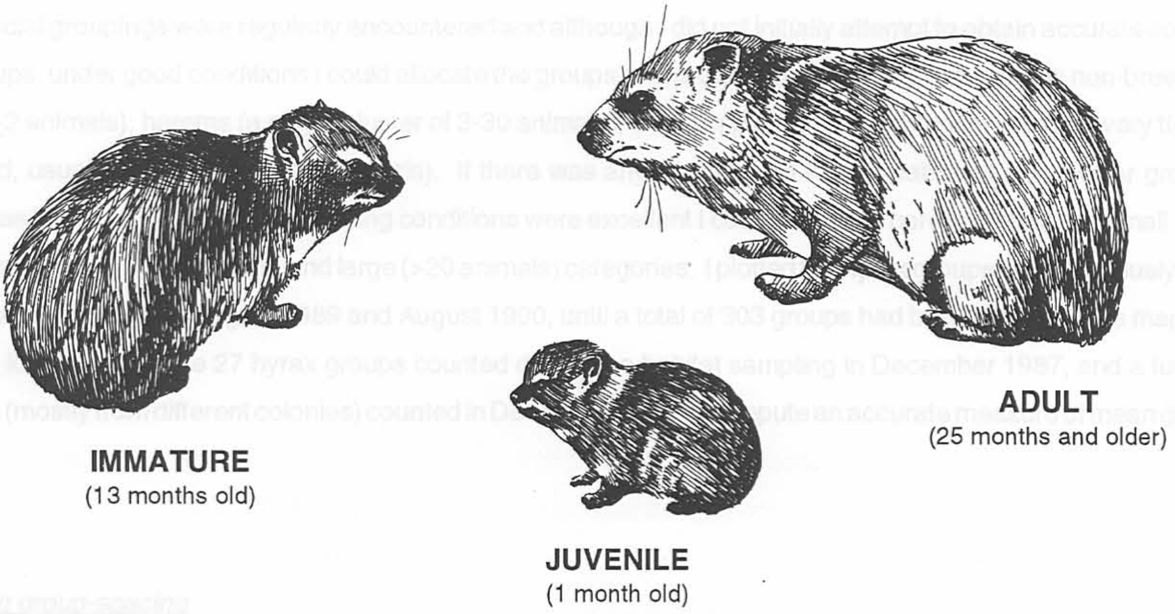


Figure 20. The three age classes discernible during counts conducted during December (@one month after the birth-pulse) in the KRNP: juveniles (average mass 0,25kg) are easily told by their small size; immatures (average mass 1,65kg) usually have a darker grey pelage than adults with bolder facial markings, they also have shorter noses and more pronounced foreheads; the eyes of adults are situated midway between nose and ears, whereas on immatures the eyes are situated closer to the nose. Adults weigh approximately 3,2kg.

is asynchronised and occurs much later in the day on cold, overcast mornings; they can remain in their crevices for two to three days when conditions are cold and wet (Coe 1962; pers. obs.). As a result of these influences I often had to repeat counts up to four times until I was satisfied with the result.

Rock hyrax in the Karoo show a distinct birth-pulse. Fourie (1983) noted that 92% of hyrax births in the MZNP (Fig. 3, page 8) occurred within four weeks (November to December) of the first birth for that season. In the Noorsveld (Fig. 3) 81% of hyrax births occurred in November (Millar 1971). Modal parturition date in this study was 12 November (see later) with the first babies appearing at the end of October. I began counts 18d after the modal parturition date so that at least 90% of females should have given birth by the start of the counts. Counts extended through the month of December and were conducted annually at sixteen colonies in the KRNP in 1987, 1988, 1989 and 1990 to assess recruitment, population composition and relative abundance.

Estimating hyrax density

Initial estimates of hyrax density from total counts of habitat strips (27 groups in 90 stretches of rock outcrop) conducted in December 1987 using Caughley's formula for unequal-sized sampling units in stratified habitats (Caughley 1977) proved unrealistic (discussion). But these counts did indicate notable consistency of group size and subsequent effort was directed at plotting all hyrax groups in the study area and accurately determining mean group size. I plotted all hyrax groups on a given slope by climbing to a commanding viewpoint (within about one kilometre range) at dawn and scanning the rock outcrops on the slope as the sun reached them. Weather affected this technique in the same way as it affected the regular counts. I used the same equipment for both methods.

Certain social groupings were regularly encountered and although I did not initially attempt to obtain accurate counts of the groups, under good conditions I could allocate the groups to one of three loose social categories: non-breeding groups (1-2 animals); harems (a single cluster of 3-30 animals); and complexes (2-4 clusters of animals, very tightly associated, usually totalling 30-45 individuals). If there was any doubt about the allocation of a particular group I classed it as 'undetermined'. When viewing conditions were excellent I could separate harem groups into small (<12 animals), medium (12-20 animals) and large (>20 animals) categories. I plotted the hyrax groups simultaneously with habitat-mapping between August 1989 and August 1990, until a total of 303 groups had been plotted in the mapped area (139 km^2). I used the 27 hyrax groups counted during the habitat sampling in December 1987, and a further 27 groups (mostly from different colonies) counted in December 1989 to compute an accurate measure of mean group size.

Measuring group-spacing

Nearest neighbour distances between groups were used in computation of the G-statistic (Brown 1975; Brown & Rothery 1978). This index has been shown to give a robust indication of dispersion pattern (Watson & Rothery 1986), and can detect regular-spacing on a small scale irrespective of larger-scale pattern. It is obtained from the ratio of the geometric mean to the arithmetic mean of the squared nearest neighbour distances. The index scales between 0 and 1 where high values indicate regularity and values less than about 0,65 indicate randomness (Nilsson, Nilsson & Slyven 1982).

Destructive sampling

Hyrax were shot during October 1989 (n=26) and October 1990 (n=26), just prior to the birth pulses, to check recruitment as determined from the counts against fecundity. The shot sample also provided information on age structure, sex ratio and body masses of the hyrax. On account of low hyrax density, destructive sampling proved time-consuming and had to be restricted so as not to interfere with other work. Weight, age, sex and reproductive details were recorded for each animal shot. Patterns of tooth eruption and tooth wear (on the maxillae) were used to determine the age of the animals (see the methods section in Chapter 10). The age distribution of 53 hyrax skulls, that were picked up in the study area (most during 1987), was determined in the same way in order to construct mortality schedules. These skulls were collected away from known predator feeding sites in order to avoid any selective bias by predators.

Behavioural observations

Chosen hyrax groups were observed in periods of five consecutive days from dawn to dusk. I tried the method of Fourie & Perrin (1986) to trap individuals in one group but abandoned this effort after no success was achieved in a two-week period. I was able to use behavioural cues to identify territorial males and other social classes in some instances. Every fifteen minutes the following parameters were recorded for each visible individual hyrax onto maps of the colony or onto a database: age (as for counts), activity, location, distance from nearest shelter, distance from overnighting outcrop, whether the animal was in the sun or the shade, whether the animal was huddling with other hyrax, and whether the animal was vigilant or performing sentinel behaviour. Meteorological conditions and the presence or absence of predators were noted at each 15min observation.

Vegetation analyses

Apparent 'vegetation zones' around hyrax colonies were investigated in the following manner. Four 30m transect lines were laid out radiating north, east, south and west from an isolated boulder colony. Every metre along these transects a quadrat (1m square) was laid alongside the transect line, and the following parameters were recorded within it: an ocular estimate of the proportion of the quadrat comprised by bare rock; the number of hyrax faeces; the number of ungulate faeces; distance to nearest large rock (shelter); distance to nearest tall shrub (shelter); and for each plant species identified within the quadrat - the name, number of plants, an ocular estimate of the proportion of the quadrat comprised by the canopy spread of that species, an ocular estimate of the proportional leaf cover within that canopy spread, and an ocular estimate of the proportion of shoots cropped on that species.

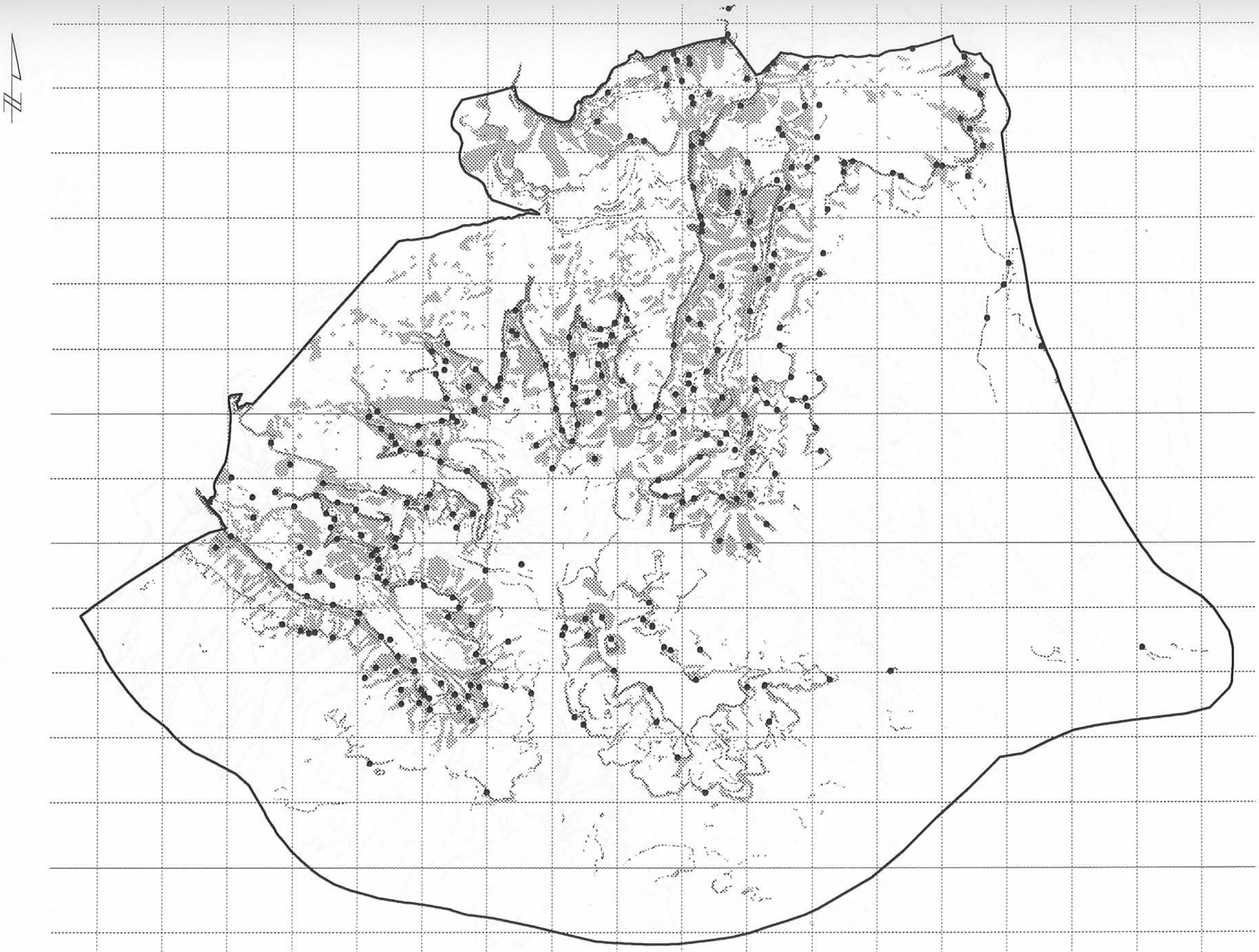


Figure 21. Distribution of hyrax groups (n=303) in relation to the refuge micro-habitats of the KRNP. Consult Fig. 16 for details on refuge micro-habitats. Upper slopes below 'toerenjies' (protrusion in top left corner) were not completely surveyed for hyrax groups. 1km grid and boundary of mapped area shown. Generated from ARCINFO coverages using ARCVIEW

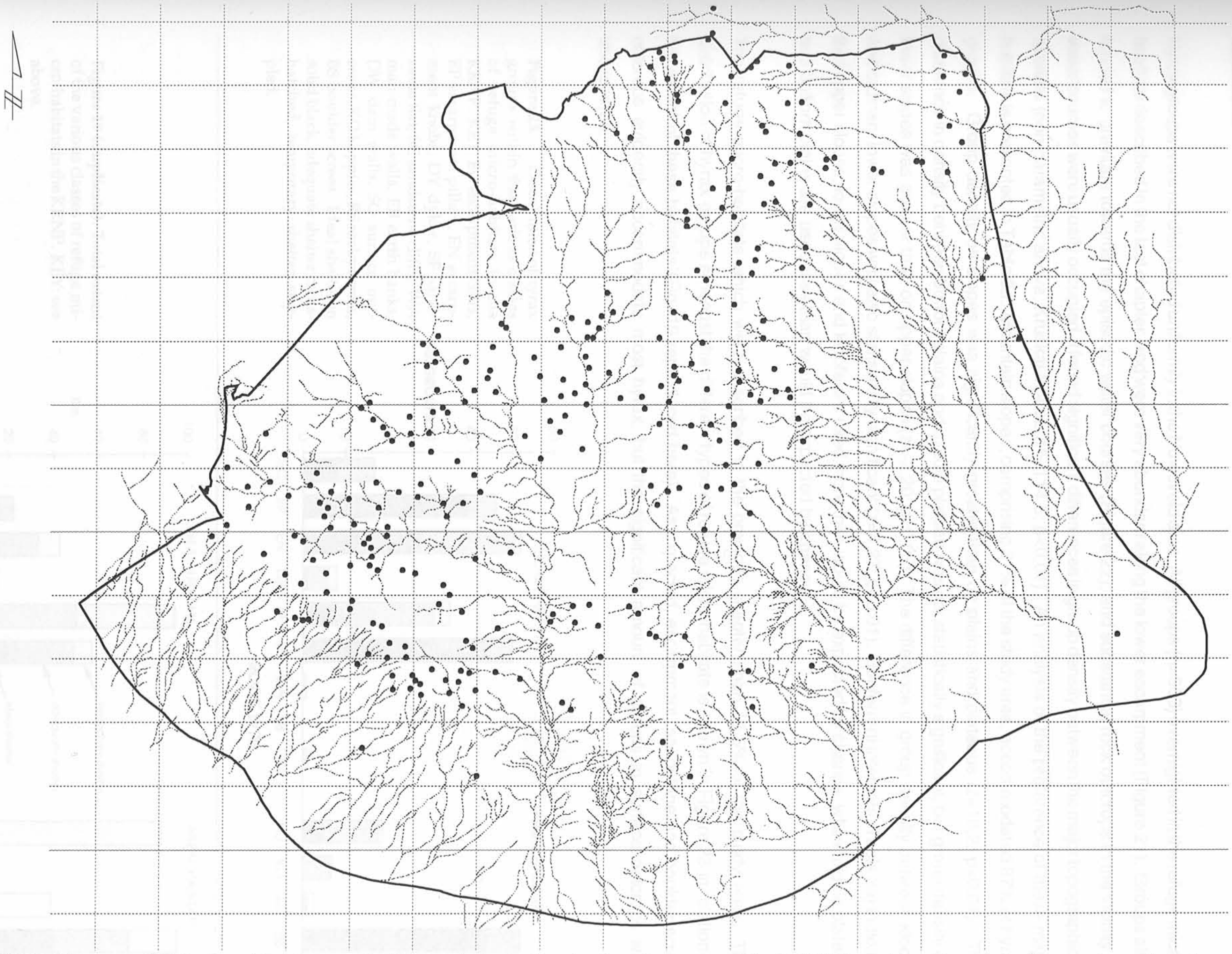


Figure 22. Distribution of hyrax groups (n=303) in relation to the episodic water courses of the KRNP (1km grid and boundary of mapped area shown) (generated from ARCINFO coverages using ARCVIEW)

RESULTS (cont.)

Habitat use

Hyrax groups were not distributed uniformly in the Nuweveld area. All groups (n=303) overnighted in the refuge micro-habitats described in the last chapter, and were very abundant along the lower escarpment (Figure 21). Groups also tended to gravitate towards the episodic water courses (Figure 22), and substantial rock outcrops in the vicinity of water courses were usually occupied. I found significant differences in group density between the major topographical habitats (non-parametric anova, Kruskal-Wallis: X^2=114,5; p<0,01). An analysis of the preference of these major habitats is presented in Table 3a. Mountain slopes, comprising 31% of the study area, accommodated 87% of hyrax groups. Group density on slopes was significantly greater than on plains and plateaus (z=10,2; p<0,01). The difference in density between bottom plains and middle plateau was not statistically significant, but group density on lower slopes was greater than on upper slopes (z=-2,20; p<0,05). The difference in group density between kloofs and ordinary lower slopes was also statistically significant (z=4,27; p<0,01). Bonferroni intervals (Table 3a) indicate that upper slopes, lower slopes and kloofs are used more than would be expected by chance, while middle plateau and bottom plains are used less than would be expected by chance.

The refuge micro-habitats which were described in the previous chapter span 16,5% of the study area. The distribution of hyrax groups amongst the different types of refuge micro-habitats is shown in Figure 23 in relation to the extent of these habitats (Fig. 19 reproduced here). As expected, escarpment, sandstone and boulder scree outcrops evidently accommodate most hyrax, but the significant amount of groups in surface outcrops was unexpected.

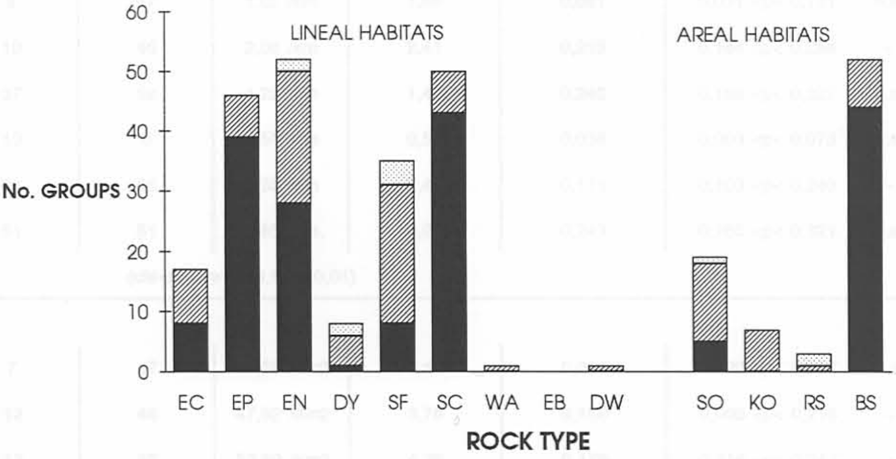


Figure 23. Distribution of hyrax groups within the various classes of refuge micro-habitats in the KRNP. KEY: EC escarpment cliffs, EP escarpment pillars, EN escarpment knobs, DY dykes, SF sandstone flat, SC sandstone cliffs, WA man-made walls, EB earth banks, DW dam walls, SO surface outcrops, KO koppies, RS rocky screes; BS boulder screes. Ideal shelter in solid black, adequate shelter cross-hatched, temporary shelter stippled.

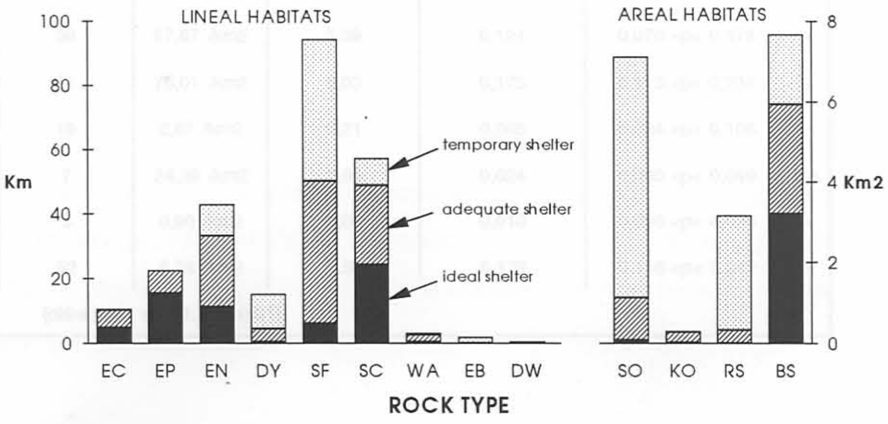


Figure 19 (duplicate). Total extent of the various classes of refuge micro-habitats in the KRNP. KEY: see above.

TABLE 3
ANALYSIS OF HYRAX HABITAT PREFERENCES

Observed and expected frequencies of hyrax groups in different habitats are compared using the Chi-square statistic which is presented beneath each analysis. A simple preference rating is provided for each habitat type by dividing proportionate use by proportionate availability, after Petrides (1975). Bonferroni confidence intervals on the expected proportional use of each habitat were calculated as described by Neu, Byers & Peek (1974) and Byers, Steinhorst & Krausman (1984). If the observed proportional use of any habitat falls outside of these intervals it demonstrates a statistically significant preference for (+) or against (-) that habitat.

HABITAT	EXTENT	EXPECTED NO. GROUPS	OBSERVED NO. GROUPS	GROUP DENSITY	PREFERENCE RATING	OBSERVED PROPORTIONAL USE	95% BONFERRONI CONFIDENCE INTERVALS	
A. preference of the major topographical habitats:								
UPPER SLOPES	4,86 km2	10	25	5,14 /km2	2,46	0,086	0,044 <p< 0,128	+
MIDDLE PLATEAU	25,60 km2	54	25	0,98 /km2	0,47	0,086	0,044 <p< 0,128	-
LOWER SLOPES	34,13 km2	72	176	5,16 /km2	2,46	0,605	0,531 <p< 0,679	+
KLOOFS	4,00 km2	8	51	12,76 /km2	6,03	0,175	0,118 <p< 0,232	+
BOTTOM PLAINS	70,24 km2	147	14	0,20 /km2	0,10	0,048	0,016 <p< 0,080	-
(chi-square = 539,7; p<0,01)								
B. preference of lineal vs. areal refuge micro-habitats								
LINEAL	4,07 km2	52	210	51,58 /km2	4,08	0,722	0,663 <p< 0,781	+
AREAL	18,89 km2	239	81	4,29 /km2	0,34	0,278	0,219 <p< 0,337	-
(chi-square = 589,0; p<0,01)								
C. preference of lineal refuge micro-habitats by length								
ESCARPMENT CLIFFS	10,49 km	9	17	1,62 /km	1,88	0,081	0,031 <p< 0,131	n.s.
ESCARPMENT PILLARS	22,38 km	19	46	2,06 /km	2,41	0,219	0,144 <p< 0,294	+
ESCARPMENT KNOBS	42,80 km	37	52	1,22 /km	1,43	0,248	0,169 <p< 0,327	n.s.
DYKES	15,67 km	13	8	0,51 /km	0,59	0,038	0,003 <p< 0,073	n.s.
SANDSTONE (FLAT)	94,67 km	81	36	0,38 /km	0,45	0,171	0,103 <p< 0,240	-
SANDSTONE (CLIFFS)	60,28 km	51	51	0,85 /km	0,99	0,243	0,165 <p< 0,321	n.s.
(chi-square = 78,5; p<0,01)								
D. preference of all refuge micro-habitats by area								
ESCARPMENT CLIFFS	0,56 km2	7	17	30,58 /km2	2,42	0,058	0,020 <p< 0,097	n.s.
ESCARPMENT PILLARS	0,97 km2	12	46	47,52 /km2	3,76	0,158	0,098 <p< 0,218	+
ESCARPMENT KNOBS	0,97 km2	12	52	53,89 /km2	4,26	0,179	0,116 <p< 0,242	+
DYKES	0,38 km2	5	8	21,11 /km2	1,59	0,027	0,000 <p< 0,054	n.s.
SANDSTONE (FLAT)	0,53 km2	7	36	67,67 /km2	5,39	0,124	0,070 <p< 0,178	+
SANDSTONE (CLIFFS)	0,67 km2	8	51	76,01 /km2	6,03	0,175	0,113 <p< 0,238	+
SURFACE OUTCROPS	7,11 km2	90	19	2,67 /km2	0,21	0,065	0,024 <p< 0,106	-
KOPPIES	0,29 km2	4	7	24,39 /km2	1,85	0,024	0,000 <p< 0,049	n.s.
ROCKY SCREES	3,33 km2	42	3	0,90 /km2	0,07	0,010	0,000 <p< 0,026	-
BOULDER SCREES	8,16 km2	103	52	6,38 /km2	0,50	0,179	0,116 <p< 0,242	-
(chi-square = 586,7; p<0,01)								

Hyrax evidently highly prefer lineal habitats and avoid areal habitats in terms of density per square kilometre (Table 3b), these trends cannot be attributed to chance. Hyrax groups in lineal habitats occur at 12 times the density of those in areal habitats.

Within the preferred lineal habitats differences also occur between their use and availability (Table 3c). All escarpment outcrop types are used in greater proportion than their availability by length but only in the case of escarpment pillars is this preference statistically significant. Flat sandstone outcrops are significantly avoided; dykes also appear to be under-utilised; while cliff-like sandstone outcrops are used in proportion to their availability. No groups were observed in earth banks. Walls and dam walls were too limited to include in this analysis, but two artificial rock structures constructed in the study area were rapidly colonised by hyrax groups.

If one considers all outcrop types in terms of their area this pattern is changed (Table 3d): all lineal habitats now appear to be used in greater proportion than their availability (as was indicated in Table 3b); in the case of escarpment pillars and knobs, and sandstone outcrops this preference is statistically significant; but in this treatment the narrower outcrop types (escarpment knobs, sandstone outcrops) now appear to be the most preferred.

Of the areal habitats in Table 3d, only koppies are used in greater proportion than their availability but this preference is not statistically significant. Surface outcrops and both types of scree (especially rocky screes) are actually avoided by hyrax, and this cannot be attributed to chance. Ideal boulder screes are only used roughly in proportion to their availability (preference rating 1,02).

The distribution of whitewash streaks indicated heavier use of cliff-like sandstone outcrops, koppies and some escarpment outcrops than did the present distribution of hyrax groups. But the relationship between density of hyrax groups and density of whitewash streaks in the Kortkloof subsample of outcrops was strong (r=0,836; p<0,01). Outcrops harbouring hyrax in the Kortkloof subsample were surrounded by more tall shrubs than outcrops without hyrax (Kruskal-Wallis H test; p<0,05).

Factors influencing use of slopes

The use of slopes (n=296; see Fig. 15, page 29) by hyrax groups was predictably influenced by the distribution of preferred outcrop types. As expected, hyrax density was high on slopes where the density of outcrop units was high (r=0,77; p<0,01) and where the density of rock crevices was high (r=0,74; p<0,01).

Hyrax density showed stronger correlations with the density of lineal habitats (r=0,81; p<0,01) than with the density of areal habitats (r=0,58; p<0,01). The strongest relationships were observed with densities of favourite outcrop types (e.g. escarpment pillars: r=0,72; p<0,01). The density of all escarpment outcrops, except those rated as temporary shelter, was the best single indicator of hyrax density (r=0,86; p<0,01). This measure alone explained nearly three quarters of the total variation in hyrax density. Weakest or negative relationships were observed between hyrax density and unpreferred habitats such as dykes (r=-0,10; p>0,10) and surface outcrops (r=-0,24; p<0,05).

A regression model (R^2 option in the SAS computer programme, see Ingraham *et al.* 1988) incorporating escarpment outcrops, sandstone outcrops and koppies (all temporary shelter excluded) explained 83% of the variation in group density. The inclusion of parameters describing the density of screes had negligible influence on the predictive value of this model. The density of large rocks on a given slope showed a closer relationship with hyrax density ($r=0,62$; $p<0,01$) than did the density of rocky screes ($r=0,48$; $p<0,01$) or boulder screes ($r=0,55$; $p<0,01$).

The relationship between group density and the density of lineal habitats ($r=0,78$; $p<0,01$) was improved when outcrops providing only temporary shelter were excluded ($r=0,81$; $p<0,01$), but was weakened again if only ideal outcrops were considered ($r=0,68$; $p<0,01$). The same trend was even more apparent for areal habitats, and held for most outcrop types treated individually.

With regard to aspect, there was no significant difference in group density between north- (7,84km^{-2}) and south- (7,72km^{-2}) facing slopes, but there were significantly more groups on east- (8,94km^{-2}) than west- (5,92km^{-2}) facing slopes if a one-tailed test could be justified (Kruskal-Wallis H test: $z=-1,75$; $p<0,05$).

Group size

Mean group size at the end of 1987 was 17,4 (n=26; s.d.=12,2), while at the end of 1989 it was 16,4 (n=25; s.d.=10,3). Non-breeding groups (mean group size=1,25; s.d.=0,5; n=8) and complexes (mean group size=32,2; s.d.=8,2; n=10) accounted for much of the high degree of variation in these samples and their relative contribution is able to profoundly influence the overall mean. Mean group size of harems was 16,4 (s.d.=7,3; n=17) at the end of 1987, and 16,4 (s.d.=5,8; n=16) again at the end of 1989. Harems comprised 82,3% of groups plotted, non-breeding groups 9,2%, and complexes 8,5%. Using these frequencies (based on the more extensive group-plotting exercise) with the relevant group sizes given above yields an overall group size of 16,2 (close to that for harems), and indicates that 82,6% of hyrax occur in harem groups, 15,8% in complexes and 0,7% in non-breeding groups.

Harems and complexes are not likely to have been missed by this group plotting method. But relatively more non-breeding groups (15,7% of sample) were observed during the more thorough total counts of habitat strips at the end of 1987. It is quite likely that some non-breeding groups were over-looked by the group plotting method. If non-breeding groups do comprise 15,7% of groups in the real population then the number of groups plotted should be increased by 7,75% to compensate for those missed and real mean group size probably approaches 15,3. Total population estimates with this compensation are 1,24% greater than estimates without.

Influence of habitat on group size

Within the sample of 53 hyrax groups counted at the end of 1987 and 1989, larger groups were associated with rock outcrops of lower (more ideal) suitability ratings ($r=-0,30$; $p<0,05$). The same trend was evident from the distribution of groups categorised during the group plotting exercise: 87% of complexes and 71% of medium/large harems occurred in ideal habitat; whereas only 43% of non-breeding groups and 38% of small harems occurred in ideal habitat. Some small harems were observed inhabiting temporary shelter.

I used a X^2 contingency table to investigate associations between the different social categories and particular rocky habitats. Certain categories were aggregated to allow calculation of adequate expected frequencies. Only two out of fifteen cells had expected frequencies less than five (viz. 4,56 and 4,80). I found a statistically significant association between certain social groupings and particular outcrop classes (X^2=17,3; p<0,05). Scrutiny of the contingency table revealed positive associations between large groups (large harems and especially complexes) and boulder screes; between medium harems and escarpment pillars or cliffs; and between small groups (non-breeders and small harems) and marginal habitats (flat sandstone outcrops, dykes, surface outcrops and rocky screes). Negative associations occurred between large groups and marginal habitats; and between small groups and escarpment cliffs or pillars. Remaining habitat types (escarpment knobs, koppies and sandstone cliffs) showed no obvious associations with any social grouping. Generally speaking, large groups and medium harems occupied the preferred habitats (as indicated by group density), while small groups were found in unpopular habitats.

Certain social groupings were also associated with habitats where an interaction of outcrop types occurred. Complexes occurred at greater frequencies than expected (and non-breeding groups at lower frequencies than expected) in kloofs where high densities of escarpment outcrops coincide with boulder screes, when compared with ordinary lower slope habitats (X^2=7,93; p<0,05).

Group spacing

Mean nearest neighbour distance amongst 291 plotted groups (Fig. 21) was 0,241km (s.d.=0,112), or when groups on the plains and plateaus were excluded 0,238km (s.d.=0,111; n=248). The nearest neighbour distances in this study yielded a value of 0,66 for the G-statistic, this indicates a dispersion pattern that is borderline between a regular and random distribution.

Population estimates, density and biomass

A total of 291 hyrax groups were plotted within the 136km^2 study area (flat surface area). At a mean group size of 16,23 hyrax, this yields a population estimate of 4723 hyrax in the study area. Compensation for overlooked non-breeding groups (see group size) increases this estimate to 4782 hyrax. The population estimate derived from the earlier method (total counts in habitat strips) was 30% greater than this.

Hyrax occur at a density of 35,2km^{-2} in the study area. Density was 69,2km^{-2} in the mountainous terrain (bottom plains excluded), or 103,0km^{-2} on the slopes (plains and plateaus excluded). Hyrax densities in the major topographical habitats are used with the extent of these habitats to extrapolate a population estimate for the Karoo National Park in Table 4. All density estimates represent hyrax numbers just after the birth-pulse at the end of 1989.

At this time of the year the population is swamped with juveniles, and mean hyrax mass is only 1650g (the calculation of this figure is described later). This figure of mean mass was used to determine biomass in the various habitats (Table 4). Overall biomass in the mountainous terrain was 1,14kgha^{-1}. The kloof habitat had the highest values of density (221,7km^{-2}) and biomass (3,66kgha^{-1}).

TABLE 4
DENSITY AND BIOMASS OF ROCK HYRAX IN THE MAJOR TOPOGRAPHICAL HABITATS AND A POPULATION ESTIMATE FOR THE KAROO NATIONAL PARK

All data refer to hyrax numbers just after the birth-pulse (in December 1989). Hyrax densities are derived from the group densities given in Table 3 and include compensation for non-breeding groups that may have been overlooked by the group-plotting method. Density estimate for the upper plateau is taken from that of the middle plateau - a topographically similar habitat. Surface areas of slopes are two-dimesnional (no compensation for gradient). The extent of the park in this analysis is as described in Chapter 2.

HABITAT STRATUM	EXTENT (km2)	DENSITY (No./km2)	BIOMASS (kg/ha)	No. HYRAX
UPPER PLATEAU	33,83	(16,0)	(0,26)	541,3
UPPER SLOPES	38,40	92,7	1,53	3559,7
MIDDLE PLATEAU	62,27	16,0	0,26	996,3
LOWER SLOPES & KLOOFS	75,86	103,5	1,71	7851,5
BOTTOM PLAINS	117,14	3,3	0,05	386,6
			TOTAL IN PARK :	13335

Population composition

A modal conception date of 27 March and a modal parturition date of 12 November were calculated from the masses of litters from pregnant females shot during October (see Fourie 1983 for method). A total of 89 counts at hyrax localities revealed that immediately after the hyrax birth pulses of 1987, 1988, 1989 and 1990, overall population composition was 35,3% juveniles (one month old); 18,1% immatures (13 months old); and 46,5% adults (25 months and older).

Three of the eighteen hyrax colonies regularly-counted disappeared during this study through emigration or mortality. A complete coverage for all years was obtained for only twelve localities. Comparisons between years are based on these 12 localities. A summary of the counts made at these localities is given in Table 5.

TABLE 5
RESULTS OF THE ANNUAL HYRAX COUNTS

The first four columns summarise annual counts made during December at twelve regular localities. The last column summarises data from all the counts (n=89) at all localities. Percentages are given in brackets. Only groups that remained extant throughout the study period were considered for the comparison of group size. Age and sex classes were separated on the assumptions described in the methods section: adults in tight groups were considered to consist of one territorial male and the remainder females; solitary adults which were loosely associated with groups were taken to be peripheral males. Mortality was determined for the two categories by comparing numbers of that category in one year with numbers of the appropriate category the following year. Annual rainfall (January to December) and rainfall for the three months prior to the birth-pulse are given in mm.

	END '87	END '88	END '89	END '90	OVERALL
TOTAL COUNT	252	185	211	188	1328
No. HAREMS	15	14	13	13	84
MEAN GROUP SIZE	22,8	16,6	19,2	18,4	
ADULTS	120 (48)	84 (45)	92 (44)	94 (50)	617 (46,5)
IMMATURES	43 (17)	29 (16)	30 (14)	53 (28)	241 (18,1)
JUVENILES	89 (35)	72 (39)	88 (42)	41 (22)	469 (35,3)
JUVENILE MORTALITY		60 (67)	42 (58)	35 (40)	(55,2 p.a.)
ADULT & IMMA. MORTALITY		79 (49)	21 (19)	28 (23)	(30,0 p.a.)
ADULT FEMALES	91 (36)	64 (35)	69 (33)	68 (36)	469 (35,3)
TERRITORIAL MALES	15 (6)	14 (8)	13 (6)	14 (7)	85 (6,4)
PERIPHERAL MALES	12 (5)	3 (2)	11 (5)	12 (6)	50 (3,8)
FEMALES/MALE	3,14	3,20	3,00	2,62	3,17
JUVENILES/FEMALE	0,97	1,13	1,28	0,60	
ANNUAL RAIN	199	301	410	186	
SEPT - NOV RAIN	61	55	211	11	

The proportion of juveniles in the population (recruitment) was higher in the years with more rainfall. Rainfall during the entire gestation period (April - November) showed the closest correlation with recruitment (r_p=0,995), but rain falling during September to November was also closely correlated (r_p=0,979) and this relationship was significant to the more appropriate Spearman's rank correlation test (r_s=1,00; $p<0,05$). Good rains falling around the birth-pulse during the one month of November also appeared to be crucial for good recruitment (r_p=0,917). Exceptional rains fell in November 1989 (page 21), and this was when hyrax recruitment was maximal during the study. This was then followed by the lowest value of recruitment in the following year when early summer rains were negligible (see rainfall pattern in Figure 25).

Juvenile mortality at seven colonies was 32% during the first six months of 1988. Evidently mortality of both age groupings was very high during 1988 but declined thereafter. Two harem groups merged and there was a significant decline in group size over this period (t-test for matched pairs; t=2,5; p<0,05), indicating an overall population decline of 27%. Subsequently there was a slight increase during 1989 and a high production of juveniles at the end of this year. Low mortality of these juveniles led to high numbers of immatures at the end of 1990. A significant population increase might have occurred at this time had there not been such poor recruitment.

Assuming that adults in a tight group consisted of a single territorial male and the rest females, and that solitary adjacent adults were peripheral males, it is indicated (Table 5) that there was a marked reduction of peripheral males during 1988 (when high mortality occurred), followed by a return to former numbers. Numbers of territorial males (one per harem) remained fairly stable, and sex ratio approximated three adult females per adult male during the study period.

Details of the hyrax shot during October 1989 and 1990 (n=52) are given in Table 6. Age-determination of these hyrax allowed a direct and more detailed appraisal of the frequency distribution of older age classes. This age structure can be assumed to closely reflect the age structure during the birth-pulse, one month later. A life table was constructed from this survival schedule (assuming that the population had ceased to decline). The proportional contribution of the second age class was borrowed from the results of the counts (immatures are more likely to be shot), and the first age class was predicted from observed recruitment values. This age distribution is shown in Figure 24. The distribution indicates that old hyrax (8 years on) comprise 5,3% of the population. Smoothing of the frequencies indicates that old animals comprise 5,9% of the population.

TABLE 6

DATA DERIVED FROM DESTRUCTIVE SAMPLING

(percentages are given in brackets)

	OCTOBER '89	OCTOBER '90	TOTAL SAMPLE
SAMPLE SIZE	26	26	52
JUVENILES (11mth)	11	6	17
SUB-ADULTS (23mth)	6	8	14
ADULTS (35-95mth)	9	10	19
OLD ANIMALS (107mth+)	0	2	2
FEMALES (excluding juvs.)	10	9	19
MALES (excluding juvs.)	5	11	16
FEMALES / MALE	2,00	0,82	1,19
No. FEMALES PREGNANT	8 (80%)	7 (78%)	15 (78,9%)
MEAN LITTER SIZE	2,25 (sd=0,46)	2,86 (sd=0,90)	2,53 (sd=0,74)
JUVENILE MASS (g)	1569 (sd=204)	1308 (sd=156)	1477 (sd=224)
SUB-ADULT MASS (g)	2565 (sd=406)	2263 (sd=262)	2392 (sd=353)
ADULT MASS (g)	2998 (sd=361)	2921 (sd=558)	2954 (sd=474)
ADULT FEMALE MASS (g)	3114 (sd=299)	3390 (sd=510)	3240 (sd=412)
ADULT MALE MASS (g)	2767 (sd=419)	2586 (sd=287)	2640 (sd=319)

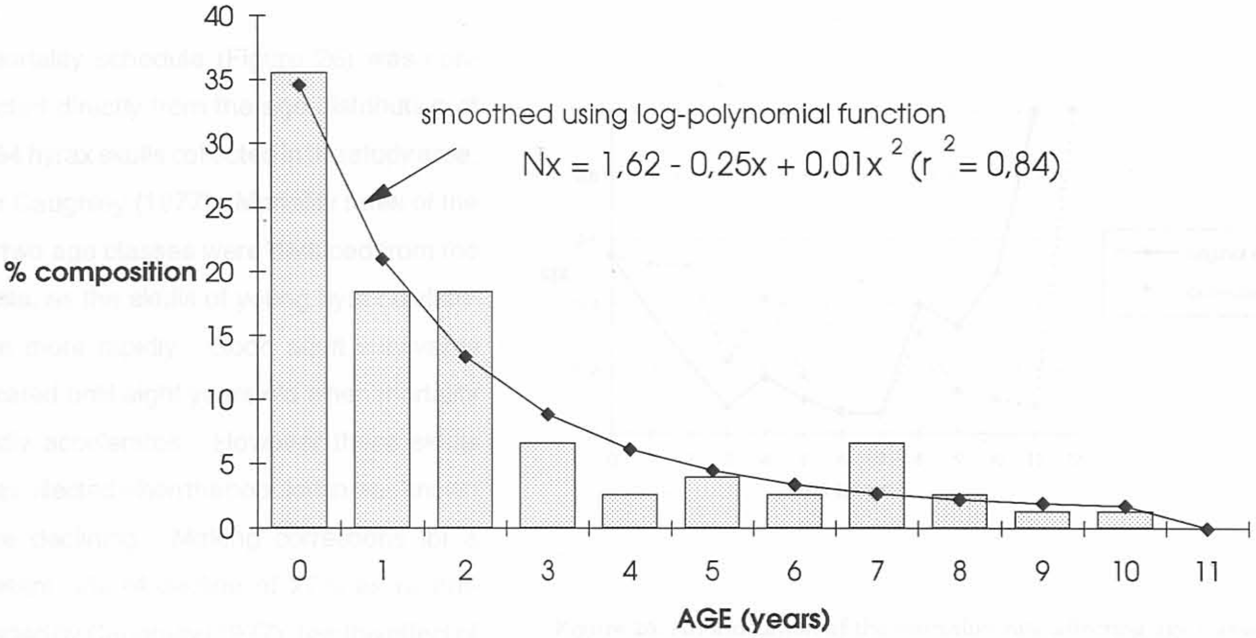


Figure 24. An indication of the age distribution of the rock hyrax population in the Karoo National Park 1989 - 1990, derived from age determination of 52 hyrax shot. Age classes 0 and 1 (which are likely to be biased in a shot sample) were predicted from the proportion of juveniles and immatures in the annual counts. The continuous line represents a smoothing of this distribution using the log-polynomial function as shown. However, evidence suggests this smoothing may be inappropriate (see discussion).

However, evidence suggests that this smoothing is inappropriate, and that irregularities in the distribution are real and reflect changes in the environment. The frequency distribution of estimated birth dates of the shot sample is plotted in Figure 25a with rainfall (Fig. 25b). The absence of hyrax born in 1984 from the shot sample coincides with a severe drought year. It appears rainfall affects sex ratio as well as recruitment. There was a strong correlation between the proportion of males in each birth year and rainfall during the preceding 12 months (r=-0,92; p<0.01) when the two oldest age classes were excluded. Females are known to live longer than males (Fourie 1983).

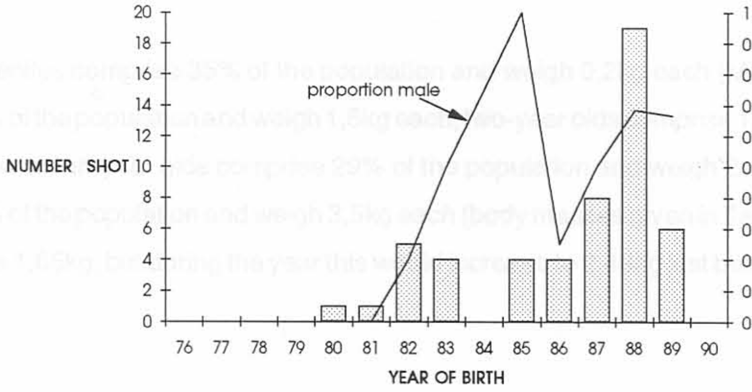


Figure 25a. Frequency distribution of birth dates estimated (see methods) for a sample of 52 hyrax shot 1989 - 1990; and the percentage of each cohort comprised by males (right-hand axis)

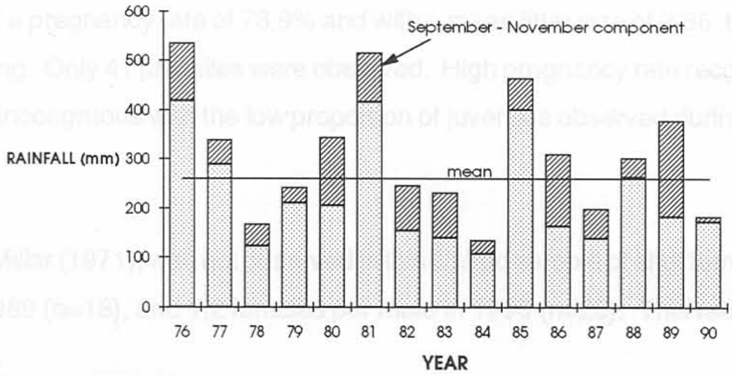


Figure 25b. Total annual rainfall (January to December) for the KRNP (rainfall immediately prior to the birth-pulses is shaded)

A mortality schedule (Figure 26) was constructed directly from the age distribution of the 54 hyrax skulls collected in the study area, after Caughley (1977). Mortality rates of the first two age classes were deduced from the counts, as the skulls of young hyrax disintegrate more rapidly. Good adult survival is indicated until eight years old when mortality rapidly accelerates. However these skulls were collected when the population was known to be declining. Making corrections for a constant rate of decline of 27% as recommended by Caughley (1977), has the effect of shifting the mortality pattern to the right (Figure 26). These mortality schedules suggest that old animals comprise 10,0% of the population, or 7,1% when corrected.

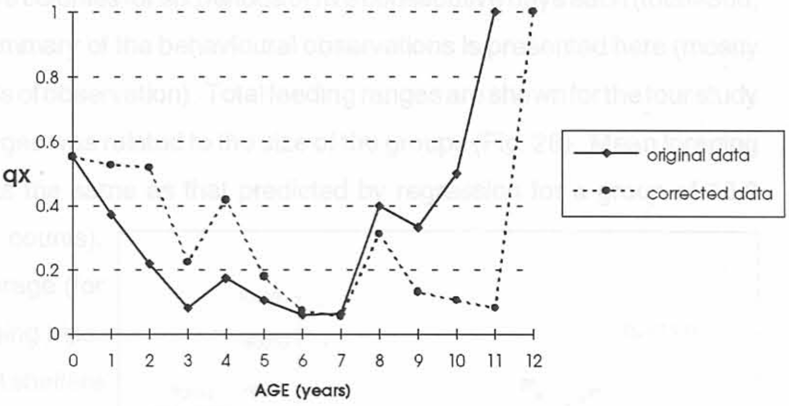


Figure 26. An indication of the mortality rate affecting age classes of rock hyrax in the KRNP, derived from age-determination of 54 hyrax skulls collected away from known predator feeding sites. Most of these skulls were collected during 1987. A corrected mortality rate is also shown for a population declining at a constant rate of 27% p.a., after Caughley (1977).

It is concluded that just after the birth-pulse juveniles comprise 35% of the population and weigh 0,2kg each (Millar 1971; Fairall 1980); one-year olds comprise 18% of the population and weigh 1,5kg each; two-year olds comprise 12% of the population and weigh 2,4kg each; three to seven-year olds comprise 29% of the population and weigh 2,8kg each; and eight to twelve-year olds comprise 6% of the population and weigh 3,5kg each (body masses given in Table 6). A mean mass for hyrax at this stage would be 1,65kg, but during the year this would increase to 2,43kg just before the birth-pulse.

Sex ratio of adults (>22 months) in the shot sample was one male to 1,2 females (Table 6). Assuming that this direct indication of sex ratio approaches that of the population, then 92 adults counted at the end of 1989 should be comprised of at least 50 females. At a pregnancy rate of 78,9% and with a mean litter size of 2,25 (Table 6), these females should have produced approximately 89 young. Eighty eight juveniles were observed. In 1990, 94 adults counted should be comprised of 51 females. At a pregnancy rate of 78,9% and with a mean litter size of 2,86, these females should have produced at least 115 young. Only 41 juveniles were observed. High pregnancy rate recorded in the shot sample collected in October 1990 is incongruous with the low proportion of juveniles observed during the counts in December 1990.

Precocious puberty of females as observed by Millar (1971), was not observed in this limited sample of shot females. Foetal sex ratio was 1,6 females per male in 1989 (n=18), and 1,2 females per male in 1990 (n=20). This ratio did not differ significantly from parity in either year.

Behavioural observations and vegetation zones

Four hyrax groups were observed at their respective colonies for six periods of five consecutive days each (total=30d; see Fig. 12, page 22 for details). A preliminary summary of the behavioural observations is presented here (mostly obtained from detailed analyses of just three periods of observation). Total feeding ranges are shown for the four study groups in Figure 27. The size of these feeding ranges was related to the size of the groups (Fig. 28). Mean foraging range for the four groups was 4,68ha, and this is the same as that predicted by regression for a group of 16,2 individuals (mean group size indicated by the counts). Within these ranges, groups travelled a daily average (for three observation periods) of 169 - 572m on foraging trips. Certain groups had two to three favourite over-night shelters which they used within their range. When conditions became very hot, one group moved to another refuge site on a cooler slope. Two of the groups showed overlap in their ranges with those of non-breeding groups (one or two individuals). There was no indication of overlap between the ranges of harem groups (but adjacent harems were not intensively studied). Hyrax foraging behaviour could be

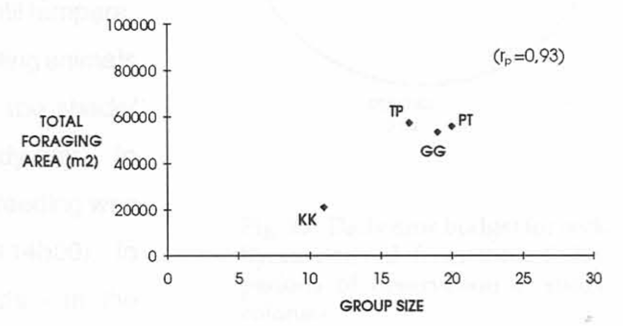


Fig. 28. The relationship between group size and foraging range for four hyrax study groups.

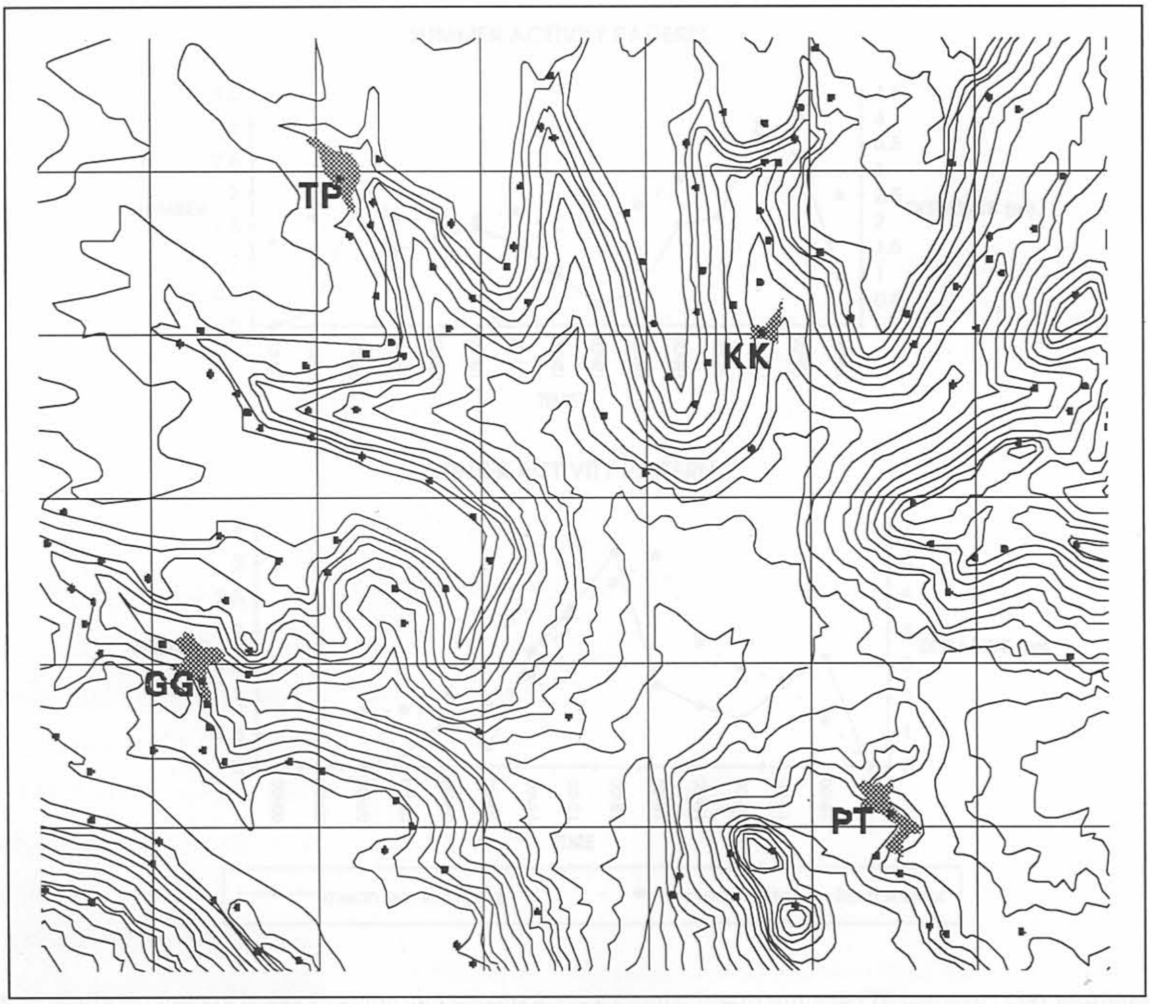


Figure 27. Total foraging ranges of the four chosen hyrax study groups, shown in relation to other groups (and 100' contours) in the Stolshoek region of the KRNP.

separated into casual feeding by individuals in the immediate vicinity of the colonies, and concerted group-feeding when all members of the group travelled some distance from the colony and fed intensively for an hour or two, usually in riparian thicket (after Sale 1965, Fourie 1983). Average daily time spent feeding by hyrax, for three of the five-day periods, ranged from 1,2h to 2,2h (see Fig. 29 for time budget), but casual feeding was not synchronised and individuals could be seen feeding over 3,5 - 7,5h of the day. Most of the time hyrax were resting in close proximity to their shelters. Sitting and huddling in the sun were the preferred postures until temperatures rose above 17^{o}C usually at about 09h00. Thereafter, resting animals were usually lying down, sometimes half in the sun, or in the shade/ shelters on hot days. Hyrax preferred to sit or stand on windy days. In winter, hyrax spent most of the morning sunning, and group-feeding was usually concentrated in one early afternoon bout (peak at @14h00). In summer, hyrax usually conducted two group-feeding bouts - in the mornings (08h30 peak) and late afternoon (17h30 peak), to avoid the hot midday period (Fig. 30). But this behaviour pattern was influenced by changeable weather conditions and by the proximity of riparian thicket.

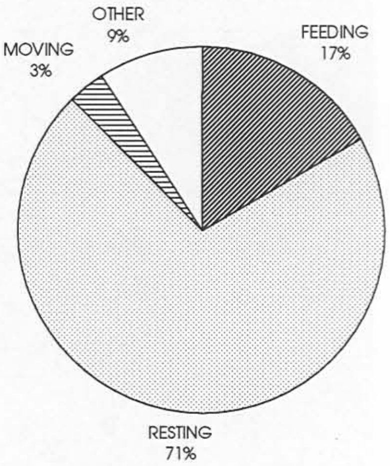


Fig. 29. Daily time budget for rock hyrax derived from three 5-day periods of observation at study colonies.

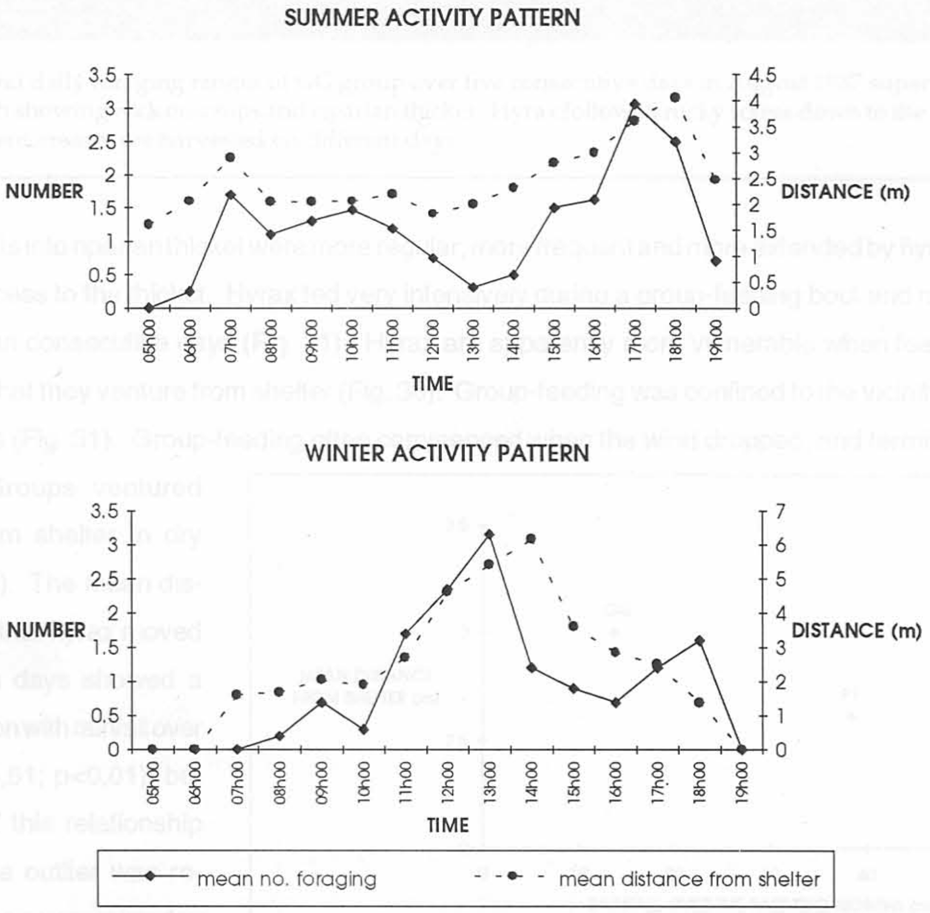


Figure 30. Daily rhythms of hyrax foraging movements for two groups: one in summer (TP January 1988); the other in winter (GG August 1987). The average pattern over five days is shown in each case, so peaks tend to be dampened by irregularities.

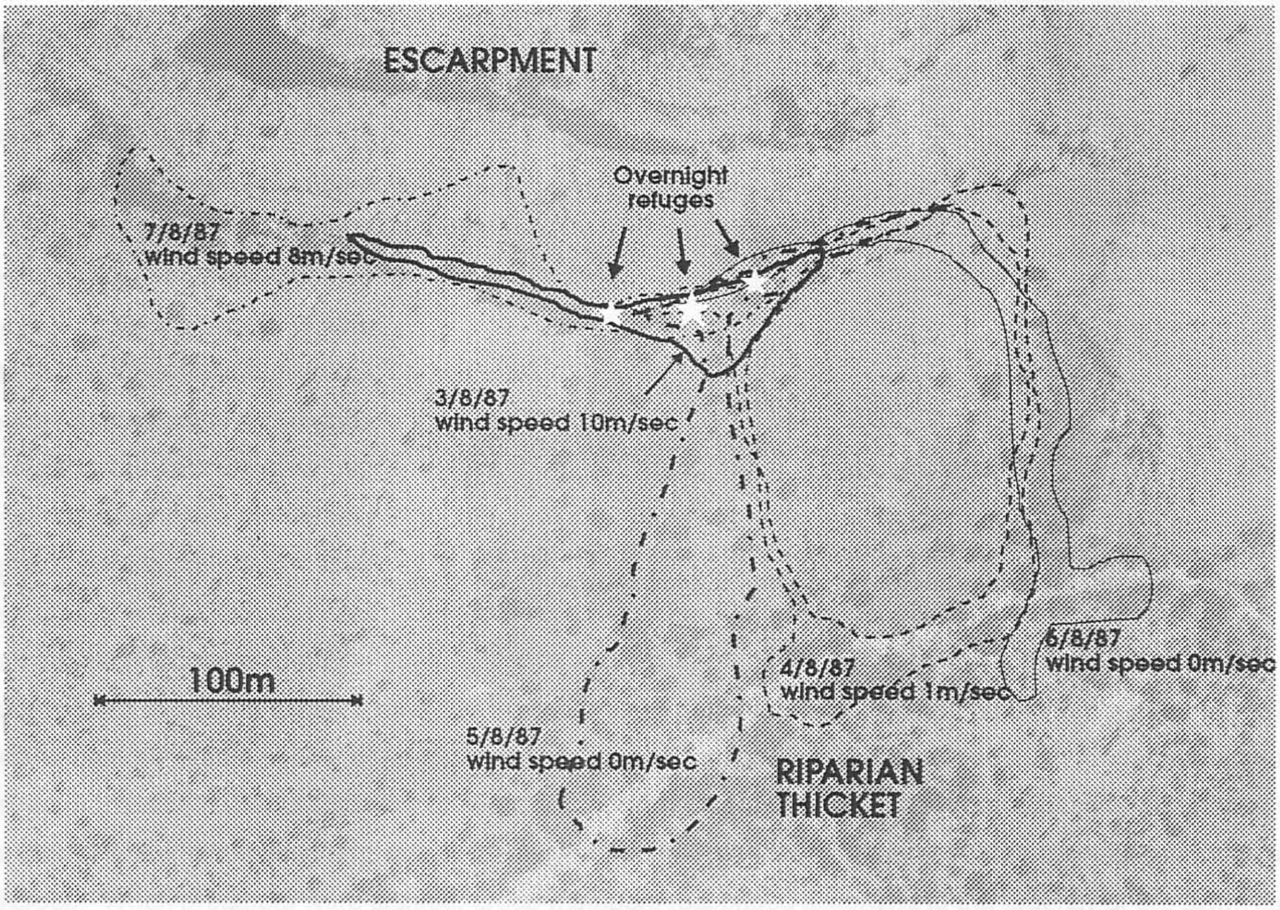


Figure 31. Total daily foraging ranges of GG group over five consecutive days in August 1987 superimposed on an aerial photograph showing rock outcrops and riparian thicket. Hyrax followed rocky screes down to the river course on still days. Different areas were harvested on different days.

Group-feeding bouts into riparian thicket were more regular, more frequent and more extended by hyrax groups which had close, safe access to the thicket. Hyrax fed very intensively during a group-feeding bout and nearly always fed in different areas on consecutive days (Fig. 31). Hyrax are apparently more vulnerable when feeding because of greater distances that they venture from shelter (Fig. 30). Group-feeding was confined to the vicinity of colony rocks on very windy days (Fig. 31). Group-feeding often commenced when the wind dropped, and terminated when high winds began. Groups ventured slightly further from shelter in dry conditions (Fig. 32). The mean distance from shelter that hyrax moved on 27 observation days showed a significant correlation with rainfall over the past 40d (r=-0,51; p<0,01), but the significance of this relationship was lost when one outlier was removed representing a very rainy day when hyrax remained in their shelters (r=-0,37; p<0,07).

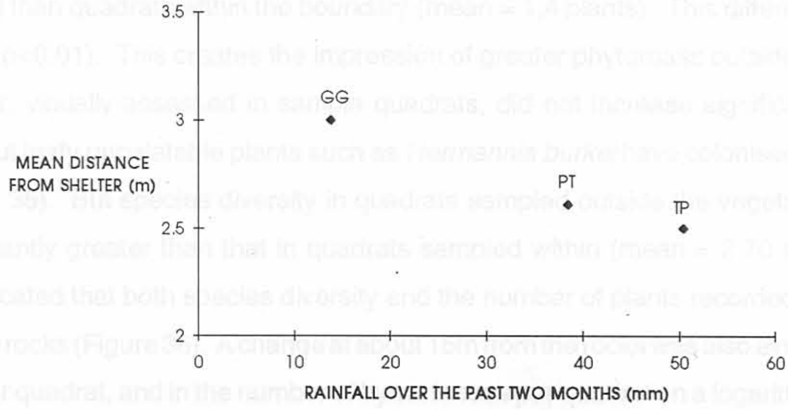


Figure 32. Average distance ventured from shelter for three groups over five days each, in relation to rainfall experienced over the past 8w.

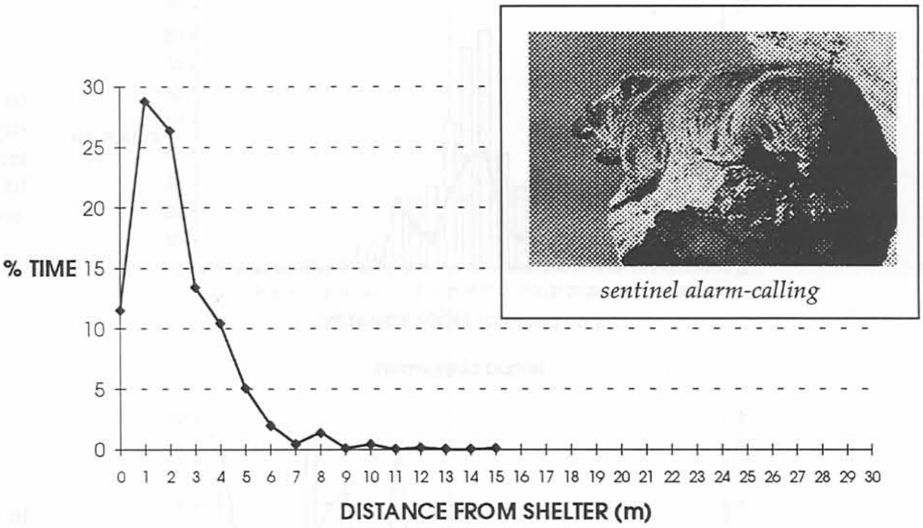


Figure 33. The amount of time that rock hyrax spend at varying distances from shelter. It should be noted that this analysis is based on 2256 sightings of individuals at three colonies over 15d, and only refers to hyrax which are visible outside or in the entrances to their crevices during the daytime.

For three periods of observations analysed thus far (2256 individual sightings), hyrax spent 96% of their time within 5m of shelter and were not observed to venture further than 15m from sanctuary (Fig. 33). Individual hyrax spent 27 - 34% of their day in a vigilant posture. Fewer animals were vigilant during group-feeding. At such times certain individuals adopted sentinel behaviour. Some recognisable individuals regularly adopted this role. They were always adults. Adult males tended to be pre-occupied with interactions with females and rival males. On one occasion a peripheral male (as defined by Fourie & Perrin 1987b) failed to warn the feeding group of an approaching Cape wildcat which it had clearly seen. It is inferred that adult females did most of the sentinel behaviour. Sentinels were in place for 20 - 37% of the time, especially when the group was travelling to and from feeding grounds. Sentinels appeared particularly vulnerable when running to catch up with the group. When predators were sighted, group members responded according to the urgency of the alarm call - usually either freezing and looking toward the sentinel or immediately fleeing for cover. Hyrax could easily distinguish between eagles that were hunting and those that were engaged in other activities (such as territorial interactions), and would take appropriate action. Hyrax were observed to employ group defence when a booted eagle *Hieraaetus pennatus* captured a juvenile (Davies 1989), but did not employ these tactics against black eagles. The intensive and casual feeding by hyrax in close proximity to rocks results in a distinct vegetation zone around regular colony rocks which is clearly visible from the air. Immediately after good rains a verdant green flush of vegetation can be seen at the entrances to rock crevices, but this soon disappears. At most colonies a clear vegetation change is permanently evident 11 - 17m from the rocks. The inner zone becomes particularly contrasting when grass growing beyond becomes lignified (yellow) in dry conditions (see Fig. 34). Quadrats beyond the clear-cut vegetation boundary contained more grass (mean = 11,5 plants) than quadrats within the boundary (mean = 1,4 plants). This difference was statistically highly significant (F=6,75; p<0,01). This creates the impression of greater phytomass outside the vegetation boundary. However leaf cover, visually-assessed in sample quadrats, did not increase significantly beyond 15m. This is because infrequent but leafy unpalatable plants such as *Hermannia burkei* have colonised the heavily grazed inner vegetation zone (Fig. 35). But species diversity in quadrats sampled outside the vegetation boundary (mean = 4,52 spp.) was significantly greater than that in quadrats sampled within (mean = 2,70 spp.) (z=7,91; p<0,01). Vegetation analysis indicated that both species diversity and the number of plants recorded per quadrat show change at about 15m from the rocks (Figure 36). A change at about 15m from the rocks was also evident in the proportion of plant shoots cropped per quadrat, and in the number of hyrax faeces per quadrat on a logarithmic scale (Fig. 37). These results are in agreement with direct observations of the distance that hyrax move from shelter (Fig. 33). Edible phytomass was estimated to be 30% greater beyond the 15m boundary.

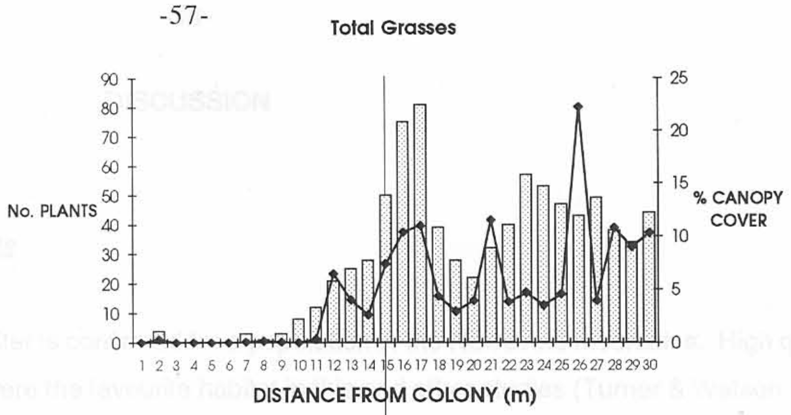


Figure 34. Change in the amount of grasses at increasing distance from a regular hyrax colony: number of grass plants per quadrat as columns; the proportion of quadrat area covered by grass leaf as a line.

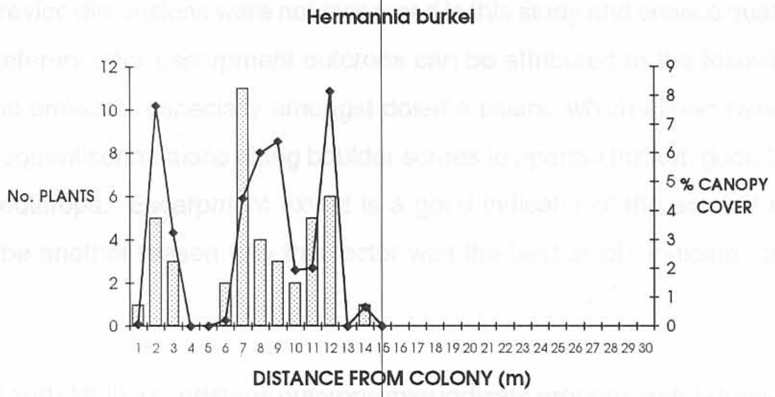


Figure 35. Change in the amount of *Hermannia burkei* at increasing distance from a regular hyrax colony: number of plants per quadrat as columns; the proportion of quadrat area covered by leaf as a line.

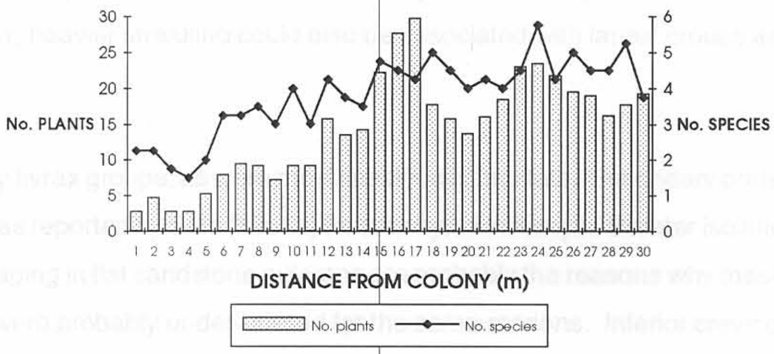


Figure 36. Change in the number of plants and the number of species per quadrat at increasing distance from a regular hyrax colony.

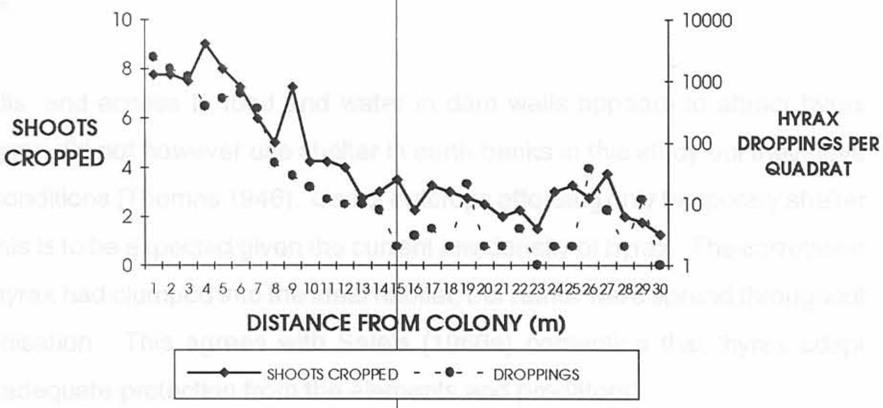


Figure 37. Change in the number of hyrax faeces (logarithmic scale), and in the index of cropped shoots (see methods) per quadrat at increasing distance from a regular hyrax colony.

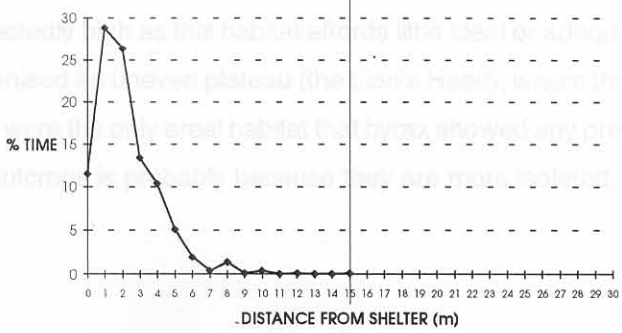


Figure 33 duplicate. The amount of time that rock hyrax spend at varying distances from shelter. (see previous page for full legend)

DISCUSSION

Distribution and the use of refuge habitats

The reliance of *P. capensis* on rocky shelter is confirmed for a population in the Nuweveld mountains. High quality crevices in hard igneous rock outcrops were the favourite habitat in this and other studies (Turner & Watson 1965; Sale 1966a; George & Crowther 1981). Crevice dimensions were not measured in this study and crevice quality can only be speculated on. The observed preference for escarpment outcrops can be attributed to the following: an extensive distribution of deep fissures and crevices, especially amongst dolerite pillars, which allows hyrax safe access to a wide and rich foraging area; frequent connections along boulder screes to riparian thicket; good lookout points; and close association with other outcrops. Escarpment extent is a good indicator of the amount of rock outcrops on a given slope, and this may be another reason why this factor was the best single indicator of hyrax density.

Heavy whitewash streaking of escarpment and cliff-like sandstone outcrops may indicate proportionately heavier use of these habitats in the past. Disease or over-exploitation of food resources might conceivably have caused a recent shift into less traditional habitats. However, heavier streaking could also be associated with larger groups and well used lookout posts on tall cliffs.

Sandstone outcrops were also favoured by hyrax groups, as were most lineal rocky habitats. Secondary preference for metamorphic and sedimentary rocks was reported by Sale (1966a) for rock hyrax in Kenya. Greater isolation and fewer (smaller?) crevices to allow safe foraging in flat sandstone outcrops are probably the reasons why these were less used than cliff-like outcrops. Dykes were probably under-utilised for the same reasons. Inferior crevices may be characteristic of vertical dolerite flows.

Abundance of shelter in man-made walls, and access to food and water in dam walls appears to attract hyrax colonisation of these limited habitats. Hyrax did not however use shelter in earth banks in this study but they have been known to do so under high density conditions (Thomas 1946). Use of outcrops affording only temporary shelter as colonies was very rarely observed. This is to be expected given the current low density of hyrax. The correlation analyses however, did not indicate that hyrax had clumped into the ideal habitat, but rather were spread throughout any habitat deemed adequate for colonisation. This agrees with Sale's (1966a) contention that 'hyrax adapt themselves to any shelter that provides adequate protection from the elements and predators'.

Use of dolerite surface outcrops was unexpectedly high as this habitat affords little ideal or adequate shelter. Most groups observed in this habitat type had colonised an uneven plateau (the Lion's Head), where the atypical surface outcrops resembled small koppies. Koppies were the only areal habitat that hyrax showed any preference for. That they were less preferred than escarpment outcrops is probably because they are more isolated, and provide less access to food.

Avoidance of rocky screes was expected, but this habitat still offers safe foraging routes to hyrax. Low use of boulder screes (rich in food and shelter) was not expected. Other researchers (Sale 1966a; Fourie 1983) suggested that this habitat was highly favoured, but did not provide quantitative evidence. This impression may be partly due to hyrax using boulder screes for foraging during the day but retreating to colonies in lineal outcrops at night (pers. obs.; Fairall pers. comm.). Time spent in the different habitats might offer a more complete impression of habitat use than that presented in this article.

Furthermore, density of screes did not prove to be a useful variable in attempts (regression models) to explain hyrax density. While screes offer safe foraging access to hyrax, evidently they are seldom used for colonies. Crevice quality is probably the reason for this. Gaps between boulders and the substrate are unlikely to afford as much space or shelter from the elements as deep fissures in the escarpment.

Comparing the surface area of a continuous stretch of lineal outcrop with the surface area of a discontinuous areal outcrop is not strictly fair, as the latter is not a true reflection of rock surface area. Some of the preference of continuous over discontinuous habitats must be attributed to this bias, but compensation is unlikely to have changed the order of habitat choice.

Differences in the use of the major topographical habitats by hyrax are largely consequential to the outcrop preferences described thus far. Slopes were favoured because they offer most of the rocky habitat (especially lineal outcrops and screes). They afford safer access to favourite foraging areas (e.g. *Acacia karoo* in riparian thickets) along an inter-connected network of lineal outcrops and screes (outcrops on plains and plateaus are usually scattered or isolated). Slopes also offer more tall shrubs as browse - especially the highly preferred (Sale 1965; Fourie 1983) *Grewia* spp. which are common around chosen outcrops (pers. obs.). Low use of the more rocky middle plateau might be due to patchy distribution of refuge, scarcity of riparian thicket, a high grass cover, and lookouts might be less effective on flat ground.

Richer vegetation on the upper slopes did not appear to induce preference of this habitat over lower slopes. The reverse situation can be explained by the high densities of hyrax groups in kloofs which make up a significant component of the lower slopes. Easy access between converging escarpment (good overnighting) and dense boulder screes and riparian thicket (good foraging) in kloofs allows close siting of large hyrax groups. Kloofs often also provide a source of water.

There was no evidence in this study that hyrax avoided the hot (and grassy) north-facing slopes unlike red rock rabbits (see next chapter). The distribution of Alpine marmots was found to be influenced by related thermoregulatory constraints (Turk & Arnold 1988), but hyrax groups in the KRNP have the ability to move when conditions get too hot. One would expect east-facing slopes to be favoured by hyrax because the early sun on these slopes affords an extra couple of hours foraging, therefore it seems reasonable to accept the one-tail statistical test which demonstrated the preference of hyrax for east-facing over west-facing slopes. There was no clear evidence in this study that strong wind prevented colonisation of certain slope aspects as observed by Sale (1966a), but wind did inhibit foraging behaviour.

Demography

The majority of rock hyrax in the Nuweveld mountains exist in many similar-sized groups spread out through the available habitat. The size of these groups must be subject to various constraints: as groups become larger, competition for food and shelter increases (Hoeck *et al.* 1982); and increased aggression in less-cohesive large groups might cause social disruption with male monopolies unsuccessful and some females unmated (e.g. Downhower & Armitage 1971). A decrease in group size however, may lead to inbreeding and greater predation risk (especially of young) through lowered vigilance, guarding and defence (e.g. Rasa 1986). One would expect that a trade-off of these various constraints would result in an ideal group size.

The relationship between group size and habitat observed in the study population probably results from competition for food and shelter in the presence of predation. Groups were larger in habitats such as escarpment pillars and boulder screes, where an abundance of large crevices allows safe access to a wide foraging range (non-breeding animals may be coerced out of these favourite habitats). Sparse crevices along flat sandstone outcrops and dykes probably cannot accommodate large groups. Large groups in boulder screes coped with inferior crevices by fragmenting, perhaps encouraging the formation of complexes in this habitat. Most multiple-harem groups occurred in kloofs where a source of abundant food and perhaps water reduces the constraints operating on increased group size, and where a dense and complicated distribution of crevices can accommodate high numbers and splinter groups. Male monopolies would be more difficult to maintain under these conditions.

Despite these influences, there was a distinct central tendency in the study population for harem groups to approach 16,4 individuals. This group size is probably advantageous in this environment. It is smaller than that observed by Fourie (1983) in the Mountain Zebra National Park (MZNP), and by Hoeck (1982) in the Serengeti, both higher rainfall areas where more rapid renewal of resources would permit larger groups. Use of this mean group size to determine a population estimate is preferred to the habitat sampling method for the following reasons: group-plotting was a more direct and extensive indication of the population; the distribution of hyrax was not very predictable for extrapolation; and habitat strips had to be chosen for practical reasons rather than randomly. Simple extrapolation of hyrax density with the extent of rock outcrops would over-estimate hyrax numbers in situations where two refuge habitats occur in close proximity to one another and where certain hyrax groups are mobile between both habitats.

In 1984 hyrax density in the KRNP was estimated at 72 - 94km^{-2} (Fairall *in litt.*). This was probably during the widespread decline (Chapter 1), for numbers apparently declined further by the time of this study. The deduced density (35,2km^{-2}) for the study area in 1989 was far lower than that (376km^{-2}) crudely estimated for the MZNP by Fourie (1983). The latter study was carried out in a wetter area prior to the widespread decline. Hyrax biomass in the most favoured kloofs (3,7kgha^{-1}) was lower than the recommended carrying capacity for sheep in the area (@16kgha-1), and did not even approach the extraordinary biomass levels (26-109kgha-1) recorded for two rock hyrax species inhabiting Serengeti koppies (Hoeck 1982). However, these latter estimates are misleading as the full foraging ranges of the animals (which included some of the surrounding grassland) were not taken into account.

The sample of shot hyrax gave the only direct indication of population composition. The shot sample indicated a much more even adult sex ratio (1,2 females per male) than that indicated by interpretation of the group counts (3 females per male) or that recorded by Fourie & Perrin (1987b) from livetrapping at colonies in the MZNP (2,4 females per male, during November). Bias in sampling adult males or females is unlikely. The high incidence of males in the shot sample suggests that the groups must have contained more than one adult male each. It is possible that adult males were being retained in groups in a sexually quiescent state (as observed by Hoeck *et al.* 1982; van der Merwe & Skinner 1982) in order to maintain an advantageous group size under low density conditions. Small groups would suffer especially high predation at low density. Peripheral males largely disappeared during 1988, they may have been incorporated into the groups. It is relevant to note that of the two colonies monitored by Fairall (*in litt.*) which both supported more than 20 hyrax initially (1981), the more exposed site (Die Gat) experienced a more drastic decline (to zero) and did not recover beyond a few individuals, while the more established and protected colony (Moordenaarsgat) did not drop below 9 individuals and had returned to former numbers by 1987.

High mortality of juveniles (@55%p.a.) recorded in this study appears to be commonplace (Fourie 1983). Juveniles suffer high predation pressure from a very wide variety of predators (e.g. Davies 1989), and this may have contributed to the evolution of a restricted breeding season (unexpected in unpredictable environments). Juvenile mortality was lighter during 1989 following heavy summer rains. Fourie (1983) witnessed similar effects in the MZNP and used population models to demonstrate the profound influence of variable juvenile mortality on hyrax population dynamics.

The heavy mortality evident during 1988 might have been linked with the earlier widespread decline. This earlier decline coincided with extremely high losses of springbok at two localities in the Karoo (Davies 1985; Liversidge pers. comm.) and of other ungulates in southern Africa (Knight pers. comm.; Williamson & Mbano 1988), suggesting a strong link with drought. Fairall (*in litt.*) stressed the importance of drought and increased predation as causative agents for the hyrax decline. Summer rains at the beginning of 1988 and at the end of 1988 were both below average for the KRNP, so 1988 could be considered a year of drought.

Skulls collected in the KRNP were the most direct indication of mortality pattern and suggested good adult survival until eight years old - this is when dental attrition becomes apparent. The evidence suggests a stable age structure with old animals comprising a small fraction (6-7%) of the population. Numbers of old animals were exaggerated by interpretation of the skull collection, unless corrected for a declining population.

The erratic karoo rainfall appeared directly responsible for annual variation in hyrax recruitment, and thus population structure. This relationship may have been more responsible for irregularities in the age distribution than the variable mortality (which can affect all age classes). Evidence for this relationship came from the distribution of birth dates in the shot sample as well as from the annual counts. Better recruitment in wetter conditions has been recorded for hyrax in other karoo localities (Millar 1971). Rainfall preceding the birth-pulse showed a very close relationship with recruitment. Moist vegetation from recent rains is probably important for lactating females.

Mean litter size recorded in this study was quite similar to that recorded elsewhere in the Karoo (Van der Horst 1941; Millar 1971; Fourie & Perrin 1987a). Fecundity data from the shot females suggested that the number of juveniles counted at the end of 1989 was a close measure of the number of juveniles actually born that year. But this is only an indication, and the adult sex ratio used in the fecundity calculation was based on a limited sample. The number of juveniles seen is likely to be a slight underestimate of recruitment. Higher fecundity of females shot one month prior to the 1990 birth-pulse was probably due to exceptionally good rains the previous summer, but it was incompatible with the low number of juveniles observed in December (which were confirmed by repeated counts). Nineteen ninety was particularly dry with very little rain falling between September and November. The low number of juveniles observed might either be due to early infant mortality within the crevices (this is unlikely to pass unseen as juvenile rock hyrax emerge on their first day, Millar 1971), or to late foetal loss - by resorption or mummification *in utero*. Higher foetal loss was observed in dry conditions by Millar (1971) and Fourie (1983), the latter reported one incidence of late foetal resorption. The ability to resorb foetuses at a late stage would be highly adaptive for hyrax in an unpredictable environment.

The relatively high incidence of adult males in the study population, as indicated by the shot sample, appears to be an effect of drought. Within the shot sample, males predominated in age classes that were born during dry conditions, while females predominated in age classes that were born during wet conditions. The study was preceded by a major drought. Greater neonatal size of males (Millar 1971) might confer greater survival of male offspring in dry conditions, but should not confer greater survival of female offspring under wet conditions. It is possible that more males were born during dry conditions, and the sex ratio amongst foetuses collected in the very wet year of 1989 (1.6 females per male, n=18) suggests that more females are born in wet conditions. More data on this topic are considered in Chapter 10. Further, large-scale collections are needed to confirm these indications but sex-biased offspring have been observed for a variety of mammals (Simpson & Simpson 1982; Verme 1983: Clutton-Brock 1985), and even for birds (Dijkstra, Daan & Buker 1990).

The relationship between rock hyrax foetal sex ratio and rainfall as suggested here may simply be an effect induced by the environment (e.g. through timing of breeding, or differential likelihood of resorption for different-sized foetuses). But the studies listed above have often linked biases in foetal sex ratio to the social status or body condition of the mother, and adaptive explanations are offered. In keeping with Clark (1978), female rock hyrax suffering from the effects of local resource depletion should produce more sons (which are likely to disperse) than daughters (which are likely to remain and antagonise local resource depletion). However, Armitage (1987) suggests that such explanations should be based on the long-term reproductive potential of the offspring.

Male hyrax have a greater reproductive potential than females if they can overcome the risks incurred by predation during dispersal, and from agonistic encounters during establishment. In populations known to fluctuate markedly, male dispersal should be most successful at the start of a population decline (during drought) when predation risk would still be low (at high density), and when prospects for establishment should begin to increase. The risk of predation for dispersing male hyrax may also be reduced during dry conditions if all hyrax are forced further from their rocks to feed.

The dramatic response of hyrax mortality and recruitment to a variable climate results in an irregular and a very dynamic population structure. Smoothing of the age distributions and the use of life tables to generalise about this structure would only be valid for a hypothetical hyrax population in a constant environment.

Behaviour

By feeding very intensively and synchronously during group-foraging bouts, and by routinely using different parts of their range on consecutive days, hyrax groups make extremely efficient use of the time that they spend away from the safety of their colony rocks. This efficiency effectively enables hyrax to minimise risky foraging behaviour (Sale 1965). Other researchers have noted that hyrax groups may travel 500m down slopes in order to forage in riparian thicket (Fourie 1983). A rich food supply and a relatively safe feeding environment in riparian thicket are the most probable explanations for this behaviour and for the tendency for colonies to be located near to river courses (Fig. 22). Sale (1965) noted that the distribution of hyrax groups in the Mackinder Valley was more influenced by vegetation quality (along streams) than by availability of refuge. Daily time allocated to feeding by hyrax in this study (2,06h) was slightly lower than that recorded elsewhere in a wetter region (2,4h - Fourie 1983), and this is suggestive that hyrax in the present study were not unduly stressed by food availability. This is to be expected given low hyrax densities and reasonable rainfall. Even so, there was some indication of groups venturing further from shelter when conditions were drier and this is supportive to Allan's (1988) speculation on variation in the availability of prey to black eagles (page 26).

Sentinel behaviour was not apparent all the time, and was only obvious during group-foraging bouts. This is when hyrax are probably most vulnerable to predation because they venture furthest from shelter and fewer individuals are vigilant. Alarm-calling is a very effective anti-predator behaviour for rock hyrax. Group members showed synchronised and well-defined responses to particular calls (as observed by Sale 1965), and it seems likely that the alarm calls convey much information on the nature of the attack as has been demonstrated for dwarf mongooses *Helogale undulata* (Beynon & Rasa 1989). It was clear though that only certain individuals proved effective at alarm-calling. Failure of low-ranking individuals to warn of danger as observed in this study has also been witnessed in vervet monkey *Cercopithecus aethiops* groups where withholding information may construe some long-term advantages to the individual (Cheney & Seyfarth 1985). An essential condition for the effectiveness of these 'early warning systems' is obviously that the alarm should be clearly audible to group members. Ineffectiveness of alarm calls is probably a major reason why hyrax did not venture far from sentinels under very windy conditions and why they did not enter riparian thicket on such days. However black eagle activity is also enhanced on windy days (Chapters 6 & 8).

High nitrate concentrations in hyrax faeces probably enable strong germination of seeds in the faeces and thus give rise to the verdant flush of vegetation around rock crevices after good rains. The same phenomenon has been observed around woodchuck *Marmota monax* burrows (Merriam & Merriam 1965). Hyrax are probably least vulnerable to predators when they can graze this luxuriant vegetation literally at their doorsteps. Predominance of unpalatable plants close to refuge sites is also a common effect of heavy grazing by small herbivores (Farrow 1917; Koford 1958; Huntly, Smith & Ivins 1986). Central-place foraging theory (Orians & Pearson 1979) predicts this, and also that plant abundance and plant species diversity should increase with distance from refuge, as observed in this study. One might expect that hyrax would feed more selectively further out from shelter in keeping with predictions and other studies (e.g. Huntly *et al.* 1986). Most studies of vegetation patterns around refuge sites used by small herbivores indicate either multiple vegetation zones radiating outward (Farrow 1917; Koford 1958; Merriam & Merriam 1965) or a gradual/clinal change in plant composition (Hall 1960; Huntly *et al.* 1986; Huntly 1987), and this is in keeping with predicted gradual changes in travel costs and in accessible feeding area (Huntly 1987; Fig. 38). However in this study, various lines of evidence point to one major vegetation zone and a clear cut-off in feeding at about 15m from refuge. This cut-off boundary appears very distinct, especially with regard to the distributions of palatable and unpalatable plants. It begs the question of why the hyrax do not travel 16m from the rocks and access a much richer food supply, and it suggests that some other factor is restricting their movements. I would speculate that the cut-off in feeding at 15m represents a trade-off between increased foraging return and increased risk of predation. The apparent absence of this phenomenon in other small, refuging herbivores may be due to the fact that most of these herbivores can modify their refuge environments, and / or the hyrax may be exposed to a greater degree of predation risk. Such trade-offs have been suggested to explain complex behaviour in a wide range of animals (reviewed in Lima & Dill 1990). Both direct observations and vegetation analyses indicated that hyrax prefer to feed and live within distinct confines of a refuge environment. This may lead to increased agonistic behaviour and reduced breeding through crowding effects and thus influence demography. It seems likely though that hyrax would venture from the refuge area under very high density conditions and they have been observed to do so while dispersing.

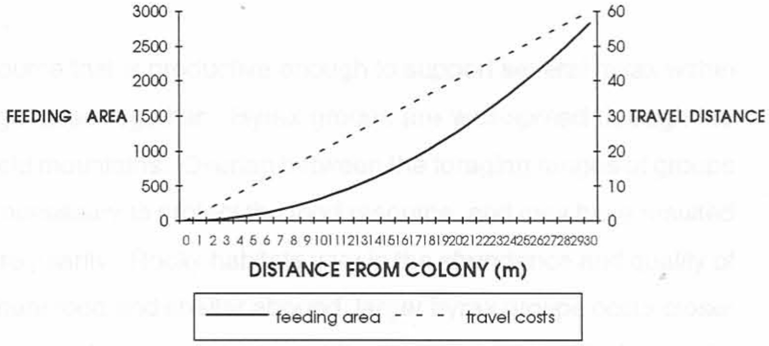


Figure 38. Model of how hyrax travel costs and the amount of accessible vegetation (food) would be expected to change at increasing distance from the colony rocks

The link between cavernicolous and gregarious behaviour

Burrowing is not an option in the hard, rocky mountains of Africa where hyrax have chosen to use the abundance of rock crevices for a comfortable microclimate, shelter from predators, and safe access to a rich forage supply. To inhabit rock crevices, hyrax have become much smaller than their ancestors (Sale 1970a), and by so doing have become vulnerable to a wider variety of predators which abound in the mountainous terrain and hunt by day, including some highly mobile raptors. Furthermore, the adaptations necessary for living amongst rocks such as short legs and a stout build make hyrax relatively slow and vulnerable in the open. Hyrax can easily be outrun by humans on flat ground (pers. obs.). Hyrax cope with this vulnerability by minimising foraging time spent away from rocks, by dispersing at night, and by living in groups (enhanced vigilance and early warnings).

Groups of animals are more conspicuous but increased predator interest is countered by increased vigilance, group defence, and by making use of sentinels. Other advantages of living in groups, such as huddling and easy procurement of mates, are more likely to be spin offs of gregariousness rather than primary causes for it. The patchy distribution of suitable crevices, which are a non-depletable but limited resource may also give added incentive to share, and provides males with the opportunity to monopolise female groups by defending this discrete critical resource (see Emlen & Oring 1977). This system leads to male dispersal and female phillopatry (Clark 1978). Sociality appears to have been encouraged in marmot species living in limited environments where they take longer to reach a safe dispersal size, and Olympic marmots can vary the timing of their dispersal to suit environmental conditions (Barash 1974). Social tolerance amongst hyrax might be encouraged for the same reasons in the arid unpredictable climate of the Karoo. The growth rate of juvenile hyrax is markedly influenced by food supply (Millar 1971).

The variability of hyrax recruitment and mortality must drastically alter population composition in response to climatic change. The observed flexibility in hyrax social organisation to accommodate these effects demonstrates the importance of maintaining a sensible group size. This group size is probably primarily a compromise between predator detection and the availability of food and shelter.

One requirement of living in groups is for a food resource that is productive enough to support several hyrax within the individual's range and to allow animals to forage close together. Hyrax groups are well-spread through the complicated network of rocky habitats in the Nuweveld mountains. Overlap between the foraging ranges of groups appears small, territoriality between groups may be necessary to protect the food resource, and may have resulted in a group dispersion pattern which tended towards regularity. Rocky habitats vary in the abundance and quality of crevices, and in the richness of accessible food. Where food and shelter abound, larger hyrax groups occur closer together. Each group occupies part of the rocky network within which they are mobile, using outcrops with high quality crevices for colony locations, and outcrops with well dispersed crevices to access their renewable food resource.

Refuge appears to be the second major requirement for group-dwelling in hyrax-sized mammals. The increased activity of groups of animals would attract attacks from predators, especially raptors, which cannot easily be outrun. All similar-sized gregarious mammals burrow or use some form of existing shelter (e.g. King 1959; Barash 1974; Cowan & Bell 1986; Rasa 1986; Herzig-Straschil 1978). Enhanced predator detection would not be an incentive for group-dwelling if the prey could not rely on an avenue for escape. In this way, the caverniculous behaviour of rock hyrax has facilitated and maybe even encouraged gregarious behaviour and the two habits have become inextricably linked.