CHAPTER 3

THE REFUGE RESOURCE

INTRODUCTION

The significance of refuge in mediating predator-prey interactions was appreciated early on in the development of predator-prey theory and empiricism. When Gause (1934) introduced prey refuge into his *Didinium - Paramecium* experiments he reversed the outcome of these experiments, with the prey surviving extinction. By protecting some prey, refuge eliminates one of two ways in which predator-prey interactions may collapse (Taylor 1984), and has generally been found to confer stability on predator-prey experiments in the laboratory (e.g. Flanders 1958; Flanders & Badgley 1963). But this stability is dependent on the effectiveness of the refuge (White & Huffaker 1969). Spatial heterogeneity offers transient refuge to prey in such experiments especially if predators tend to aggregate in areas of high prey density and if their movements are less effective than those of their prey (Pimentel, Nagel & Madden 1963; Hastings 1977; Takafuji 1977; Maly 1978). Most laboratory experiments indicated increased stability with increased spatial heterogeneity (Huffaker 1958; Huffaker, Shea & Herman 1963). Diffusion models have predicted that such spatial heterogeneity may arise endogenously from the interaction if an homogenous environment is sufficiently large (McMurtrie 1978; Hilborn 1979).

In agreement with laboratory experiments, factors representing protection for a fraction or a number of prey were found to confer stability upon early predator-prey models such as the Lotka-Volterra and Nicholson-Bailey models (Leslie & Gower 1960; Bailey, Nicholson & Williams 1962; St Amant 1970; Hassell & May 1973) - greater stability being conferred when a fixed number rather than a fixed proportion of the prey was protected (Hassell 1976). In the case of prey moving randomly between refuge and hostile environments, diffusion models predict that interactions can only be stable if the refuge habitat exceeds a minimum critical size (Kierstead & Slobodkin 1953; Gurney & Nisbet 1975). But the early predator-prey models have been found to be inherently unstable and biologically unrepresentative in some important regards. It is now preferred to model the predator functional response on predator-prey ratios (*per capita* resources) rather than simply prey density (Berryman 1992; Slobodkin 1992), especially for heterogeneous environments (Arditi & Saïah 1992) with enrichment. Ratio-dependent theory has also demonstrated the importance of refuge, and generally affords a better fit to field situations (marriage between theoretical and empirical studies of predation has been a problem in the past, see Hansson 1988a). Akçakaya (1992) used ratio-dependence between predator, prey and food resources together with a simple refuge factor to correctly predict the periodicity and amplitude of snowshoe hare *Lepus americanus* cycles.

Field studies do not always indicate that prey refugia confer stability on interactions. In fact there is mounting evidence that refuge can give prey populations the advantage, certainly in relatively simple ecosytems, leading to oscillations (limit cycles) and sometimes destructive interaction between prey populations and their food resources. Vole cycles in northern Europe show a clear positive correlation with snow cover which protects increases in vole populations from an immediate response by generalist predators but not from a delayed response by specialist mustelids (Hansson & Henttonen 1985; Hansson 1988b). Likewise, dense stands of spruce *Picea mariana* and willow *Salix* spp. or alder

Alnus spp. thickets afford refuge to snowshoe hares in a habitat mosaic, permitting population increase before the obligate predators such as Canadian lynx Lynx canadensis catch up with the changes in hare density (Wolff 1980). Reluctance of spotted hyenas to enter bush and woodland following migrating Serengeti wildebeest and a consequent low ratio of predator to prey in this region may be responsible for occasional destructive interaction between wildebeest and their food resources in the Serengeti (Kruuk 1970, 1972a).

Prey refuges can take many forms in nature, but refuge to one prey may have the opposite effect for another. Snow protects voles and lemmings from raptors but it renders large ungulates more vulnerable to attack by wolves (Nelson & Mech 1986) - and the behavioural response to this vulnerability is an increase in group size (Heard 1992; Jedrzejewski, Jedrzejewski, Okarma & Ruprecht 1992). Like snowshoe hares, hazel grouse Bonasa bonasia favour densely-vegetated habitats for protection from goshawk Accipiter gentilis attack (Lindén & Wikman 1983). Grass rats Arvicanthis blicki in Kenya also find refuge in dense vegetation but population irruptions may lead to these rodents eating down their refuge and exposing themselves to heavy predation (Brown 1976, p. 105). Australian house mice Mus domesticus minimise predation risk by favouring protective habitats especially on moonlit nights, but they do not show this behaviour in areas where predators are absent (Dickman 1992). Increased exposure of prey when vegetation cover is thin during the dry season has been offered as an explanation for the timing of raptor breeding seasons in Africa (Moreau 1950). So refuge may have far-reaching consequences on the behaviour of both prey and predator. Herrera and MacDonald (1989) suggest that ponds on Venezuelan floodplains afford protection from predators and a rich food supply worth defending to capybaras Hydrochoerus hydrochaeris, and this has led to territorial behaviour by groups in this species. Territorial behaviour is also evident in lagomorphs that use cover. particularly those unable to create their own burrows (Cowan & Bell 1986; Brown, Southwick & Golian 1989). Many small mammals, especially rodents, are able to modify their environment and create refuge by burrowing. But burrows are not very permanent features and are not always effective at preventing predation, especially in soft substrates (Myers & Parker 1975; Murie 1992). Habitats which afford good protection from predators are often occupied by more dominant individuals in a prey population, forcing subordinates into suboptimal, risky buffer zones (Jenkins, Watson & Miller 1964; Bigalke 1970). The concept of a displaced, vulnerable component of the prey population confers. stability to predator-prey models (Smith 1972; Jones 1978). Besides using spatial refuges, many prey populations find refuge in time. Synchronised breeding confers safety in numbers to the highly vulnerable juveniles of many animals (e.g. Murie 1944; Kruuk 1970, 1972a; Hughes & Richard 1974), and certain vulnerable insect imagos (Lloyd & Dybas 1966a&b).

Rock hyrax in the Karoo show a distinct birth-pulse, mostly in November (Millar 1971; Fourie 1983), and this suggests that the juveniles might be heavily hunted because synchronised breeding is not usually expected in unpredictable environments. Rock hyrax are extremely refuge-dependent in space. Their refuge normally takes the form of crevices in rock outcrops and boulder screes, and has been described superficially by Turner & Watson (1965), George & Crowther (1981), Hoeck (1982), Fourie (1983), and in some detail by Sale (1966a). The minimum size for crevices used by hyrax appears to be set by the size of the animals (George & Crowther 1981), while large crevices which would permit entrance of felid predators are avoided (Sale 1966). Besides rock outcrops, hyrax have been observed to use dongas, stone walls, culverts under roads, and the burrows of suricates *Suricata suricatta* and aardvarks during population irruptions (Thomas 1946). Rock hyrax are nearly always seen in very close proximity to their refuges and

minimise the time they spend foraging away from the rocks (Sale 1965; Turner & Watson 1965; Fourie 1983). Dispersion often occurs at night (A. Root & R. Pellow in Hoeck 1982; pers. obs.). Besides protection from predators, rock crevices afford a comfortable microclimate to hyrax (Turner & Watson 1965; Sale 1966a; Fourie 1983). Rock hyrax are thermally labile - they can allow their body temperature to drop by a few degrees at night and then use the microclimates around their refuge resource to thermoregulate during the day (Sale 1970b; Louw 1971; Louw, Louw & Retief 1972; McNairn & Fairall 1984). The first few hours of every morning are usually spent 'sunning' on the rocks, especially on karoo winter days (Fourie 1983).

Refuge used by rock hyrax is unusual in comparison with other forms of refuge used by smaller mammals for the following reasons: it is relatively permanent; it cannot be modified by the animals; it provides shelter for a fixed number of individuals; it is highly effective against nearly all predators; and it occurs in an extensive and patchy distribution within mountainous habitats. For these reasons, rocky refuges can be expected to confer a very real measure of K or carrying capacity on the landscape for hyrax populations, and a high degree of stability on the interaction between rock hyrax and their predators. Although rocky habitats afford hyrax with safe access to a fixed area of vegetation, the number of hyrax that this food resource should support might vary with the effects of enrichment by rainfall. Allan (1988) speculated that a pattern of poor breeding by black eagles in wet years and good breeding in dry years might reflect the distance that hyrax must venture from refuges to feed and thus their vulnerability to predation. Previous population models of rock hyrax (Fairall, Vermeulen & van der Merwe 1986; Swart *et al.* 1986) make the simple assumption that hyrax are protected at low densities and vulnerable at high densities. For modelling to accurately reflect hyrax populations in the Karoo I felt that accurate measurement of the refuge resource (this chapter) and accommodation of the effects of rainfall enrichment (see Chapter 12) would be essential.

While the significance of refuge is widely accepted in theory, its influence in field situations is not yet fully understood (Crawley 1992: p. 487). To compare empirical observations on the influence of refuge to rock hyrax with theoretical predictions introduced above, a detailed study of the refuge resource was warranted (it should be noted that the same refuge resource is also used by red rock rabbits and by black eagles for nest sites). I also hoped that by studying the densities of hyrax in sample units of rocky habitat, I would be able to extrapolate a population estimate of hyrax in accordance with the extent of these habitats. A general description of the nature and origins of karoo rocks was given in Chapter 2. This chapter provides a detailed description and analysis of the refuge micro-habitats found in the KRNP. The relationship of prey and predator to these habitats is examined in later chapters.

METHODS

Categorization of refuge habitats

Rocky habitats in the KRNP can be broadly divided into 'lineal' outcrops such as escarpment which are clearly distributed along one dimension, and 'areal' habitats such as screes which are clearly distributed in two dimensions. The principal rocky and other microhabitats that potentially afford shelter to rock hyrax (Figure 14) were further classified as follows in terms of substrate, form, situation and distribution. Dykes are lineal habitats and derive from vertical dolerite intrusions where the substrate has been exposed as strings of discontinuous (scattered) knobs. Horizontal dolerite intrusions, known as sills, are more common (98% by area of outcrop). The tops of sills can be exposed in an areal fashion either as discontinuous knobs on the surface of plateaus (surface outcrops), or as small continuous (solid) caps protecting cones of shale bedrock (koppies). Particularly large outcrops of rock are exposed in a lineal fashion at the edge of the dolerite sills. Most of these 'escarpment' outcrops are dolerite but sandstones may also be exposed, especially at the base of large cliffs. Some deflected dolerite sills may also be exposed just above or below the escarpment edge. These variants are all considered escarpment. Sheer cliffs of dolerite weather along perpendicular cooling joints - with time this 'columnar weathering' may produce an alignment of tall pillars which may erode further to form a discontinuous string of knobs. Escarpment outcrops may occur in any one of these three lineal forms. Horizontal sandstone lenses in the KRNP are either exposed on slopes or by river action on the bottom plain, as lineal outcrops of continuous rock surface. They can be broadly separated into tall cliff-like outcrops (where vertical planes > horizontal planes) or flat outcrops (where horizontal planes > vertical planes). The latter usually occur on gentler slopes. Weathering of dolerite sills and sandstone lenses produces screes on the slopes immediately

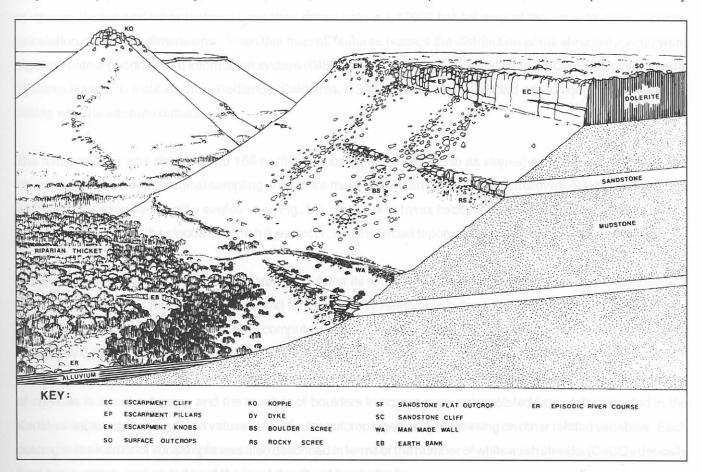


Figure 14. A detailed topographical diagram of the KRNP illustrating the classes of refuge micro-habitats available to rock hyrax, and the substrates from which they derive.

beneath these outcrops. Screes can be defined as discernible clusters of loose rocks and have a discontinuous, areal distribution. Rocky screes (most rocks <0,7m high) usually derive from the sandstone outcrops. Boulder screes (most rocks >0,7m high) nearly always derive from the larger escarpment outcrops. Sandstone rocks are used in the construction of lineal walls for roads and kraals which can afford refuge to hyrax. Alluvium is exposed as small lineal cliffs and banks along river courses in valley bottoms and it is also used in the construction of dam walls. All potentially afford refuge to hyrax.

Habitat mapping

Detailed habitat-mapping was conducted over 136km² of the Nuweveld mountains and surrounding plains. Compensation for the angle of lower slopes increased these surface areas by 5,8%; while compensation for the angle of upper slopes increased these surface areas by 9,6%. So the total mapped area represents 139km² of real surface area. This area encompassed four complete black eagle territories, and parts of four other adjacent territories (Chapter 6). Every rock outcrop (n=3365) within this area was viewed and outlined on 1:10000 aerial photographs of the region (supplied by International Aviation Services Pty. Ltd., Pretoria). Each outcrop was numbered and described in terms of various parameters and these details were then loaded onto an attribute database (details below). The aerial photographs were subject to distortion, so a 500m grid was superimposed onto the photographs from 1:50000 topocadastral maps of the area using various landmarks. The rock outcrops, water courses, stretches of riparian thicket and other features were then drawn onto a 1:17000 habitat map of the area, to allow accurate calculation of outcrop dimensions. From this map all features (except the distribution of tall shrubs/thickets) were digitised onto a geographical information system (GIS) of the core area of the park using ARCINFO (Environmental Systems Research Institute, Inc., Redlands, California, USA). Features were loaded with unique labels to enable linking with the attribute database.

The mapped area was stratified into 166 sections (subsequently referred to as slopes) on the basis of aspect and topography to provide ecological sampling units more meaningful than grid squares (effectively subdividing the area as it would be seen by foraging eagles - see Fig. 15). In this way hyrax habitat could be considered in terms of the outcrops themselves, the slopes on which they occur, and the broad topographical habitats described in Chapter 2.

Each outcrop mapped was assigned an area code (after its respective slope), an outcrop class and a number; and was then described in terms of substrate and form, suitability rating (see below), height, length, and surface area. Correlation analyses (R² option in the SAS computer program, see Ingraham, Luginbuhl, Schlotzhauer & Watts 1988) on an early database of 786 outcrops (the Kortkloof sub-sample) had indicated that these might be the more important descriptive variables relating to hyrax distribution. Values for three other parameters: width of outcrop; the number of crevices in linear outcrops; and the number of boulders in screes were extrapolated from data recorded in the Kortkloof subsample using mean values for particular outcrop types or by regressing on other related variables. Each outcrop in the Kortkloof subsample was also described in terms of the number of whitewash streaks (CaCO₃ deposits from hyrax urine), and an index of the local density of large shrubs.

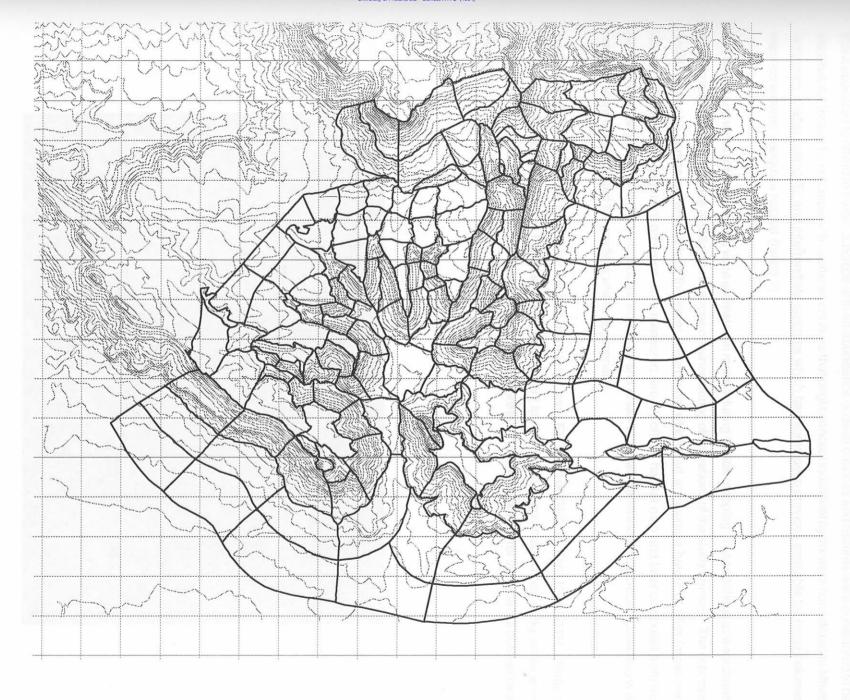


Figure 15. The area within the Karoo National Park where detailed habitat mapping was conducted and its subdivision into slopes (1km grid and 100' contours shown)

The suitability rating of an outcrop was assessed rather subjectively in terms of the nature and extent of the shelter that it appeared to afford to hyrax: outcrops with an abundance of deep crevices and fissures were considered to be ideal habitat (rating 1); outcrops with scattered crevices that might conceal individual hyrax were considered to afford temporary shelter (rating 3); and intermediate outcrops which had some deep crevices available for hyrax colonies were considered adequate habitat (rating 2).

The height and width of rock outcrops were estimated in metres during habitat mapping. These estimates were drawn from considerable experience at judging distances obtained during observations of the study animals. The outcrops could usually be compared with cliffs of the lower escarpment which had an average height of 35m (measured directly). Widths of escarpment outcrops were measured directly off the habitat map and later computed from the GIS, as were lengths of all linearly-distributed outcrops, and areas of all two-dimensional outcrops. Dimensions of outcrops were compensated for gradient where appropriate.

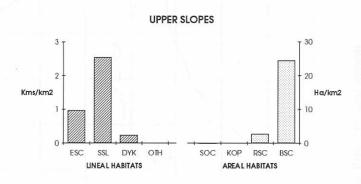
Surface areas for the continuous linear habitats were taken as: LENGTH*HEIGHT + LENGTH*WIDTH. Surface areas for the discontinuous linear habitats (dykes; escarpment knobs) which encompassed non-rocky areas were taken simply as LENGTH*WIDTH. Surface areas of koppies were taken from the formula for the area of a demisphere: $(\pi d^2)^*0.5$

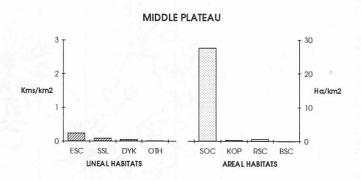


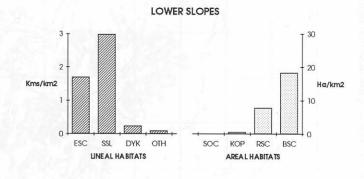
RESULTS AND DISCUSSION

Extent and distribution of refuge micro-habitats

The distribution of the major classes of rocky habitats is shown in Figure 16 for the mapped area of the park. The distribution of episodic water courses (drainage routes) is shown in Figure 17 for the same area. Riparian thickets growing along these water courses provide important feeding habitat for hyrax as well as some protection from eagles (Chapter 4). Good access to this habitat is found on the slopes and bottom plains, but not on the middle plateau. It is evident that availability of rock outcrops varied markedly between the major topographical habitats (Fig. 16). Densities of the main outcrop types in the different topographical habitats are illustrated in Figure 18 (data given in Table 1, page 20; statistical comparisons presented on page 69). All mountain slopes in the mapped area have consistently high densities of rock outcrops, and these major habitats account for 84% of all lineal outcrops by length and 98% of all screes by area. The distribution of lineal outcrops within lower and upper slopes are basically similar, but upper slopes (being less convoluted and steeper) contain relatively shorter stretches of very tall escarpment outcrops which have resulted in high densities of boulder scree. All outcrop types are scarce on the plains and plateaus except for surface outcrops which occupy a significant area of the middle plateau. The upper plateau (not mapped) is very similar to the middle plateau and is also characterised by surface outcrops of dolerite.







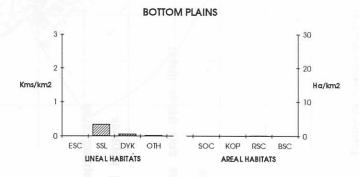


Figure 18. Densities of the principal refuge micro-habitats in the major topographical habitats of the Karoo National Park. Lineal and areal habitats had to be shown on separate scales. KEY: ESC escarpment, SSL sandstone lenses, DYK dykes, OTH other lineal outcrops, SOC surface outcrops, KOP koppies, RSC rocky screes, BSC boulder screes.

Figure 16. Geographical information system of the principal refuge micro-habitats within the Karoo National Park (1km grid shown) generated from ARCINFO coverages using ARCVIEW

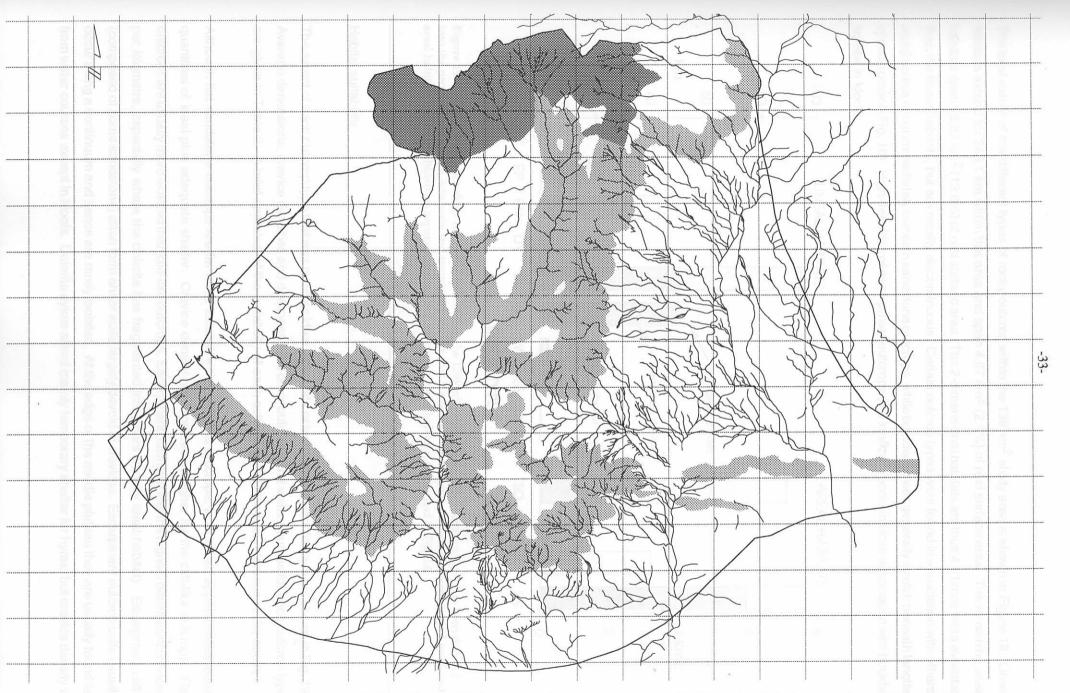


Figure 17. Routes of the episodic water courses in the Karoo National Park shown against the major topographical habitats within the mapped area (1km grid shown) generated from ARCINFO coverages using ARCVIEW

The total extent of the different types of rocky outcrop within the 139 km² study area is shown in Figure 19. Lineal habitats extend for 248.1 km within this area and span 4.07 km² (2.9%) of real surface area. The remaining areal habitats span 18.89 km² (13.6%) of real surface area. The 2-dimensional habitats are thus 4.6 times more available than the linear habitats, but are mostly discontinuous. Certain outcrop types were found in association with others: rocky screes occur immediately beneath sandstone outcrops, while boulder screes generally stretch beneath lengths of escarpment (Fig. 16). High densities of escarpment outcrops (4.9 km/km²) occur in close association with boulder screes in kloofs.

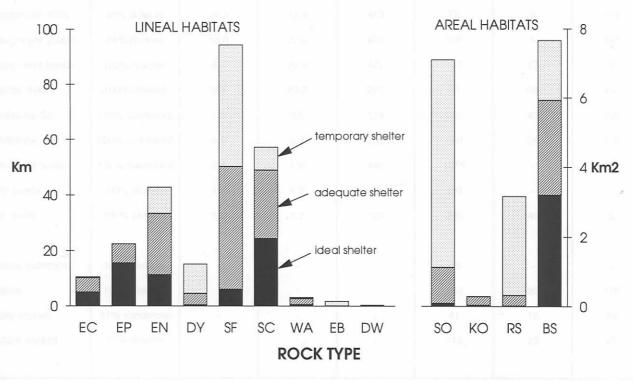


Figure 19. Total extent of refuge micro-habitats within the 139km² mapped area. Each outcrop type has been divided into the proportion of ideal, adequate and temporary shelter that it affords to rock hyrax (see habitat mapping). Lineal and areal habitats had to be shown on separate scales. For abbreviations of habitats, see legend in Fig. 14.

Habitat suitability

The extent of each outcrop type that was rated as ideal, adequate or temporary shelter for hyrax is shown in Fig. 19. Average dimensions, crevice densities and distances from other outcrops and water courses for each outcrop type are given in Table 2. A brief appraisal of the suitability of each outcrop type follows, in reference to the above.

Although flat sandstone outcrops are far more extensive than cliff-like outcrops, both afford approximately equal quantities of ideal plus adequate shelter. Crevice density per kilometre is higher for the cliff-like outcrops. Flat outcrops are usually more isolated than cliff-like outcrops. Escarpment outcrops offer the highest densities of crevices per kilometre, especially where the dolerite has fragmented into pillars (mostly ideal habitat). Escarpment cliffs (comprised of some sandstone) often form sheer walls largely devoid of crevices. Escarpment outcrop units usually occur along a continuum and hence are rarely isolated. At the edge of the middle plateau they are usually found far from water courses except in kloofs. Dolerite dykes afford mainly temporary shelter for hyrax, but crevice density is

TABLE 2
ATTRIBUTES OF THE PRINCIPAL REFUGE MICRO-HABITATS
AVAILABLE TO ROCK HYRAX IN THE KAROO NATIONAL PARK

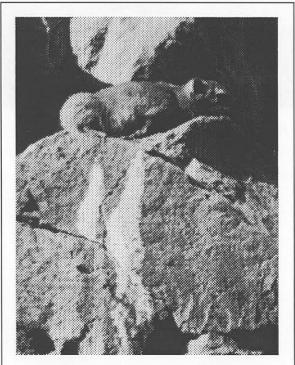
ROCK TYPE	SUBSTRATE	mean height	mean width	CREVICE DENSITY		mean distance to outcrop	mean distance to water course
				No/km	No/ha	(m)	(m)
a refuge anymor	ment at rock hi	rax in this stu	dy la diffirent	fromthating	nost other stu	iles so lur. F	bel-hvmxar
Escarpment cliffs	46% dolerite	24,3	17,8	413	78	9	111
Escarpment pillars	94% dolerite	18,0	22,6	676	156	5	192
Escarpment knobs	100% dolerite	4,3	21,0	421	187	17	100
Dolerite dykes	100% dolerite	0,9	23,2	229	95	66	69
Sandstone flat	100% sandstone	1,5	3,5	134	238	43	115
Sandstone cliff	100% sandstone	5,3	5,2	230	200	25	106
Man-made walls	100% sandstone	2,4	1,6	440	1275	retykess and s	saves rounb
Earth banks	100% aluvium	1,9	1,2	42	139	i) but this ov	evanuat muk
Dam walls	100% aluvium	3,0	1,7	125	286	40	5
Surface outcrops	100% dolerite	dense vegel	ellon found o	n today outo	46	ra in Africa.	Of the may
Koppies	100% dolerite	order models			133	39	176
Rocky screes	57% sandstone	ethin forces	ediction of the sale		41	16	84
Boulder screes	77% dolerite	to pint, resignati		-	113	22	75

reasonable. Dykes are the only lineal habitats that stretch vertically down slopes, often running closely parallel to water courses, but usually far from other outcrops. Sandstone walls have exceptionally high densities of shallow crevices, providing mostly adequate shelter for hyrax. Earth banks have the lowest density of crevices, and only afford temporary shelter for hyrax. Earthen dam walls afford adequate shelter for hyrax colonies. Both earth banks and dam walls occur along water courses.

The dolerite surface outcrops and the predominantly sandstone rocky screes have very low densities of crevices per hectare and are made up of large areas of scattered rock suitable only as temporary shelter for hyrax. In the rocky screes, small rocks covered an estimated 48% of ground cover, large rocks (>0,7m) occurred at average densities of 27ha⁻¹, and average density of boulders (>2m) was 0.4ha⁻¹. Dolerite koppies provide similar crevice densities to escarpment outcrops, but afford mostly adequate shelter. Koppies are usually far from water courses and other outcrops. Crevices are far denser in boulder screes than rocky screes. Boulder screes contain an average of 57 large rocks ha⁻¹, 2.0 boulders ha⁻¹ and a ground cover of 25% small rocks. Many boulder screes contain very high densities of boulders, interspersed with impenetrable riparian thicket, thus affording an extensive ideal habitat, rich in food and shelter. Boulder screes and especially rocky screes occur in close association with other outcrops, and both tend to accumulate in depressions and along drainage routes (close to water courses).

Most adequate and ideal hyrax habitat is contained within escarpment, sandstone and boulder scree outcrops (Fig. 19), and one would expect these habitats (especially escarpment pillars and boulder screes) to accommodate most hyrax. Remaining outcrop types are either limited in extent (e.g. walls, koppies) or largely unsuitable for permanent colonies (e.g. dykes, surface outcrops, rocky screes). Crevice quality was not measured in this study but is speculated on in later chapters.

The refuge environment of rock hyrax in this study is different from that in most other studies so far. Rock hyrax are usually found in the igneous rock outcrops of Africa, particularly granite and its derivatives which may form large rounded domes with well scattered crevices as in the northern Cape (George & Crowther 1981), and in parts of the Matobo Hills (Gargett 1990), or isolated koppies which often comprise habitat islands in a sea of grassland as in the Serengeti (Turner & Watson 1965; Hoeck 1982) and parts of the Matobo Hills (Gargett 1990). Hyrax also inhabit boulder screes found along fault scarps and lateral glacial moraines in Kenya (Sale 1966) which are probably less isolated. The dolerites and sandstones of the eroded karoo landscape give rise to a patchy, but more contiguous network of escarpment and sandstone outcrops running across the slopes transected by dykes and screes running down the slopes. The substrates in the KRNP and MZNP are similar (see Fourie 1983) but this network of rocks appears to be more extensive and connected where the Great Escarpment is well-developed as at Beaufort West (pers. obs.). Another difference between this and other hyrax studies is that the short karoo shrubs in the KRNP afford less protection to hyrax than the dense vegetation found on rocky outcrops elsewhere in Africa. Of the major topographical habitats in the KRNP, clearly the mountain slopes should afford the best rocky network for safe feeding and dispersal by hyrax, but an irregular patchwork of surface outcrops should also permit some access to vegetation on the plateau habitats, while a few thin, long sandstone lenses should provide access to riparian thickets along river networks on the bottom plains. The variety of refuge habitats in the KRNP form an interactive mosaic of varying potential combinations of food and shelter, and this should be reflected in the distribution pattern of rock hyrax. One might anticipate that the interface between escarpment and boulder screes would provide the most suitable conditions for hyrax.



Vigilant hyrax sunning in a favourite spot. Note the whitewash streaks on the rocks from CaCO₂ in hyrax urine.