CHAPTER 5

DISTRIBUTION AND ABUNDANCE OF ALTERNATE PREY

PART 1: RED ROCK RABBITS

INTRODUCTION

Red rock rabbits (*Pronolagus* spp.) are nocturnal and generally solitary lagomorphs that occur in a wide range of rocky habitats in southern and eastern Africa (Ansell 1960; Smithers 1971; Peddie 1975; Skinner & Smithers 1990). They do not burrow and can often be found lying up in a form, relying on crypsis and dextrous escape over rocks to evade predators. Such habits suggest some behavioural affiliation with hares but the chromosome complement of red rock rabbits establishes their evolutionary identity as rabbits (Robinson 1981). Their small hindlimbs suggest that escape from predation involves the use of cover, rather than sheer speed (Cowan & Bell 1986), and indeed they are observed to find refuge amongst loose rocks, in rock crevices and in dense vegetation where they create an open nest and bear their altricial young (Skinner & Smithers 1990).

They are predominantly grazers (Stewart 1971) and produce copious amounts of characteristic disk-shaped faecal pellets which they deposit in regular middens (Peddie 1975; Skinner & Smithers 1990). This suggests an unselective, bulk-feeding habit which may be a consequence of restrictions on movement imposed by refuge requirements (Cowan & Bell 1986). Demographic information can often be easily obtained from regular defecation habits (Putnam 1984): faecal pellets (and pellet groups) have been successfully used to estimate abundance of deer (Davis 1982), water voles (Woodroffe & Lawton 1990), and leporids (Taylor & Williams 1956; Angerbjörn 1983; Krebs, Gilbert, Boutin & Boonstra 1987). The use of middens or latrines has been associated with territoriality in mammals as widely varying as water voles (Woodroffe & Lawton 1990), rabbits (Mykytowycz 1966), badgers (Kruuk 1978; Roper, Sheperdson & Davies 1986), deer (Green 1987), antelopes (Owen-Smith 1977) and rhinoceros (Owen-Smith 1971). Pepler (1990; pers. comm.) implicates a territorial habit in Smith's red rock rabbit, *Pronolagus rupestris*.

Smith's red rock rabbits (here-on referred to as red rock rabbits) are numerous in the KRNP, and early observations indicated that they were an important alternate prey for black eagles (see Chapter 9). To provide a comprehensive understanding of the predator-prey system under investigation, it was necessary to find out how many red rock rabbits there were in the different habitats of the KRNP. A study of red rock rabbit habitat selection was facilitated by the prevalent use of middens in this cryptic species. Numbers of rabbits could be linked to numbers of middens on the basis of faecal accumulation rates on middens. Field work and analysis for this investigation was jointly carried out by Elsabe Aucamp (for an honours project) and myself. The study also suggested a link between use of middens, territoriality and the use of refuge, which is relevant to this thesis on predation. This chapter is divided into two parts: in the second section, data on the distribution and abundance of other potential prey species (mostly from incidental sightings, and the helicopter counts - see Chapter 2) are considered.

METHODS

Straight-line transects of one kilometre in length were conducted randomly in each of the major topographical habitats of the KRNP until the number of middens encountered exceeded the sample size recommended by Burnham, Anderson & Laake (1980). Approximately 18 transects were completed for each habitat except the bottom plains where no middens were encountered. The route of each transect was noted and marked out for possible future repetition. The size, perpendicular distance from the transect line and the position along the transect for each midden encountered was recorded, along with a visual assessment of the local microhabitat for each midden. The microhabitat variables recorded are described in Table 7. To compare microhabitats of the middens with microhabitats available, the same variables were recorded regularly every 250 paces along each transect line. These latter recordings also provided data for comparisons of the major topographical habitats.

TABLE 7

A DESCRIPTION OF THE MICROHABITAT VARIABLES THAT WERE VISUALLY ASSESSED FOR EACH MIDDEN AND AT REGULAR INTERVALS ALONG EACH TRANSECT LINE

VARIABLE	RATING	DESCRIPTION
SLOPE	0	flat
	1	gentle slope
	2	steep slope
	3	sheer cliff
ORIENTATION	-	N, NNW, NW, WNW, W ... etc.
ALTITUDE	1	bottom plains (910m)
	2	lower slopes, gentle (988m)
	3	lower slopes, intermediate (1065m)
	4	lower slopes, steep (1143m)
	5	middle plateau (1220m)
	6	upper slopes, gentle (1373m)
	7	upper slopes, intermediate (1525m)
	8	upper slopes, steep (1678m)
	9	upper plateau (1830m)
LOCAL ROCK TYPE	0	no rocks
	1	small loose rocks (most <10cm high)
	2	large loose rocks (most >15cm high)
	3	boulder scree (most >1m high)
	4	sandstone lens outcrop
	5	surface knoll of dolerite on plateau
	6	dolerite/sandstone escarpment
DISTANCE TO ROCKS	m	estimated distance to nearest substantial rock outcrop that could potentially afford secure shelter to a rabbit
DISTANCE TO WATER	m	estimated distance to the nearest episodic water course
PLANT COVER	0-9	0% plant cover - 90% plant cover (occular estimate)
BUSH:GRASS RATIO	0-9	0%shrub/100%grass - 90%shrub/10%grass (occular estimate)
DENSITY OF LARGE SHRUBS	0	no large shrubs
	1	scattered large shrubs
	2	thicket
	3	dense trees

Overall midden density in mountainous terrain was assessed using a fixed width transect based on the frequency distribution of middens at varying distances from the transect line. Midden densities in each of the major topographical habitats were assessed using both the model of Eberhardt (1968) for transects of indefinite width, and the Fourier series estimator for ungrouped data recommended by Burnham *et al.* (1980).

As part of an intensive, localised study, all middens (n=56) in a 12,3ha study area at Mountain View on the upper plateau were plotted on an aerial photograph. The spacing pattern of these middens was investigated using the G-statistic as described in the previous chapter (pages 39-40).

Twenty to 45 of these middens (mean=35) within the Mountain View study area were cleared of fresh faecal pellets every second day for an eight-day period in January 1990 and two further eight-day periods in July 1990. The area was also regularly screened to check for faecal pellets distributed away from middens. The literature was consulted for estimates of defecation rates of *Pronolagus* and similar species, so that faecal accumulation rate per midden could be used to indicate the ratio of animals to middens.

Further to this, three rabbits were captured on the Mountain View study area by the method of Pepler (1989), and force-fed a liquid paste consisting of a fluorescent pigment and Pro-nutro cereal (Nutri product, Milchik, R.S.A.) diluted with water. The paste was introduced past the back molars of the animal using a syringe. This stimulated swallowing and proved more successful and less risky than stomach intubation when practised on domestic rabbits. Different pigments were used for the different individuals. The rabbits were captured and released during periods of faecal pellet collections, and the collections from each midden were inspected under ultra-violet light to trace the subsequent movements and defecation rate of each treated rabbit.

A third indication of the ratio of animals to middens was obtained from energetic considerations. Mean mass for a faecal pellet was assessed in summer and winter by collecting ten pellets from each of ten middens in the Mountain View study area, and drying these at 65°C for four days before weighing. The energy content of ten summer pellets and ten winter pellets was assessed by bomb calorimetry. From the average faecal accumulation rate, it was possible to predict the average amount of faecal energy accumulating per midden per night. The amount of energy digested that this represents was then estimated from appropriate figures of digestive efficiency obtained from the literature, and this figure was compared with predicted energy requirements of an average rabbit.

Fresh faecal pellets were collected from a further 63 middens outside the Mountain View study area during the course of line-transect sampling in order to check for differences in midden use between the major habitats. This was necessary to ascertain whether the ratio of animals to middens determined in the Mountain View study area could be extrapolated to other areas of the park.

RESULTS

Appraisal of the major topographical habitats

Significant variation in the physiognomy of the major topographical habitats was revealed by the microhabitat assessments along the transect lines. Non-parametric, one-way analysis of variance (Kruskal-Wallis tests) showed statistically significant differences between the major habitats for the following parameters: plant cover (X^2=127,3; d.o.f.=4; p<0.01); bush to grass ratio (X^2=109,7; d.o.f.=4; p<0.01); density of large shrubs (X^2=97,1; d.o.f.=4; p<0.01); distance to rocks (X^2=83,8; d.o.f.=4; p<0,01); and distance to water (X^2=71,6; d.o.f.=4; p<0,01). After aggregation of appropriate local rock type categories, contingency table analysis revealed statistically significant differences between the major habitats for this parameter also (X^2=66,3; d.o.f.=8; p<0,01). For values of these parameters in the major topographical habitats refer to Table 1 (p. 20).

Density of middens in the major topographical habitats

By plotting the number of middens encountered at varying intervals to the transect line (Fig. 39), it was established that most, if not all, middens within 3m on either side of the transect line were detected. A total of 187 middens were detected within this fixed width transect 6m wide and 73000m long (bottom plains excluded). An overall density of 427 middens/km^2 of mountainous terrain is inferred.

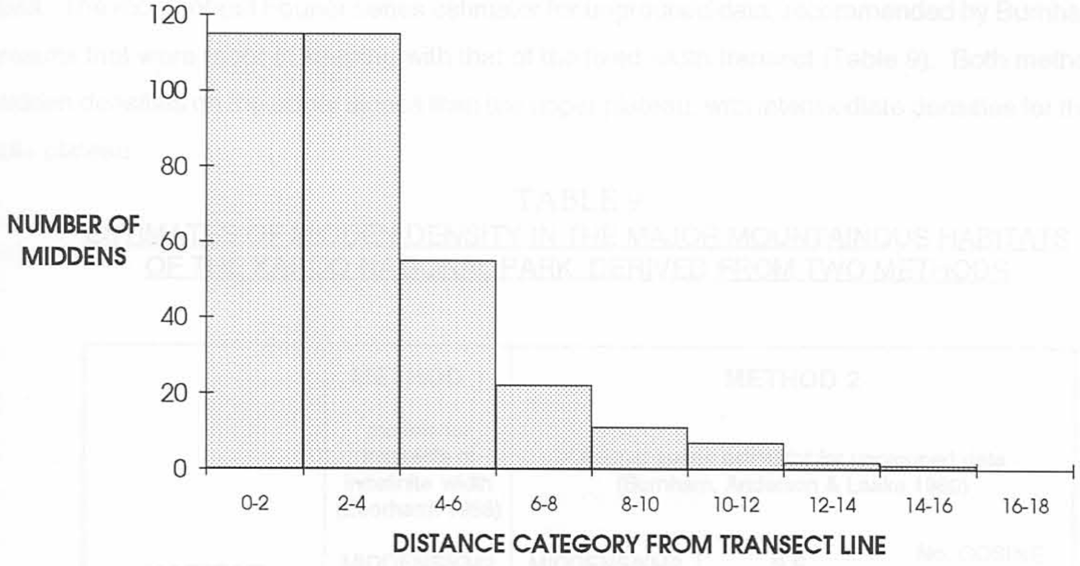

Figure 39. Frequency histogram showing the number of middens detected at varying distance categories from the transect line. It was assumed that all middens within 3m of the line were detected (see text).

There was no significant difference in the number of middens encountered per transect for the four mountainous habitat types. However, there was a significant difference in the mean perpendicular distances that middens were

TABLE 8

NUMBER OF MIDDENS ENCOUNTERED AND THEIR AVERAGE PERPENDICULAR DISTANCES FROM LINE TRANSECTS COMPLETED IN THE MAJOR TOPOGRAPHICAL HABITATS

HABITAT	TOTAL NUMBER OF TRANSECTS	TOTAL NUMBER OF MIDDENS	MEAN PERPENDICULAR DISTANCES (m)	MEAN NUMBER OF MIDDENS PER TRANSECT
UPPER PLATEAU	19	76	3,06 (sd=2,15)	4,00 (sd=2,98)
UPPER SLOPES	18	80	2,60 (sd=1,93)	4,44 (sd=2,59)
MIDDLE PLATEAU	18	92	3,94 (sd=3,21)	5,17 (sd=4,05)
LOWER SLOPES	18	79	3,24 (sd=2,35)	4,39 (sd=3,47)
BOTTOM PLAINS	4	0	-	-
TOTAL	77	327		
1-WAY ANOVA ON MOUNTAINOUS HABITATS (bottom plains excluded)			F=4,30 p<0,01	F=0,40 p>0,10

detected from the transect line for the different mountainous habitats (Table 8). In particular, most middens were detected close to the transect line on the upper slopes, especially when compared with those encountered on the middle plateau.

Eberhardt's (1968) model for transects of indefinite width yielded very high estimates of midden density in the major habitats when compared with the fixed-width transect (Table 9). Furthermore, the fit of the probability of detection curve to the raw data was only close for one habitat, the lower slopes, and was not statistically significant for the upper slopes data. The more robust Fourier series estimator for ungrouped data, recommended by Burnham *et al.* (1980) yielded results that were more in keeping with that of the fixed width transect (Table 9). Both methods suggested higher midden densities on the upper slopes than the upper plateau, with intermediate densities for the lower slopes and middle plateau.

TABLE 9

ESTIMATES OF MIDDEN DENSITY IN THE MAJOR MOUNTAINOUS HABITATS OF THE KAROO NATIONAL PARK, DERIVED FROM TWO METHODS

HABITAT	METHOD 1	METHOD 2		
	models for transects of indefinite width (Eberhardt 1968)	Fourier series estimator for ungrouped data (Burnham, Anderson & Laake 1980)		
	MIDDENS/KM2	MIDDENS/KM2	S.E.	No. COSINE TERMS
UPPER PLATEAU	417,3	401,9	55,4	2
UPPER SLOPES	651,3	552,7	79,4	3
MIDDLE PLATEAU	524,1	474,8	73,3	3
LOWER SLOPES	471,7	415,6	58,1	2

Smaller-scale habitat preference

There was no significant association between midden density and altitude. However, midden density did vary with orientation. Within the lower slopes habitat type, there was a statistically significant difference in the number of middens encountered per transect between slopes of varying aspect (Kruskal Wallis 1-way anova: X^2=9,2; d.o.f.=3; p<0,05). Particularly low numbers of middens were encountered along transects on northerly aspects (mean=0,4; n=5). High numbers of middens were encountered along transects on southerly (mean=6,8; n=4) and westerly (mean=5,8; n=6) aspects. The same trend was apparent within the upper slopes habitat type, but small samples of especially northerly aspects (n=1) precluded any tests.

There was a tendency for more middens to be encountered along transects running across gentle slopes (mean=5,3; n=13) than along transects running across steep slopes (mean=3,9; n=23). This tendency was not statistically significant. However, a X^2 contingency table comparing observed frequencies of middens for the various slope ratings with expected frequencies (as derived from the microhabitat assessment loci) revealed a statistically significant association between middens and slope rating (X^2=7,9; d.o.f.=2; p<0,05). As indicated previously, middens were positively associated with gentle slopes and negatively associated with steep slopes. Flat areas appeared to be used roughly in proportion to their availability.

There was no evidence that local plant cover or the density of large shrubs might influence the distribution of middens. However, midden loci had higher average bush:grass ratios (more shrubby) than microhabitat assessment loci when compared for each transect. This difference was statistically highly significant (t-test for matched pairs: t=3,27; p<0,01).

Middens on the lower slopes occurred significantly closer to episodic water courses than expected from the microhabitat assessment loci (unequal variances t-test: t=2,53; d.o.f.=130,5; p<0,05). No such differences were obtained for the middle plateau or upper slopes. By contrast, middens on the upper plateau occurred significantly farther from the water courses than expected from the microhabitat assessment loci (equal variances t-test: t=-2,63; d.o.f.=167; p<0,01).

Midden loci on plateaus occurred closer to substantial rock outcrops (mean=39,5m; s.d.=73,3; n=168), than expected from microhabitat assessment loci (mean=74,2m; s.d.=135,0; n=185). This difference was statistically highly significant (unequal variances t-test: t=3,04; d.o.f.=289,3; p<0,01). There was no evidence for association between midden loci and substantial rock outcrops on either of the slope habitats.

The observed frequencies of the various rock categories associated with midden loci were compared with their expected frequencies derived from the microhabitat assessment loci. On the plateaus there was a statistically highly significant association between middens and certain rock types (X^2=63,6; d.o.f.=4; p<0,01). In particular, middens were negatively associated with non-rocky areas and positively associated with large loose rocks and boulders (as an aggregated category). On the slopes, where non-rocky areas are negligible (Table 1, page 20), middens were positively associated with small loose rocks at the expense of all larger outcrops (X^2=16,1; d.o.f.=3; p<0,01).

Distribution of middens at Mountain View

The 56 middens located in the rocky 12,3ha study area at Mountain View represent a density of 455 middens/km^2 which is compatible with those estimates given previously. Analysis of the nearest-neighbour distances between these middens yielded a G-value of 0,67 indicating a dispersion pattern that was borderline between regular and random.

Faecal accumulation rate

Eleven collections of faecal pellets were made from the Mountain View middens spanning the three sampling periods. The first collection in each sampling period was excluded from analyses because of ambiguity in the classification of fresh (<2 days old) faecal pellets. A total of 9223 fresh pellets were collected during the remaining eight samples which represent the accumulations of 463 midden nights. A nightly accumulation rate of 19,9 faecal pellets per midden is inferred. The accumulation of pellets varied widely between middens and also between collection dates. No faecal pellets were found outside of middens despite searching.

Although collections of fresh faecal pellets from middens within the Mountain View study area were generally smaller than those collected elsewhere (n=63), we could detect no significant differences between the study area and other habitats in this regard.

Recovery of faecal pellets marked with fluorescent pigments

The first captured rabbit treated with fluorescent pigment received high dosages of the pigment over an extended capture period. After release of this rabbit a total of 201 marked faecal pellets were detected, distributed over eight middens up to six nights after release. The second and third captured rabbits received single doses of pigment and were released immediately. Fewer marked faecal pellets were detected from these rabbits (totals=107 and 81). These pellets were distributed over three middens each and were collected up to four nights after release for both individuals.

Energy content of faecal pellets

Faecal pellets collected during July were heavier (mean mass=0,238g; s.d.=0,025; n=100) than those collected during January (mean mass=0,207g; s.d.=0,037; n=80). This difference was statistically significant (Mann-Whitney U test: $z=2,18$; $p<0,05$). Mean mass (dry weight) for all pellets weighed was 0,223g. Energy content of pellets was very similar for the two periods: ten pellets assessed in January had an average energy content of 19,05KJ/g (s.d.=0,32); ten pellets assessed in July had an average energy content of 19,08KJ/g (s.d.=0,51). An average faecal pellet contains 4,25 kilojoules of energy.

DISCUSSION AND POPULATION ESTIMATE

Middens as indicators of habitat preference

Most census methods employed concurred that red rock rabbit middens occur at densities of about 400-500 km^{-2} in the rocky, mountainous habitats of the Karoo National Park. Little faith can be placed in the excessive density estimates derived from Eberhardt's (1968) model for transects of indefinite width, as this model did not adequately describe the probability of detection curve. The robust Fourier Series estimator provided estimates of density (with reasonable standard errors) that were more compatible with density estimates derived from the fixed width transect and the mapping of middens at Mountain View.

Although encounter rates for middens were not significantly greater per transect in the upper slopes habitat, greater densities in this habitat can be inferred from perpendicular distance data which indicate lower detectability of middens in this more difficult terrain. Both models for density estimation presented the same order of habitat preference: upper slopes > middle plateau > lower slopes > upper plateau. Preference for upper slopes over lower slopes might be due to generally taller vegetation, better distribution of boulder outcrops and the absence of northerly aspects. Comparable densities might have been found for lower slopes if northerly aspects had been excluded. Such high densities on slopes are probably permitted by a close dispersion of large rock outcrops and the near absence of non-rocky areas. Preference of the middle plateau over the upper plateau as indicated by midden density is probably due to a large proportion of unsuitable (non-rocky) terrain in the latter habitat type.

Despite documented accounts of a dietary preference for grasses by *Pronolagus* spp. (Stewart 1971; Peddie 1975), this study showed that middens occurred at significantly lower density in very grassy areas. Some shrubs may be required to provide shade and cover for resting rabbits. But north-facing aspects tend to be the most grassy areas, and these slopes may simply be too hot during the day to offer comfortable resting spots. Thermoregulatory constraints have been shown to influence the dispersion of other small mammals such as the Alpine marmot (Turk & Arnold 1988).

Gentle slopes were the favoured gradient in this study. Widely-dispersed loose rocks on gentle slopes probably afford ideal escape routes for red rock rabbits, and indeed middens were positively associated with this rock category. The less rocky flat areas (plains and plateaus) were neither preferred nor avoided overall. Steep slopes were avoided, possibly because this habitat encompasses difficult terrain, with bare screes covering wide areas.

The observed relationship between the distribution of middens and that of episodic water courses is obscure. Avoidance of water courses on the upper plateau may be a consequence of the fact that most water courses in this habitat are situated in non-rocky, small valleys (unlike all other habitats). Water courses on the lower slopes, by contrast, descend through gulleys which afford shelter amongst rocks and riparian thicket. Rabbits might also be attracted to such thickets on the lower slopes for moisture in the vegetation. There was no evidence that middens were aggregated around water courses on the more mesic upper slopes.

The low frequencies of middens and microhabitat assessment loci encountered on large substantial rock outcrops did not indicate that these features were significantly preferred. However, middens were definitely aggregated around such outcrops in the plateau habitats. This is probably due to these features being in short supply on the flat areas. Rabbits inhabiting the mountain slopes are probably never far from such outcrops, especially on the boulder-strewn upper slopes. It seems likely that the rabbits require access to these features within their ranges.

Large rock outcrops are probably important to red rock rabbits for the refuges they provide in rock crevices. The observation that red rock rabbits can also lie up in forms amongst the vegetation suggests that rock crevices are required as shelter from predators rather than from the elements. Availability of such refuge might be more critical for the survival of juvenile rabbits than adults. Although *Pronolagus* spp. are recorded to nest amongst dense vegetation (Skinner & Smithers 1990; Pepler 1990), it seems likely that interstices under or between rocks would be used by red rock rabbits in the less vegetated Karoo. Indeed two juvenile rabbits, when flushed, were observed to find sanctuary in holes under small boulders (pers. obs.).

Middens as indicators of rabbit abundance

The present conversion of estimates of midden density into estimates of rabbit abundance using faecal accumulation on middens is based on two preliminary assumptions that require justification. First, it is assumed that all faecal pellets are deposited on middens. Secondly, it is assumed that faecal accumulation rate in the Mountain View study area is representative of all habitats in the park.

Wild rabbits *Oryctolagus cuniculus* also use middens or 'dung-hills' for territorial purposes, and it has been shown that only a proportion of faecal pellets are deposited on these dung-hills (Mykytowycz & Gambale 1969). However, *O. cuniculus* (unlike *P. rupestris*) is a social species and use of middens in this species serves to define boundaries between groups, and varies with the social status of the individual (Cowan 1987). Middens of red rock rabbits are large, more frequent and appear to be more regularly spaced. In justification of the first assumption, no faecal pellets were found away from middens, even when searching with ultra-violet light to illuminate pellets marked with fluorescent pigment at night.

The absence of a significant difference between fresh faecal accumulations on middens in the various habitats is considered to be justification for the second assumption. The tendency for larger samples to be collected on middens outside the Mountain View study area is probably due to these being first collections - when separation of fresh pellets is more ambiguous.

Recovery of faecal pellets marked by fluorescent pigment from treated rabbits was disappointing. It appeared that the pigments were voided from the rabbits' digestive tracts too rapidly for meaningful evaluation of defecation rate and the number of middens visited. Some pellets were evidently overlooked on the first collection after release and picked up in later collections. But recovery of marked faecal pellets did indicate that daily defecation rate probably exceeds 150 pellets and that single animals range over at least 3-8 middens.

Although the deposition of faecal pellets on middens at Mountain View appeared highly variable, regular clearing of a large number of middens should have yielded a reliable estimate of average faecal accumulation rate per midden per night (19,9 pellets). Peddie (1975) reported that a captive *P. randensis* produced approximately 21g of faecal pellets per day (dry weight). This would correspond to 94 faecal pellets using our data which would indicate a ratio of approximately 4,7 middens per rabbit. However, the captive animal was a juvenile and was fed a high quality diet.

Oryctolagus cuniculus can produce up to 820 faecal pellets per day (Taylor & Williams 1956). The literature suggests lower defecation rates for other leporids: *Lepus timidus timidus* produced 200-450 faecal pellets per day (Lampio 1952); while *Lepus timidus scoticus* produced 208 (33-450) faecal pellets per day (Flux 1970). If red rock rabbits produce about 250 pellets per night, a ratio of 12,6 middens per animal is inferred.

The energy content of winter and summer faecal pellets was very similar but larger pellets were collected during winter. This might be due to a higher proportion of juveniles in the population during summer, or to rabbits consuming greater quantities of bulk food during winter.

The digestive efficiency of most leporids is about 50% (Slade & Hintz 1969; Holter, Tyler & Walski 1974; Mautz, Walski & Urban 1976; Walski & Mautz 1977). Therefore, 85KJ of faecal energy accumulating on the average midden each night can be taken to represent roughly 85KJ of energy digested, and 72KJ metabolised (80-90% of digested energy is usually metabolised by leporids: Walski & Mautz 1977). The field metabolic rate of a red rock rabbit weighing 1,62kg (mean mass given by Skinner & Smithers 1990) is calculated at $1280KJd^{-1}$, using Nagy's (1987) equation for eutherian herbivores. This is close to values estimated for black-tailed jackrabbits *Lepus californicus* of comparable mass (Shoemaker, Nagy & Costa 1976; French & Heasley 1981). It can be concluded that faecal energy accumulating on 17,8 middens represents sufficient energy metabolised to fulfil the requirements of a single adult rabbit. Actual ratio of middens per animal would be lower than this because a proportion of the population is comprised of juveniles with lower total metabolic requirements. Considering faecal production and accumulation rates (above) as well, the ratio of middens per animal probably lies between 13 and 18. It is concluded that a relationship of 15 middens to a single rabbit is realistic.

Estimates of rabbit abundance in the topographical habitats and the Karoo National Park using this ratio are given in Table 10. Midden density in the mountainous terrain of the park probably corresponds to an overall density of 30 rabbits/km^2, and biomass levels of about 45kg/km^2 (using a mean mass of 1,5kg). Density of *P. randensis* was estimated to be far higher (265 rabbits/km^2 of koppie habitat) in the wetter Matobo Hills National Park in Zimbabwe (Peddie 1975). The population size estimated for red rock rabbits in the Karoo National Park (n=6652) is approximately half that estimated for rock hyrax in the park (n=13335). Red rock rabbits are approximately twice as abundant on the rocky plateaus as rock hyrax, but the latter outnumber red rock rabbits by a factor of three on the mountain slopes (Table 4, page 48). Together these two small herbivores comprise the major component of the park's herbivore biomass, especially in the rocky areas. It should be noted that red rock rabbit numbers appear to be highly variable: there was a ten-fold difference in the number of rabbits encountered in 1987 and in 1989 (see Fig. 40b, p. 81).

TABLE 10
POPULATION ESTIMATE FOR RED ROCK RABBITS IN THE VARIOUS MAJOR HABITATS OF THE KAROO NATIONAL PARK

The extent of the park in this analysis was as described in Chapter 2. Surface areas for the respective habitats were determined by use of an image analyser and were compensated for gradient on the lower slopes (increased by 5,8%) and on the upper slopes (increased by 9,6%). Midden densities were derived using the Fourier Series Estimator (see text). An average ratio of 15 middens per rabbit was used to predict rabbit numbers (see text).

HABITAT	SURFACE AREA (km2)	MIDDEN DENSITY (No./km2)	NUMBER OF MIDDENS	NUMBER OF RABBITS	RABBIT DENSITY (No./km2)
UPPER PLATEAU	33,8	401,9	13596	906	26,8
UPPER SLOPES	42,1	552,7	23263	1551	36,8
MIDDLE PLATEAU	62,3	474,8	29566	1971	31,7
LOWER SLOPES	80,3	415,6	33356	2224	27,7
BOTTOM PLAINS	117,1	0	0	0	0
MOUNTAINOUS TERRAIN	218,5	456,8	99781	6652	30,5
ENTIRE PARK	335,6	297,3	99781	6652	19,8

Middens as indicators of territoriality

As stated in the introduction middens or latrines are associated with a territorial function in a diverse array of mammal species. Many of these mammals have evolved different ways of depositing olfactory signals on such latrines to advertise presence in their territory. This suggests strong selective pressure for this behaviour in territorial species. *Oryctolagus cuniculus* conveys olfactory signals via strategically distributed dung-hills by coating faecal pellets with a secretion from the anal gland and by 'chinning' on proximate landmarks, and the anal glands of territorial leporids are much larger than those of even closely-related non-territorial species (Mykytowycz 1968). Enlarged anal glands in red rock rabbits would be highly suggestive that middens fulfil a territorial function. Fresh faecal pellets on red rock rabbit middens are indeed characterised by a shiny, waxy coating (pers. obs.). Aggression and chasing, which often ensue between red rock rabbits after one has been disturbed from its area, are also highly suggestive that this species is territorial (Pepler 1990, pers. comm.).

Unlike most other territorial lagomorphs however, *Pronolagus* species are solitary. Dung-piles of *O. cuniculus* are mostly maintained by dominant animals in each group, and are often clustered on the boundaries between groups (Mykytowycz & Gambale 1969; Cowan 1987). Such latrines probably help stabilise relationships between neighbouring groups as in badgers (Roper *et al.* 1986). Red rock rabbit middens were not clustered in our Mountain

View study area. If all faecal pellets of this species are deposited on middens, the middens need to be practically placed within each individual's range for access, but sufficiently spaced to act as strategic indicators of presence (which would require regular visits).

Why should *P. rupestris*, unlike most solitary lagomorphs (including two other species found in the KRNP), be territorial? Territories are defended areas (Noble 1939), and territorial behaviours (such as acts of defence and the exclusion of rivals from fixed areas) are usually only warranted when some resource is economically defensible (Brown 1964). Cowan & Bell (1986) point out that there is greater potential for competition amongst leporids that rely on some form of cover, and that these species are more often territorial. The pika, *Ochotona princeps*, is also a solitary and territorial lagomorph (Svendsen 1979). Like red rock rabbits, pikas do not burrow and rely on interstices amongst rocks on talus slopes for their refuge requirements. Crevices and fissures, irregularly distributed through rocky terrain, appear to comprise a critical resource that is worth defending by vulnerable small mammals in predator-rich environments (red rock rabbits were easily captured by black eagles and caracals once detected away from cover - pers. obs.). Lagomorphs have no control over this resource and must defend what is available. Escape routes to such refuge sites are probably required by adult rabbits, but the crevices might also be critical as safe nest sites for raising young.

DISTRIBUTION AND ABUNDANCE OF ALTERNATE PREY

PART 2: NOTES ON OTHER SPECIES

During the course of fieldwork, attempts were made to gather as much information as possible on other potential prey of black eagles in the KRNP, besides rock hyrax and red rock rabbits. This was done primarily to provide a framework for understanding black eagle feeding habits (Chapter 9). Besides conventional prey recorded for black eagles such as hares, game birds, small antelope (see Chapter 9), notes were kept of larger animals which may provide food to the eagles in the form of juveniles or carrion. While conducting fieldwork in the KRNP between 1986 and 1990, detailed notes were kept of the time spent in the field and locations visited. All potential prey seen were recorded, and where possible I also noted details of local habitat conditions for each sighting (using the variables as listed in Table 7, page 67). Each May (1987 onwards) the National Parks Board conducted total counts of all large ungulates in the park by helicopter (Randall *in litt.*).

A total of 567h were spent walking through the KRNP in the course of fieldwork. Most of this walking was conducted in mountainous terrain to and fro hyrax colonies and eagle nests. Prey sightings while specifically observing hyrax were excluded while calculating relative abundance of hyrax to avoid bias. A total of 1304 potential prey animals were sighted. Relative frequencies and relative biomass of the different prey species are presented in Table 11. For scientific names, consult Appendix 2.

Detailed census techniques (Chapters 4 & 5) indicated that rock hyrax outnumber red rock rabbits by a factor of two in the KRNP, yet hyrax and red rock rabbits were encountered at a ratio of 26:1 while walking in the park. This disparity reflects the cryptic and nocturnal nature of red rock rabbits, and suggests that rock hyrax should be relatively much more available to black eagles foraging at similar times and in similar places to myself.

TABLE 11

INCIDENTAL OBSERVATION OF POTENTIAL PREY SPECIES IN THE KRNP

Ungulate lambs refer to lambs of medium-sized animals e.g. springbok; mountain reedbuck and grey rhebok are not included in the frequency and biomass analysis because they are not preyed on as adults; the figure of 905 hyrax was derived from relative encounter rates when this species was not specifically being searched for (n=443h); all mass estimates from Skinner & Smithers (1990) and Maclean (1985); consult Appendix 2 for scientific names.

SPECIES	N	% FREQUENCY	ADULT MASS (kg)	BIOMASS (kg)	% BIOMASS
rock hyrax	905	69,40	3,20	2896,0	47,46
red rock rabbits	35	2,68	1,62	56,7	0,93
Cape hares	4	0,31	2,04	8,2	0,13
scrub hares	5	0,38	3,60	18,0	0,29
steenbok	31	2,38	11,10	344,1	5,64
klipspringer	212	16,26	11,90	2522,8	41,34
grey duiker	4	0,31	11,00	44,0	0,72
large ungulate lambs	32	2,45	5,00	160,0	2,62
mountain reedbuck	46	-	-	-	-
grey rhebok	41	-	-	-	-
yellow mongoose	1	0,08	0,83	0,8	0,01
small grey mongoose	14	1,07	0,80	11,2	0,18
Cape wildcat	2	0,15	4,30	8,6	0,14
Cape fox	2	0,15	4,10	8,2	0,13
greywing francolin	53	4,06	0,39	20,7	0,34
karoo korhaan	4	0,31	0,75	3,0	0,05
SUMMARY:					
HYRAX	905	69,40	-	2896,0	47,46
LAGOMORPHS	44	3,37	-	82,9	1,36
SMALL ANTELOPES	247	18,94	-	2910,9	47,70
UNGULATE LAMBS	32	2,45	-	160,0	2,62
CARNIVORES	19	1,46	-	28,8	0,47
GAME BIRDS	57	4,37	-	23,7	0,39
TOTAL	1304	100		6102,3	100

Different species of lagomorphs in the park exhibited similar flushing behaviour (distances) to one another (pers. obs.), so their encounter rates should reflect relative densities. From encounter rates it appears that Cape hares *Lepus capensis* and scrub hares *Lepus saxatilis* occur at approximately one eighth of the numbers of red rock rabbits, with respective population sizes estimated at 760 and 950 (Table 12). However, much of the habitat sampled on foot was the preferred mountainous habitat of red rock rabbits - this occupies about 80% of the total park area. Cape hares prefer the short arid scrub on the plains (Table 13), and scrub hares prefer taller vegetation. These habitats were probably under-represented when walking, so the populations of these leporids may be under-estimated.

Numbers of most other prey species in the KRNP cannot be predicted from encounter rates because of variation in visibility and behaviour. However, some inferences may be drawn by marrying the encounter rates with the results of the helicopter censuses. Klipspringers *Oreotragus oreotragus* are likely to be overlooked by helicopter count but not by groundwork. Klipspringer were encountered roughly five times more often than mountain reedbuck *Redunca fulvorufula* or grey rhebok *Pelea capreolus* on foot. Populations of these species were reliably estimated at @250 each over the study period from the helicopter census. Relative encounter rates on the ground suggest that the KRNP may accommodate about 1200 klipspringer. Population estimates of steenbok *Raphicerus campestris* and grey duiker *Silvicapra grimmia* in Table 12 are based on their relative encounter rates in comparison with that of klipspringer. These are only intended as a rough indication of numbers, both are likely to be minimum estimates because both of their preferred habitats (bottom plains for steenbok; riparian thicket for grey duiker) were under-represented by foot-sampling.

TABLE 12

POPULATION ESTIMATES FOR VARIOUS POTENTIAL PREY SPECIES IN THE KRNP

See text for methods

SPECIES	method	ESTIMATE
rock hyrax	Chapter 4	13335
red rock rabbits	Chapter 5	6652
Cape hares	sighting ratios	760
scrub hares	sighting ratios	950
steenbok	sighting ratios	200
klipspringer	sighting ratios	1200
grey duiker	sighting ratios	50
springbok	helicopter census	1285
mountain reedbuck	helicopter census	220
grey rhebok	helicopter census	276
small grey mongoose	sighting ratios	210

The springbok population in the park (average 1285 individuals) can be expected to produce about 450 lambs each year on the basis of a production efficiency of 35% under cropping (Davies 1985). These lambs would only be vulnerable to black eagle attack for maybe one month in the year. Availability of other ungulate lambs may be estimated in a similar way.

The encounter rates in Table 11 suggest that rock hyrax may comprise roughly 69% of the potential prey available to black eagles, and only about 47% of the available prey biomass. It should be borne in mind though that rock hyrax are very obvious when sitting on rock outcrops but may not necessarily be available to hunting eagles. Small antelope species and the lambs of larger ungulates comprise about 21% of the number of potential prey available, but a much larger proportion (50%) of the available biomass.

Distribution of prey sightings between major habitats (Table 13) mainly reflects my movements but gives an indication of habitat tolerance. More frequent encounters with red rock rabbits on plateaus than on slopes is not in agreement with midden distributions (this chapter) but may reflect different flushing tendencies in the different habitats. All Cape hare sightings were on flat ground (70% bottom plains). Most scrub hares (91%) were seen on flat ground, especially in the taller vegetation of the upper plateau (64% sightings). Disparity between the distributions of these two species may relate to rainfall and vegetation cover. Scrub hares were not consistently found in riparian thicket as expected. Most carnivores were seen on the bottom plains, but most Cape wildcats and caracals (sightings and scats) were located near or on rocky outcrops, along with potential prey species such as hyrax, red rock rabbits and klipspringers (detailed analysis in Chapter 7). Nearly all (95%) klipspringer sightings were on mountain slopes. Of the game birds, karoo korhaans *Eupodotis vigorsii* frequented the bottom plains, greywing francolins *Francolinus africanus* the upper plateau. Grey duikers and steenbok were most often seen on the bottom plains, especially along episodic water courses. Grey rhebok were seen on the slopes and especially the upper plateau. Mountain reedbuck were seen lower down often along river courses on gentle, lower slopes. Most springbok (84%) were recorded on the bottom plains, but towards the end of fieldwork they appeared to be moving up into the lower slopes (perhaps from population pressure on Lammetjiesleegte).

TABLE 13
DISTRIBUTION OF SIGHTINGS OF POTENTIAL PREY SPECIES WITHIN THE MAJOR HABITATS OF THE KAROO NATIONAL PARK

Larger mammals (last 5 spp.) and ostriches were not sampled extensively; (*) sightings of caracal and wildcat are supplemented by locations of recognisable scats; escarpments may be combined with their respective slopes.

SPECIES	BOTTOM PLAINS	LOWER SLOPES	LOWER ESCARPMENT	MIDDLE PLATEAU	UPPER SLOPES	UPPER ESCARPMENT	UPPER PLATEAU
rock hyrax	15	155	172	11	7		24
small mammals		3	1	1			4
red rock rabbit		2	5				11
Cape hare	7			1			2
scrub hare	2		1	1			7
yellow mongoose	2	1					
small grey mongoose	9	4					
zorilla		1					
Cape fox	2						
bat-eared fox	1	4					
Cape wildcat (*)		3	5				
caracal (*)	1	12	15				
vervet monkey	1						
greywing francolin	1	3					18
karoo korhaan	2						
ostrich	17						
grey duiker	4	3					
steenbok	47	6		2			
klipspringer		65	13	5	16		
grey rhebok	1	6			11		39
mountain reedbuck	2	13					
springbok	384	70					5
kudu	3						
red hartebeest	5						
black wildebeest	2						
gemsbok				1			
mountain zebra	3	5		4	5		5

Encounter rates with rock hyrax during fieldwork showed a decline in 1988 and in 1990 which corresponded to declines as indicated by colony counts (Chapter 4) at the start and end of those respective years (Fig. 40a). This indicates that incidental encounter rates can indeed give a real indication of change in density. The hyrax declines corresponded to rainfall patterns following an apparent 3-4y cycle (Chapter 2). Summer rainfall at the start and end of 1988 comprised the low 'trough' of this cycle (Fig. 40f). Four other species showed declines reaching a 'trough' in 1988 and subsequently recovering, these were klipspringer and steenbok (as indicated by encounter rates on the ground - Fig. 40c), and kudu and grey rhebok (as indicated by helicopter census - Fig. 40d). Helicopter counts actually suggested that klipspringers and steenbok were lowest in May 1989. Red rock rabbits and small grey mongooses also exhibited population 'troughs' but lowest numbers for these species were reached a year earlier in 1987 (Fig. 40b). It may be that populations of such smaller animals respond more rapidly to rainfall effects. Only red rock rabbits and rock hyrax showed any indication of declining in 1990 when the period of lowest rainfall followed the period of highest rainfall. The prevalence of pronounced population declines in seven species in the KRNP corresponding to rainfall patterns indicates that a dry period in 1987 - 1988 was a very real ecological event for this region. The vegetation was probably already highly stressed from a more devastating drought in the early 1980's, so relationships between vegetation and consumers may have been more responsive than usual. The figures do suggest that the cyclic rainfall pattern may be encouraging osscilations in herbivore numbers. However, population change in springbok and mountain reedbuck (as indicated by helicopter census - Fig. 40e) showed no indication of a drought-related decline. Evidence of a decline in some herbivore species and not in others is puzzling but it may be explained if the requirements of selective browsers such as kudus and steenbok were in excess of their preferred food resources; while mixed feeders such as springbok (perhaps on a lower plane of nutrition) may have had more *per capita* resources to see them through the drought.

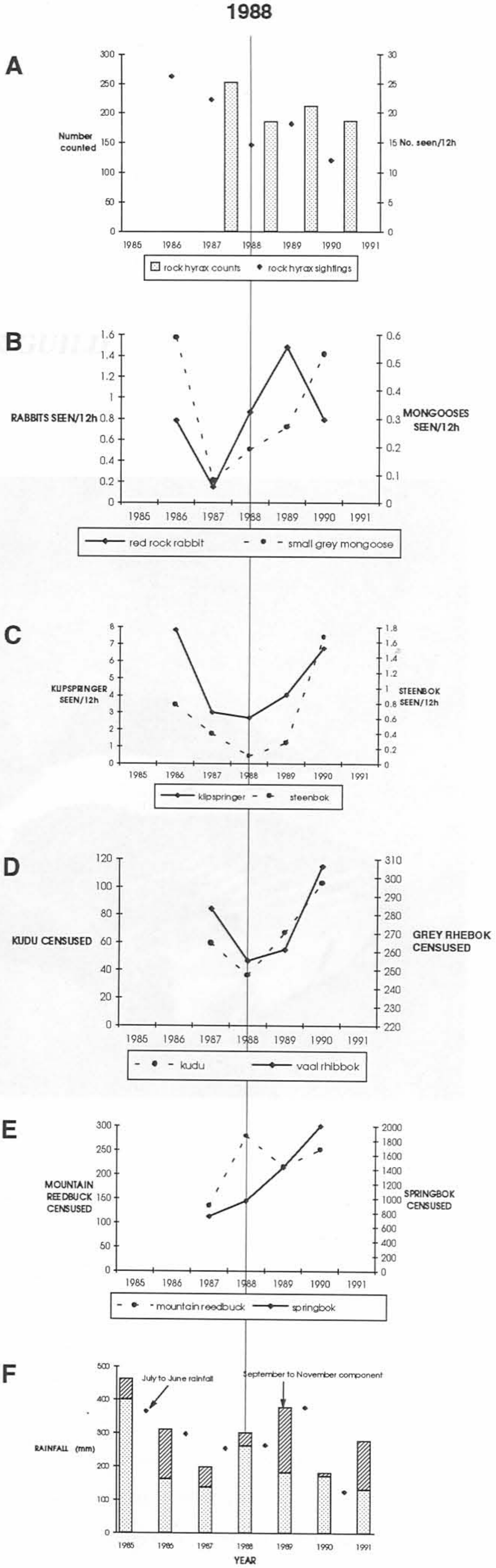

Fig. 40. Population change of various species in the KRNP in relation to rainfall. (D & E from Randall *in litt.* - see text for detail)