CHAPTER 7

DISTRIBUTION, ABUNDANCE AND FEEDING HABITS OF CARACALS AND OTHER PREDATORS

INTRODUCTION

The prime objective of this chapter was to collate as much information as possible about other predators besides black eagles which may be responsible for the loss of individuals from the hyrax population. The only other major predator of adult rock hyrax in the study area was the caracal, so most of the attention in this chapter is directed at this species, and some relevant general information on caracals is provided here. Initial plans to undergo a major investigation of caracal home range and movements involving radio-telemetry proved largely unsuccessful. So extensive reference is made in this chapter to other studies of caracals in similar karoo environments. Limitations on field work precluded detailed study of all predators in the KRNP, but for modelling purposes (Chapter 12) it was important to have an informed awareness of the potential impact of non-eagle predation on hyrax under more 'normal' conditions of hyrax density, and to use all the information available to try and gauge the capacity of the numerical and functional responses that these predators might show to changes in the hyrax population.

Although not as prey-specific as black eagles, caracals are considered to be an important predator of rock hyrax in the Karoo. Rock hyrax remains occurred in 7 - 9% of stomachs from caracals killed in control operations in the Cape (Pringle & Pringle 1979; Stuart 1982); in 22% of caracal scats collected in the Karoo National Park (Palmer & Fairall 1988); and rock hyrax comprised 53% of prey items identified in caracal scats collected in the Mountain Zebra National Park (MZNP) (Moolman 1984, 1986a). In the MZNP in the eastern Karoo, where black eagles may be nest-site limited (pers. obs.) and hyrax occur at high densities (Fourie 1983), caracals are considered the major hyrax predator and their relationship to this prey has been modelled mathematically (Swart *et al.* 1986).

The distribution of caracals is sympatric with that of black eagles up through the Afro-montane belt, but extends around the perimeter of the Sahara into west and north Africa, and through Arabia into Asia and India (Stuart 1984). They are not found in the equatorial forests and true deserts. At their northern limit they are considered endangered, and it is only in the Cape Province and parts of Namibia that they abound, especially in rocky terrain, and pose a threat to domestic livestock (Stuart 1984). Like black eagles, they hold a controversial position with farmers in these regions (Chapter 11), but their damage to livestock is generally considered more severe (Stuart 1981), and their role as predators of pest species such as hyrax is less well-known. Caracals are powerful predators for their size. Adult males can attain masses of up to 20 kg (Pringle & Pringle 1979). They readily kill adult antelope which may be twice their size, such as springbok and mountain reedbuck (Grobler 1981) and, unlike black eagles, are known to kill adult sheep and goats. Domestic livestock remains were found in 26 - 55% of stomachs from caracals killed in control operations in the Cape (Pringle & Pringle 1979; Stuart 1982); and comprised 23% of identifiable prey in scats collected from farmland around the MZNP (Moolman 1984, 1986b). Single caracals have been known to kill up to 21 sheep or goats in sporadic occurrences of surplus killing (Skinner 1979; Stuart 1986), and this has made them extremely unpopular with farmers.

Caracals are not known to be truly territorial. They are distributed in a flexible system of overlapping home ranges which in the Cape Province may vary from 15 - 56 km^2 for males and from 6 - 18 km^2 for females (Stuart 1982; Norton & Lawson 1985; Moolman 1986a, 1986b). Overlap of home ranges within the sexes is small, but a male's range may encompass those of a few females. Juvenile caracal remain in their mother's home range until independent. A female caracal becomes sexually mature at a year old; has a gestation period of 2,6 months; and may produce up to four kittens per litter at any time of the year (Stuart 1982). Up to six kittens per litter have been recorded in captivity (Kralik 1967). The flexible spatial organisation plus high propensity for population increase means that, in contrast to black eagles whose numbers are maintained relatively constant by the number of available breeding territories and by a conservative reproductive rate, caracals are able to exhibit a pronounced 'numerical' response to changes in prey density over time. The breeding potential of caracals is not much less than that of rock hyrax (Chapter 4), but hyrax can show a very rapid response to rainfall effects, so some time-lag in the numerical response by caracals might be expected.

Besides hyrax and domestic livestock, caracals are known to prey on a wide variety of other animals and can thus be considered 'generalist' predators. Early diet studies indicated that caracals fed on a range of small prey especially rodents and lagomorphs, as well as arthropods and vegetable matter (Bothma 1965; Smithers 1971; Viljoen & Davis 1973; Skinner 1979). More recent and extensive work in the Cape reveals that a range of ungulate prey, including full-grown antelope, fulfil most of caracal food needs in this region (Pringle & Pringle 1979; Grobler 1981; Stuart 1982; Moolman 1984; Palmer & Fairall 1988). Caracals are able to survive during periods of low hyrax availability in the Karoo by subsisting on these alternative prey types. It is possible that caracals may 'switch' to a diet of hyrax when these prey become super-abundant, and in this way show a 'functional' response (Holling 1959, 1965) as well as a numerical response to increases in hyrax numbers. This functional response has been shown to be of great significance in predator-prey relationships. In southern Sweden for instance, a wide variety of generalist predators which could subsist on alternate prey were able to prevent cycling in vole populations by an efficient functional response (Erlinge 1987; Erlinge, Goransson, Hansson, Hogstedt, Liberg, Nilsson, Nilsson, von Schantz & Sylven 1983; Erlinge, Goransson, Hogstedt, Jansson, Liberg, Loman, Nilsson, von Schantz & Sylven 1984, 1988).

There were few other predators capable of killing adult hyrax in the study area. A single pair of martial eagles hunted mostly outside of the park. Tawny eagles were not seen in the study area. Leopards *Panthera pardus* have not been seen in the area for decades, and brown hyenas *Hyaena brunnea* pass through only very rarely. Domestic dogs *Canis familiaris*, black-backed jackals and Cape foxes *Vulpes chama* were not encountered in the rocky areas around hyrax colonies, and hyrax have been known to successfully chase off adult black-backed jackals (Fourie 1983). Human predation on hyrax has not occurred in any magnitude since proclamation of the park in 1976. However, Juvenile hyrax are vulnerable to a variety of numerous, smaller 'secondary' predators in the park most notably: small grey mongoose, Cape wildcat, Cape eagle owl *Bubo capensis*, jackal buzzard *Buteo rufofuscus*, booted eagle; and possibly gymnogene *Polyboroides typus*, white-necked raven *Corvus albicollis*, Cape cobra *Naja nivea* and rock monitor *Varanus exanthematicus* (for all scientific names after first mention, see Appendix 2).

METHODS

Caracals were captured in six cage traps carefully located alongside well-used game tracks. The traps were baited with varying combinations of blood, offal, feathers, and also faeces and urine sand from captive caracals (obtained from Vrolijkheid Nature Conservation Station). Trapping was organised by S. Klemm in the first half of 1988. All traps were positioned in the park, with most positions in the kloofs surrounding Stolshoek. The traps were visited every morning. When a caracal was captured, it was held against the side of the trap by moving cross-bars through the wire mesh, and given an initial intramuscular injection of Rompun (at dosages of up to 1,5 ml depending on estimated body mass) followed by a second intramuscular injection of Ketamine hydrochloride (at dosages of up to 100 mg depending on estimated body mass). The dosage of Ketamine necessary to anaesthetise the first captive caracal was much higher (125 mg for a 5 kg cat) in the absence of an administration of Rompun. The drugged cats became tractable after several minutes and were successfully anaesthetised for a couple of hours. During this time various details (sex, mass, body dimensions) were recorded, and the animals were fitted with radio collars (provided by Dr. Neil Fairall of CDNEC) which operated in the frequency range of 144,125 - 151,851 MhZ.

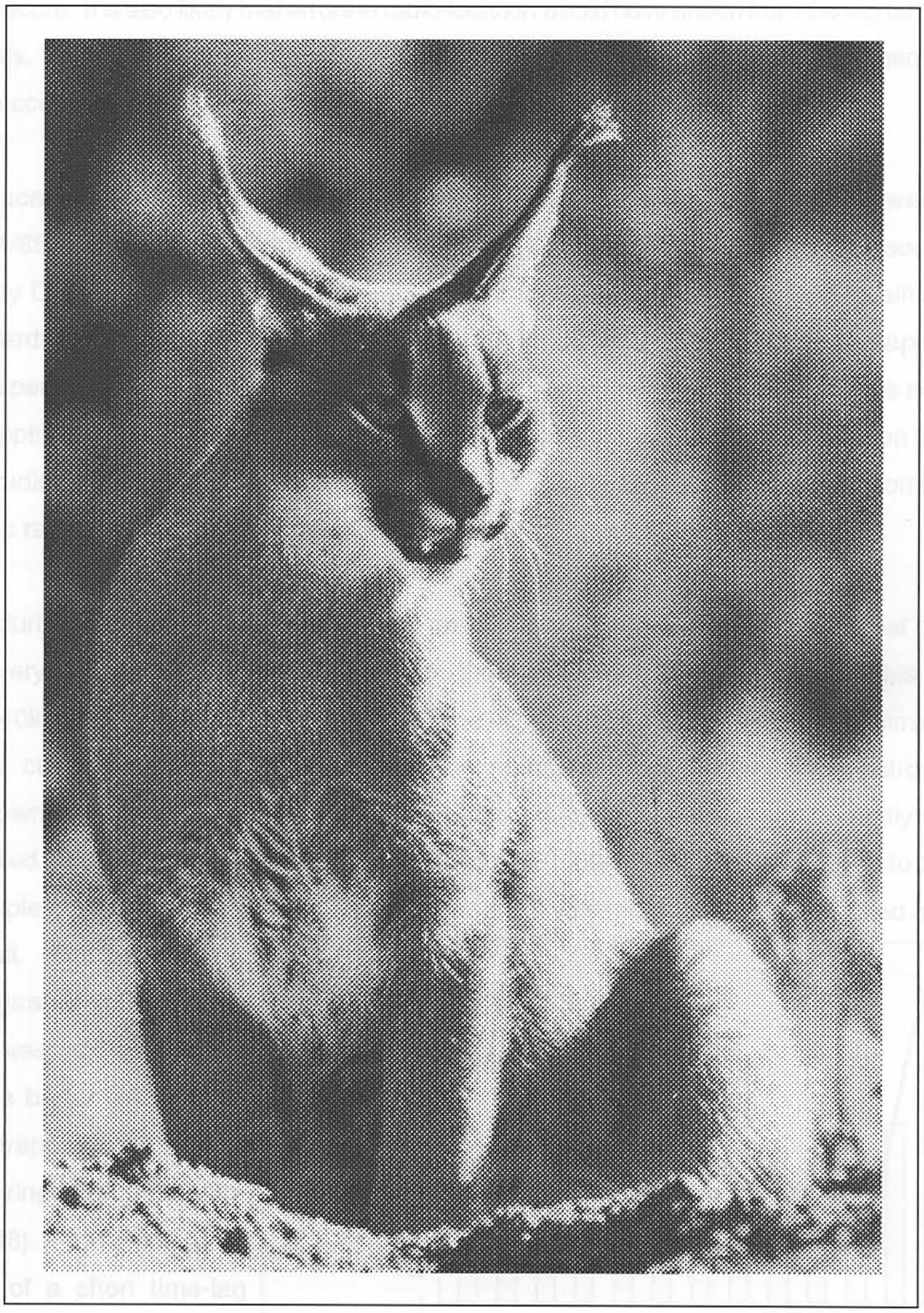
Throughout 1988 efforts were made to obtain two simultaneous bearings on each of the fitted transmitters from known positions in the park. This always involved two observers in radio contact from various positions overlooking the park. It was thought that previous difficulties in obtaining bearings on radio-collared caracals in the mountainous terrain (N. Fairall pers. comm.) might be overcome by conducting radio locations from the upper escarpment at 910 m above most of the park. Radio-locations of the caracals were also attempted while walking around the convoluted lower escarpment on moonlit nights.

Throughout fieldwork for the present study, scats of caracals and Cape wildcats were collected while walking around the park. Most were collected during 1987. The amount of effort spent in each habitat type in the course of fieldwork was not analysed, but all major habitats were extensively covered while plotting out rock outcrops and monitoring hyrax groups and eagle nests (Chapters 3, 4 & 6). Caracal scats were also collected while walking fixed one km transects in the various major habitat types to assess the midden densities of red rock rabbits (Chapter 5). This permitted more direct comparison between the habitats in which scats were deposited and the habitats available. The same micro-habitat variables recorded for each red rock rabbit midden (Table 7, page 67) were recorded for each caracal scat collected. Scat locations would present a biased impression of habitat selection by caracals if they were located strategically for social purposes but unlike European lynx *Lynx lynx* or Canadian lynx, caracals do not use middens and scats tend to accumulate in the areas that are used most by the cats (Grobler 1981; L.C. Moolman pers. comm.). Cape wildcat scats can be distinguished because they are smaller and usually partly or wholly buried (Palmer & Fairall 1988). Details of habitat and activity were also recorded for any direct observations of caracals and other carnivores or raptors in the course of fieldwork.

Scat analyses were carried out by G. van Dyk at the Mammal Research Institute in the following manner. Scats were initially treated using the same method as Palmer & Fairall (1988): they were dried, weighed and measured in the laboratory, and then broken apart by hand; but in the present analysis hairs were identified by taking cross sections of sample hair from each scat (after Keogh 1983), rather than using imprints of the hair (as did Palmer & Fairall 1988).

Using Keogh's methodology, cross section reference slides were also made up for the hair of any potential mammalian prey occurring in the KRNP which were not described in Keogh's paper (material obtained from the Transvaal Museum). Caracal diet was then expressed as percentage occurrence of each hair type in the 100 scats analysed.

Data on caracal captures in control operations were obtained from CDNEC and from private farmers in order to provide information on the relationship between numbers caught and rainfall patterns (P. Norton *in litt.*; J.H. Swiegers *in litt.*).



Felis caracal

RESULTS

Trapping success and radio-tracking of caracals

Four caracals were captured and fitted with radio collars between January and May 1988. Details of these cats are provided in Appendix 4. Efforts to radio-locate these caracal were made on 17 nights, over approximately 70h. Although signals of most cats could be detected regularly from one trig. point on the upper escarpment immediately above Stolshoek (known as 'Toerentjies'), a simultaneous triangulation was only obtained on one occasion from other known localities along the upper escarpment. This was attributed to the fact that as one moves along the upper escarpment away from this trig point, the view of the convoluted terrain of the kloofs in which the cats were residing became more obscure. It is also likely that errors in radio-location would have arisen from the signal bouncing off rocky slopes in the kloofs. When efforts to radio-locate the caracals by walking along the lower escarpment on moonlit nights also proved unsuccessful, further radio-tracking efforts were discontinued at the end of 1988.

The first two caracals were captured during 349 trap nights at seven trap localities on the lower slopes between 25/1/88 and 10/4/88. This yielded a trapping success rate of 175 trap nights per caracal. The second two caraçals were captured by Dirk Brand and his assistant during 172 trap nights at fourteen trap localities on the middle plateau and towards Doringhoek between 25/4/88 and 16/5/88. This latter effort yielded a trapping success rate of 86 trap nights per caracal. These workers also re-trapped one of the caracals but this was not included in the estimates of trapping success. A different area was chosen for this second trapping session in the hope that it would facilitate radio-tracking. Unfortunately this did not help. If both trapping sessions are combined, the overall trapping success rate for the KRNP in 1988 was 130 trap nights per caracal.

Trapping effort during control operations of caracal on the farm Montana near Victoria West owned by Jannie Swiegers was very intense leading up to and throughout the present study period. This farm is situated approximately 140km NNW of the present study area, and experienced a similar 3-4y cyclic climatic regime to that of Beaufort West, culminating in the drought of 1984. The numbers of caracals that were destroyed each year on this farm are shown in Figure 59 along with the total rainfall experienced each year. Evidently a high number of caracals were killed during the wet period between 1979 and 1981, but numbers killed dropped to a minimum during 1985 after a couple of very dry years. Subsequently, progressively more caracals were killed during a period of improving rainfall. The relationship between trappings and rainfall the previous summer was not statistically significant, but a better relationship emerged when trappings were compared with a moving average of rainfall (r=0,6; p=0,08). The two patterns are suggestive of a short time-lag between rainfall events and the numbers of caracals killed, which may vary from six to twelve months.

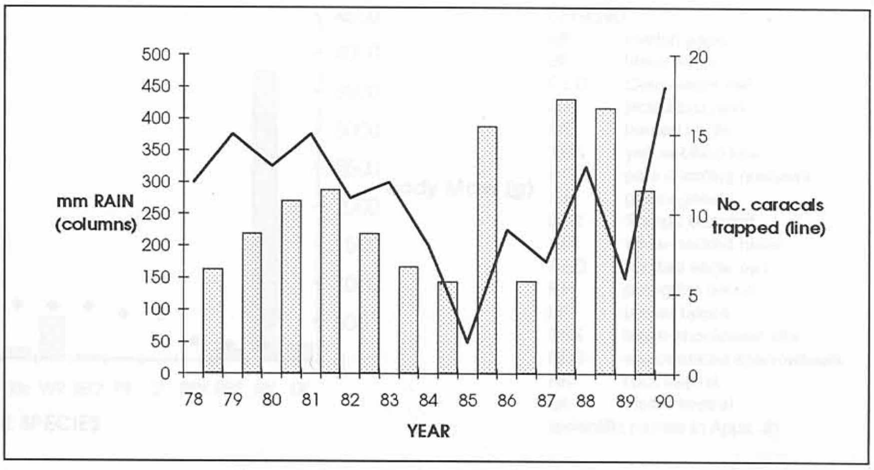


Figure 59. Records of the number of caracals killed in control operations on the farm Montana, near Victoria West, in relation to rainfall patterns (July to June). Data provided by J. Swiegers (*in litt.*).

Relative abundance of other predators

Relative abundance of terrestrial predators, as encountered by myself in the course of fieldwork (138 sightings), is shown in Figure 60a, in relation to average body mass. Baboons (n=84) and mongooses (n=34) were the most frequently encountered terrestrial predators (86% of sightings). Caracal sightings (n=6) slightly outnumbered Cape wildcat sightings (n=4). Most of these sightings were made during daylight.

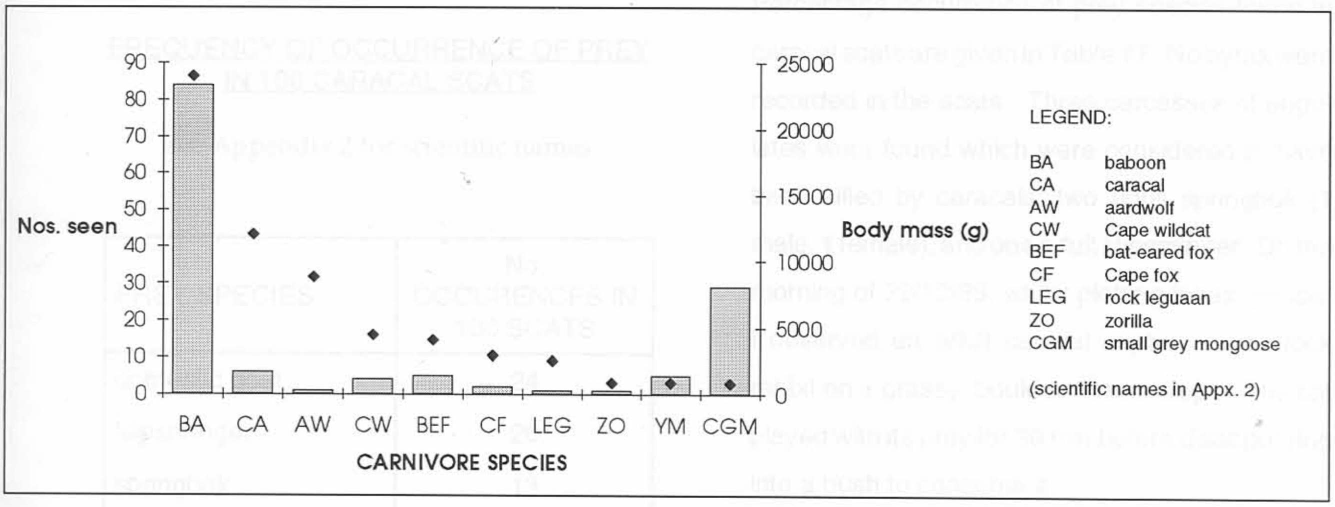


Figure 60a. Relative abundance of carnivores and other terrestrial predators in the KRNP, as indicated by incidental sightings of these species during fieldwork. (diamonds denote adult mass)

Relative abundance of avian predators, as encountered by myself in the course of fieldwork (783 sightings), is shown in Figure 60b, in relation to average body mass. Black eagles (n=328) and rock kestrels (n=291) comprised the bulk (79%) of these sightings. However 65% of black eagle sightings were made on routine visits to nests. Undoubtedly the frequency of these visits introduced bias into the sample. If these visits are excluded then black eagle sightings still outnumber those of all other raptors which are potential secondary predators of juvenile hyrax (booted eagles, gymnogenes, pale chanting goshawks, buzzards and white-necked ravens) at a ratio of 1,4 : 1,0. It is inferred that at least 1,5 of these smaller avian predators occur per black eagle territory (more details on raptor abundance are given under habitat selection).

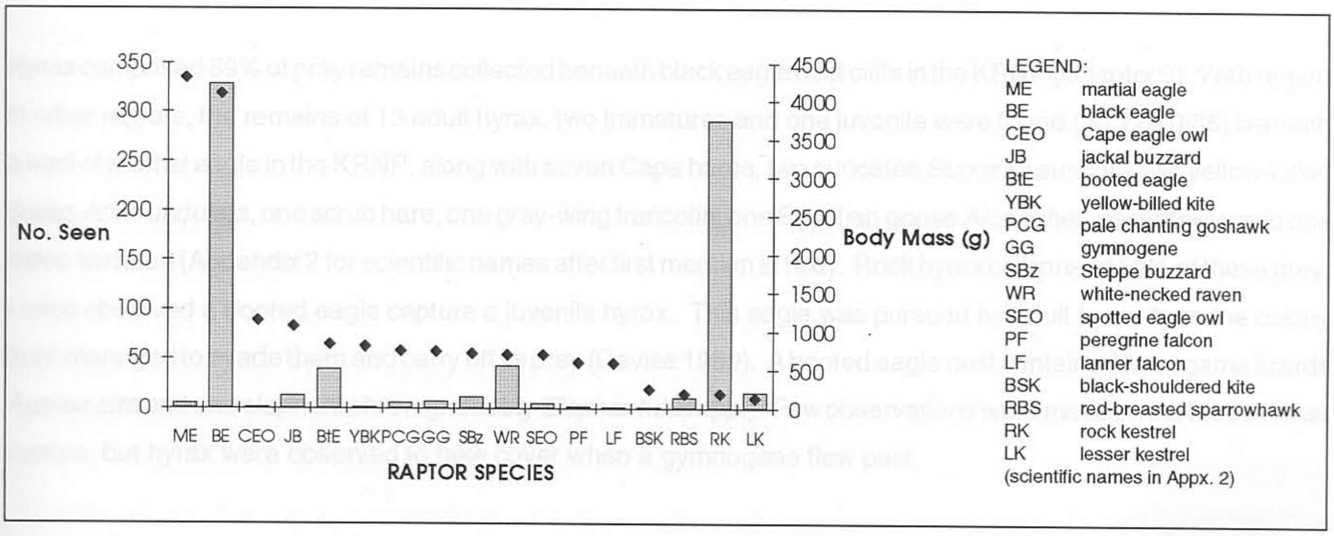


Figure 60b. Relative abundance of raptors and other avian predators in the KRNP, as indicated by incidental sightings of these species during fieldwork. (diamonds denote adult mass)

Feeding habits

TABLE 17

FREQUENCY OF OCCURRENCE OF PREY IN 100 CARACAL SCATS

see Appendix 2 for scientific names

PREY SPECIES	No. OCCURENCES IN 100 SCATS
domestic goat	24
klipspringer	20
springbok	13
mountain reedbuck	10
birds	10
steenbok	4
mongoose	3
lagomorphs	2
bat-eared fox	2
grey duiker	2
ground squirrel	1
arthropods	1

Percentage occurrence of prey species found in caracal scats are given in Table 17. No hyrax were recorded in the scats. Three carcasses of ungulates were found which were considered to have been killed by caracals: two adult springbok (1 male, 1 female), and one adult klipspringer. On the morning of 29/12/89, whilst plotting hyrax groups, I observed an adult caracal capture a red rock rabbit on a grassy, boulder-strewn slope. The cat played with its prey for 30 min before disappearing into a bush to consume it.

Few data were gathered on the feeding habits of other carnivores. On the morning of 16/12/87 I watched an adult Cape wildcat stalk and chase juvenile hyrax unsuccessfully. Adult hyrax fled from a Cape wildcat on another occasion. Small grey mongooses were observed to ignore juvenile hyrax even when these were isolated from their group and vulnerable. I did not observe baboons or any other potential terrestrial predators attacking hyrax.

Hyrax comprised 89% of prey remains collected beneath black eagle nest cliffs in the KRNP (Chapter 9). With regard to other raptors, the remains of 13 adult hyrax, two immatures and one juvenile were found (on 12/10/86) beneath a nest of martial eagle in the KRNP, along with seven Cape hares, two suricates *Suricatta suricata*, two yellow-billed ducks *Anas undulata*, one scrub hare, one grey-wing francolin, one Egyptian goose *Alopochen aegyptiacus* and one karoo korhaan (Appendix 2 for scientific names after first mention in text). Rock hyrax comprised 52% of these prey. I once observed a booted eagle capture a juvenile hyrax. This eagle was pursued by adult hyrax from the colony but it managed to evade them and carry off its prey (Davies 1989). A booted eagle nest contained two agama lizards *Agama atra* and one elephant shrew (probably *Elephantulus* spp.). Few observations were made on the food of other raptors, but hyrax were observed to take cover when a gymnogene flew past.

Habitat selection

Most caracal scats were recovered from the lower slopes and upper plateau. This distribution appeared to be disproportionate to the extent of these and other major habitat types (Figure 61). But the overall extent to which these habitats were sampled was not analysed. Most fieldwork was conducted on the lower slopes and middle plateau. However, transect sampling of the major habitats for red rock rabbit middens (Chapter 5) permitted comparison of caracal scat distribution with effort per habitat (Figure 62), but only 17 scats were recovered on these transects. In this analysis lower slopes were again indicated as an important caracal habitat, and middle plateau to a lesser extent. Poor scat recovery along transects on the upper slopes and plateau may have been due to taller vegetation. Few transects were conducted along the upper escarpment.

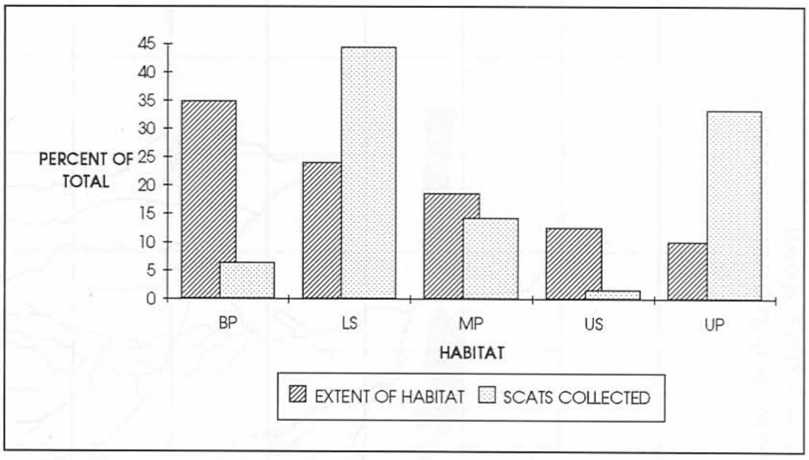


Figure 61. Proportional recovery of all caracal scats from the major topographical habitats in the KRNP, in relation to the proportional extent of those habitats within the park.

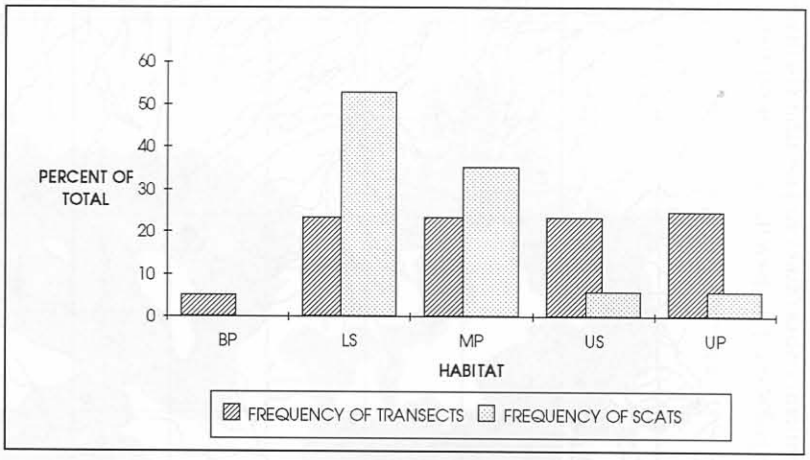


Figure 62. Proportional recovery of caracal scats during field transects conducted through the major topographical habitats in the KRNP, in relation to proportional sampling effort.

Many of the scats collected in the plateau habitats during the course of fieldwork were found close to the respective escarpments. This association is apparent in Figure 63 and is not likely to be entirely due to extra effort along the escarpments. On the lower slopes and valley bottoms, most caracal scats and all successful trappings were located along river courses (Figure 63). All sightings of caracals were in boulder or rocky scree habitats except one on Lammetjiesleegte (plains). Most of these sightings were either late evening (@18h30) or in the morning before 09h30, but two observations of active caracals at 11h00 and 14h45 were made on cool days. Detailed micro-habitat analyses of the limited transect data revealed some tendency for caracal scat loci to be situated closer to major rock outcrops than were habitat assessment loci, on both lower slopes ($t=-2,12$; $p<0,10$) and the middle plateau ($t=-1,82$; $p=0,10$). I could not detect any association between caracal scat loci and drainage routes or density of tall shrubs from these limited data. When compared with habitat assessment loci, caracal scat loci were associated with areas of sparser cover on the lower slopes ($t=-2,0$; $p<0,05$), and with non-grassy areas on the middle plateau ($t=-2,2$; $p=0,05$). The overall evidence suggests that caracals use all the mountainous habitats in the KRNP, especially the lower slopes; and that they tend to gravitate towards escarpment outcrops on the plateaus, and towards river courses and boulder screes in the valleys.

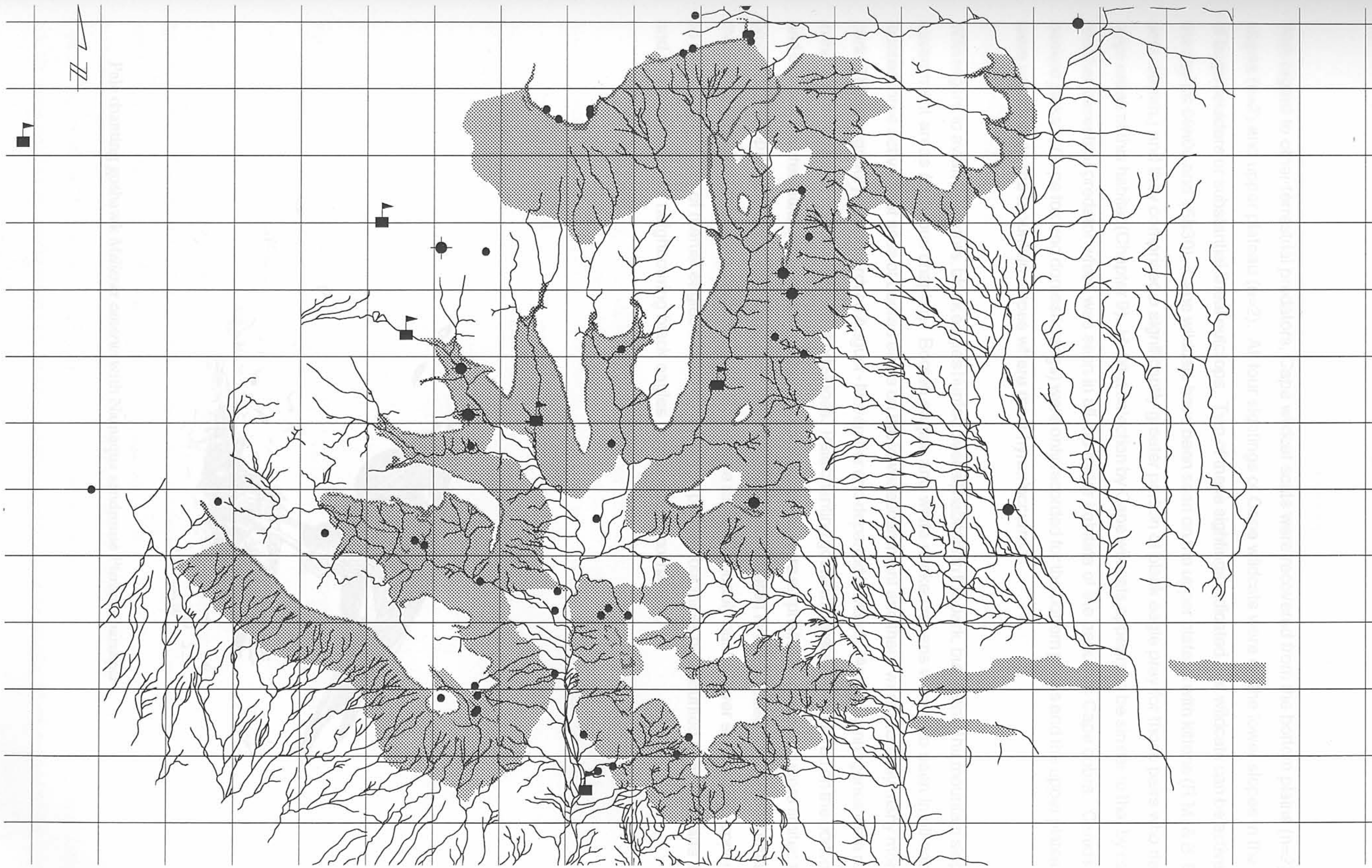
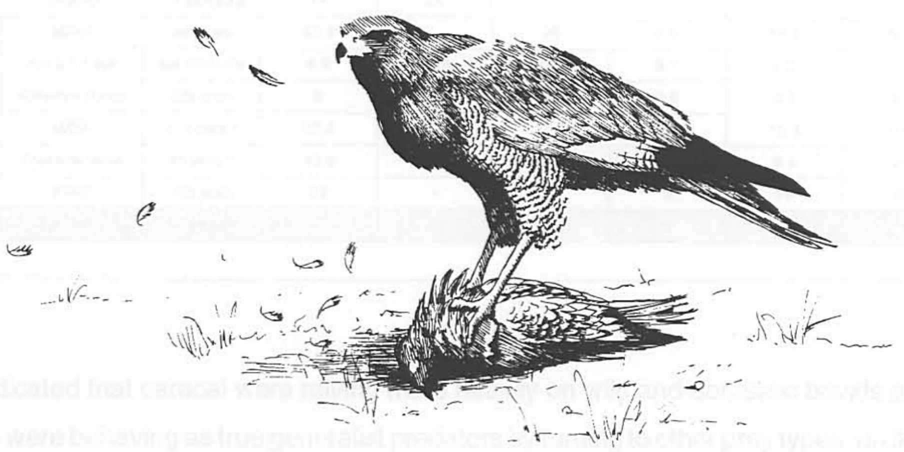


Figure 63. The distribution of caracal scats (small, solid circles), sightings (large, solid circles with cross pieces) and trap localities (solid box with flag) within the KRNP, in relation to episodic drainage routes (continuous lines), mountain slopes (grey) and escarpment (dark grey). One kilometer grid is shown.

With regard to other terrestrial predators, Cape wildcat scats were recovered from the bottom plains (n=2), lower slopes (n=2) and upper plateau (n=2). All four sightings of Cape wildcats were on the lower slopes in the vicinity of large boulders or substantial lineal outcrops. Two of these sightings indicated that wildcats can be active during the day (at 09h00 and 15h30). Cape wildcats have been seen on the upper plateau with kittens (R.M. & B. Randall pers. comm.) and they comprised a significantly greater portion of black eagle prey for those pairs who defended large areas of this habitat (Chapter 9). Habitat selection by Cape wildcats appears to be similar to that by caracals. Another terrestrial predator which was seen in all the major habitats of the park was Cape cobra. Canids (black-backed jackals, Cape fox and domestic dogs) were only recorded for the bottom plains and the upper plateau - they were not seen on the mountain slopes where most hyrax occurred.

With regard to avian predators, black eagles hunted over all habitats in the park, but mainly the mountain slopes and escarpment areas (previous chapter). Booted eagles and white-necked ravens were also seen in all habitats. I located three active nest sites of booted eagle on the lower escarpment and there were probably many more in the park. These migratory raptors arrived August - November and departed in March - April. Gymnogenes were recorded in the kloofs and along the escarpments and slopes. Pale chanting goshawks were encountered on the bottom plains and one pair was resident on the middle plateau. Jackal buzzards were surprisingly scarce and were limited to a few pairs on the upper plateau. Cape eagle owls were also only encountered in this habitat but their nocturnal habits masked any relative indication of abundance. Both these raptors probably hunted over some of the upper slopes as well. A single pair of martial eagles nested on the upper plateau but these birds hunted mostly outside the park and were excluded by neighbouring black eagles from prime hyrax habitat.



Pale chanting goshawk *Melierax canorus* with Namaqua sandrouse *Pterocles namaqua*

DISCUSSION

Feeding habits

Total absence of hyrax in the present analysis of caracal scats was not expected. Studies in the eastern Karoo have concluded that hyrax can comprise as much as 53% of caracal food (Grobler 1981, Moolman 1984, 1986a - see Table 18). This indicates that hyrax are not safe from caracals on account of the largely nocturnal habits of this cat. An investigation of caracal scats in the KRNP conducted three years prior to the present study recorded hyrax in 22% of scats (Palmer & Fairall 1988). Palmer (1985 unpubl.) employed feeding trials on captive caracal to compute correction factors for under- or over-estimation of prey types from scat analyses, and using various methods concluded that the observed frequency of occurrence of hyrax in caracal scats from the KRNP (22%) indicated that hyrax comprised between 12% and 29% of caracal food. Scats analysed by Palmer and Fairall were collected in 1984 when hyrax were declining from asymptotic numbers reached during the late 1970's to early 1980's, and the hyrax may have been vulnerable due to drought conditions (N. Fairall pers. comm.). The present study was conducted after the hyrax population had declined by an estimated factor of four (N. Fairall pers. comm.; Chapter 4), and the most likely explanation for the absence of hyrax as prey in the present study is that the reduced hyrax population was now well protected within its carrying capacity as defined by the extent of rocky habitat, and that the animals were simply not vulnerable to attack by mammalian carnivores. So the best indication for the relative contribution of hyrax to caracal food in the KRNP under more normal circumstances is about 20%, and it is conceivable that this might vary between 0 - 50%.

TABLE 18

COMPOSITION OF CARACAL DIET IN VARIOUS REGIONS OF THE CAPE

all values expressed as frequency of occurrence in the various sampling units, except Moolman (1984, 1986a) who expressed each value as a percentage of the total identifiable prey items

				DIET COMPOSITION						
SOURCE	DATE	STUDY AREA	METHOD	HYRAX	DOMESTIC STOCK	WILD BOVIDS	SMALL CARNIVORES	LAGOMORPHS	RODENTS	BIRDS
Pringle & Pringle (1979)	1972-75	Bedford	103 stomachs	14	55	-	-	-	-	-
Grobler (1981)	1979-80	MZNP	200 scats	53,3	-	20	0,9	10,6	5,3	5,3
Stuart (1982)	1980-81	SW & E Cape	394 stomachs	6,8	27,8	31,4	5,2	5,2	9,8	7,4
Stuart (1982)	1980-81	Robertson Karoo	248 scats	9	16,8	10,9	2,9	5,2	50	5,2
Moolman (1984, 1986a)	1982-83	MZNP	100 scats *	52,5	-	13,5	5,1	15,3	8,5	4,3
Moolman (1984, 1986a)	1982-83	Craddock farms	85 scats *	30,3	22,5	12,4	-	9,4	24	2,1
Palmer & Fairall (1988)	1984	KRNP	100 scats	22	-	28	2	19	39	2
Present Study (1993)	1987	KRNP	100 scats	-	24	50	5	2	1	10

The present study indicated that caracal were relying more heavily on wild and domestic bovids and birds. So it appears that caracals were behaving as true generalist predators by turning to other prey types, unlike black eagles which were successfully pursuing hyrax prey at low density (Chapter 9). Had we found a large proportion of hyrax in caracal diet, this would have been difficult to reconcile with the observation that black eagles were accounting for nearly all of the mortality of the adult hyrax age classes (Chapters 10 & 12). These findings suggest that black eagles are far more efficient at catching hyrax than are caracals. Unlike the wide-ranging black eagles which can detect hyrax at great distances and cover these distances at great speed (Chapter 6), caracals must rely on stalking and ambushing their prey. A certain threshold prey density or vulnerability may be necessary for caracals to become adept at supplementing their diet with hyrax. Caracals may also be more successful predators of hyrax where black eagles are restrained by other factors such as dense vegetation or the absence of nest sites.

Red rock rabbits are an abundant potential prey species for caracals in the KRNP (Chapter 5). Having actually witnessed a caracal capture this prey, a greater reliance on lagomorphs was expected than that revealed from the present scat analyses. Lagomorphs comprised up to 15% of prey in other caracal scat studies (Table 18), and are usually underestimated in scat analyses (Palmer 1985 unpubl.). But estimation of red rock rabbit numbers in the KRNP was conducted during 1989 - 1990, and sightings of this prey in the course of fieldwork suggested a ten-fold increase in abundance from very low numbers in 1987 to a peak in 1989 (Chapter 5). Fluctuations in rabbit numbers appeared to be much more amplified than those of other prey, including hyrax. The notion that caracals were hard-pressed to catch hyrax and rabbits leading up to and during 1987 concurs with a heavier reliance on large prey items and on domestic stock as revealed by the present study. Normally, caracals in conservation areas do not kill domestic stock (see Table 18), but there was some evidence of caracals moving out into farmland from the park in the present study.

Although Cape wildcats are generally considered to be predators of murids (Skinner & Smithers 1990), and although no hyrax remains have been found in Cape wildcat scats from the KRNP (Palmer & Fairall 1988) or from the eastern Robertson Karoo (Stuart 1982), adult hyrax observed in the present study certainly perceived wildcats as a threat and young hyrax only narrowly escaped capture by this predator. It is highly likely that young hyrax are sometimes captured, especially naive animals immediately after the birth pulse. Like caracals, Cape wildcats do not appear to be strictly nocturnal, so diurnal prey are still vulnerable to them. I could find no evidence in the literature for hyrax predation by the other likely mammalian predators encountered in the present study (Cape fox, small grey mongoose, baboon). Hyrax predation by these species is probably extremely rare. Stuart (1982) recorded hyrax in 0,5% of stomachs from 114 black-backed jackals killed in control operations in the Cape. This predator was not encountered during fieldwork but has been seen occasionally on the upper plateau. Leopards are known to prey heavily on hyrax in Cape mountains (Norton, Lawson, Henley & Avery 1986) but were not present in the KRNP. The only other terrestrial predator which may pose a serious threat to at least juvenile hyrax in the KRNP (because it can pursue its prey into shelter) is the Cape cobra, but little information is available on feeding habits or density.

Black eagles and martial eagles were the only raptors encountered in the KRNP which were considered large enough to kill adult rock hyrax. Hyrax comprised 7% of prey remains collected from martial eagle nests around the Cape, and were more prevalent under cliff nests of this eagle (Boshoff, Palmer & Avery 1990). Young hyrax are recorded as prey for jackal buzzards (Steyn 1982), booted eagles (Davies 1988), pale chanting goshawks (J.H. Swiegers pers. comm.), and Cape eagle owls (on moonlit nights) although this raptor preys mostly on *Pronolagus* (Gargett & Grobler 1976; Steyn & Tredgold 1977). It is not possible to quantify the amount of the diets of these smaller raptors that is fulfilled by hyrax in the KRNP, but it is likely that all might show an immediate functional response to prey on young hyrax when these prey become super-abundant.

Abundance

Estimates of home range size for male and female caracals in the Cape are given in Table 19 along with corresponding trapping success rates and rainfall for each study area. There was no statistically significant relationship between trapping success and rainfall, so regression of density on rainfall was not enabled. By assuming non-overlapping home ranges within the sexes, and totally overlapping home ranges between the sexes, it is possible to use the values of home range size to estimate likely ranges of caracal density. I used the ratio of juvenile to adult caracals given by Grobler (1981). If caracal densities in the KRNP approached those in the S W Cape, then the average black eagle territory of 24km^2 should accommodate 0,48 male, 1,31 female and 1,20 juvenile caracals. If caracal densities approached those in the MZNP, then the average black eagle territory in the KRNP should accommodate 1,58 male, 4,00 female and 3,71 juvenile caracals. These extremes provide convenient, likely biological limits to the range of caracal density in the Cape. But our trapping success rate suggests that an intermediate density of approximately 1,0 male, 2,69 female and 2,47 juvenile caracals is most likely for the KRNP, and would concur with intermediate rainfall (between that in MZNP and Robertson Karoo). This prediction indicates that the KRNP (330km^2) might accommodate 14 male, 37 female and 34 juvenile caracals. The black eagle population in the KRNP is estimated at about 30 birds (including juveniles and non-breeders - see Chapter 6), so caracals probably outnumber black eagles at a ratio of nearly three to one.

TABLE 19

TRAPPING SUCCESS RATES AND HOME RANGE ESTIMATES FOR CARACAL IN VARIOUS REGIONS OF THE CAPE

recaptures of caracals are excluded from calculations of trapping success in all studies except Moolman (1986a & b) for the MZNP

SOURCE	STUDY PERIOD	STUDY AREA	ANNUAL RAINFALL mm	Nos. TRAPPED	TRAP NIGHTS PER CARACAL	HOME RANGE SIZE (KM2) FEMALE	MALE
Grobler (1981)	1979-80	MZNP	398	1	538		
Stuart (1982)	1980-81	W Cape	237 - 1500	7	472	18,2	48,0
Norton & Lawson (1985)	1981-82	W Cape	<1500	2	500	18,0	56,0
Moolman (1986a & b)	1982-83	MZNP	398	21 *	90	5,5	15,2
Moolman (1986a & b)	1982-83	Cradock farms	398	13	146		19,0
Brand (1989)	1985	Calitzdorp	@300	2	246		
Brand (1989)	1986	Laingsburg	@210	8	151		
Brand (1989)	1987	Grahamstown	@470	11	124		
Brand (1989)	1987	Robertson	237	9	121		
Fairall (in litt.)	1984	KRNP	260	1	@400		(similar MZNP)
Present study (1993)	1988	KRNP	260	4	130	-	-

In 1984 Fairall (*in litt.*) and co-workers recorded greater frequencies of visits by caracals to scent posts in the Stolshoek region of the KRNP than in the recently proclaimed Doringhoek region. This difference subsequently disappeared, so it may have been caused by control operations at Doringhoek up until 1984.

Home range size for Cape wildcats is not known for the Cape. It is also not known for certain whether all areas of the park were used by wildcats. They may have been excluded or predated from some areas by caracal. The ratio of sightings of caracals to wildcats is the only clue available for wildcat numbers in the park. If this ratio is assumed to be representative of actual numbers (and that wildcats have a similar population structure to caracals), then the KRNP would contain about 34 adult Cape wildcats (and about 23 juveniles), and an average black eagle territory would contain about 2,5 adult wildcats (and about 1,7 juveniles). However, little confidence can be placed in these estimates and it is not possible to estimate the numbers of any other terrestrial predators in the KRNP with any certainty from available data.

Habitat selection

Both adult and juvenile hyrax are evidently susceptible to attack by black eagles and caracals throughout the park, and especially in their main areas of occurrence on mountain slopes. Results on habitat selection by caracals in the present study were similar to those observed by Moolman (1986a) for the MZNP, in that caracals were associated with large rocks (boulder scree) and riparian thicket. This may be due to shade-seeking behaviour and the need for cover when stalking prey. Observations in the present study are also in agreement with Moolman's (1986a) findings that caracals can be active during the day, particularly at temperatures below 22^{o}C. Escarpments and dry river courses probably afford convenient pathways for caracal movement and two of the caracal sightings in the present study were of animals crossing from one valley into another via a neck in the lower escarpment. Such features were found to be ideal caracal trapping sites by Brand (1989). Avoidance for grassy areas on the middle plateau and thicker plant cover on the lower slopes as indicated by the microhabitat analysis may simply be due to a preference by caracals for the less vegetated rocky areas in these habitats.

An aim of the present study of habitat selection by caracals was to predict in which areas hyrax would be vulnerable to attack by caracals, in case this might influence hyrax foraging behaviour. Hyrax are undoubtedly vulnerable to caracal attack in the vicinity of their rock outcrops, but they are probably more vulnerable when foraging away from their rocky shelters in riparian thicket. Thick vegetation along dry river courses may afford hyrax protection from black eagles, but not necessarily from attacks by caracals. It is likely that hyrax are only safe in riparian thicket over the midday period when caracals are less active (Moolman 1986a). Hyrax have an effective anti-predator strategy involving early warning and escape routes (Chapter 4). This strategy would be severely impeded in the dark, so predation by felids and owls might provide strong selective pressure opposing any development of nocturnal habits by hyrax.

Higher diversity and probably density of smaller, generalist predators such as Cape wildcat, jackal buzzard and Cape eagle owl, on the upper plateau is puzzling, but it may be due to dense vegetation supporting denser small mammal populations. Prevalence of these and other predators such as pale chanting goshawks and canids on the plateau and plains habitat types is probably not too crucial to hyrax populations, because most hyrax occur on the mountain slopes. But it is very clear that while adult hyrax face only two major enemies in the KRNP, juvenile hyrax may face **up to nine** potential predators in certain habitats.

Capacity for population change

The wide variation in numbers of caracal trapped on the farm Montana between 1978 and 1990 suggests that caracal density is very variable and that this predator might show a strong numeric response to changes in prey density. The rainfall-related pattern indicates that even intense persecution of this species does not appear to be the major influence on numbers. Caracal populations in the Cape appear particularly resilient to very heavy persecution, and numbers have actually gradually increased over the last few decades while black-backed jackal numbers have gradually declined (P. Norton *in litt.*). This indicates a very high potential for population increase. Unfortunately there are no direct data for observed rate of increase for natural caracal populations. But lines of best fit plotted through the increase and decline phases of the caracal trapping data for Montana do give some indication of the potential rate at which caracal numbers may change on Karoo farmland. While the influence of movements cannot be removed from this pattern, it at least provides some biological indication of the capacity of the numeric response on a localised basis. If it is assumed that numbers killed were directly related to numbers available, these analyses indicated a population decline at a rate of 34% per annum past a midpoint for the decline phase in July 1983, and a population increase at a rate of 22% per annum past a midpoint for the increase phase in December 1987. The drought in 1984 represented a very severe ecological event, so it is unlikely that caracal numbers would ever change much more dramatically than this. Good rains must first elicit a response in prey numbers before caracal numbers change, and a time-lag of about six months between rainfall events and caracal population response would appear appropriate for any modelling purposes.

Raptors are renowned for their ability to converge on localised irruptions of prey (e.g. Malherbe 1963). This facility enabled raptors to suppress cyclicity in vole populations in western Finland by efficient, density-dependent predation of the voles (Korpimäki 1985a, 1993). There are no data available for estimating the numeric response of generalist raptors (or other terrestrial predators) in the Karoo for modelling purposes. It is unlikely that this response would be as effective on localised hyrax irruptions as it is on rodent irruptions.

Food requirements of the caracal population

Estimates of the food needs of wild caracals can only be based on captive feeding trials and energetic predictions. Stuart (1982) found that eight captive caracals (mostly adult) needed an average of 586g (wet weight) meat per animal per day. This ranged from 485gd^{-1} for small females to 835gd^{-1} for large males. The three captive adult caracal used in Palmer's (1985 unpubl.) feeding trials consumed an average of 679gd^{-1} each. Grobler (1981) monitored the food requirement of a tame but free-ranging young male caracal (weighing 11,2kg) at 796gd^{-1}, and predicted that a wild adult caracal would need roughly 1000g of meat per day and a wild juvenile caracal would need about 500gd^{-1}.

Palmer & Fairall (1988) used standard metabolic scaling (Kleiber 1961) to predict the energy requirements of a 12kg caracal at rest, and increased this estimate by 50% (after Schmidt-Nielsen 1983) for the additional energy requirements of a free-living adult caracal, to yield a figure equivalent to 3150KJd^{-1}. Assuming the overall energy content of meat consumed by caracals to be 22KJg^{-1} dry matter (see Chapter 8), a dry matter concentration in this meat of 30% (see Chapter 8), and an assimilation efficiency for this carnivore of 80% (e.g. Golley, Petrides, Rauber

& Jenkins 1965; Farrell & Wood 1968; Litvaitis & Mautz 1976; Moors 1977), then in order to achieve this energy requirement of 3150KJd^{-1}, a wild caracal would need to consume 597g wet weight of meat per day. This is much lower than Grobler's (1981) estimate for wild adult caracal.

Nagy (1987) has shown that the field metabolic rates of wild animals are often far greater than those of captive animals, and that field metabolic rate can show a different relationship to body mass than does basal metabolic rate. This author provides various equations for estimating field metabolic rate of different groupings of animals. I used equation no. 18 for eutherians and the same assumptions on metabolisable energy content of caracal food given above to predict the food requirements of free-living male, female and juvenile caracals. The average body masses of 13,5kg for adult males and 10,5kg for adult females were calculated from data provided by Pringle & Pringle (1979) and Stuart (1982). Juvenile caracal were assumed to weigh 5kg. These data and calculations predict that in the wild an adult male caracal needs 1447g (wet weight) of meat per day; an adult female caracal needs 1179gd^{-1}; and a juvenile caracal needs 645gd^{-1}. In complete contrast to the predictions of Palmer & Fairall (1988), these predictions are far greater than those of Grobler (1981). Predictions of the food energy required by free-living black eagles using Nagy's (1987) formulae proved unrealistically high (Chapter 8), so it is possible that the predictions for caracals are also over-estimated.

Using the estimates of caracal abundance given earlier together with the predictions of field food requirements from Nagy's (1987) equation, caracals in the KRNP (330km^2) need to consume a total of 86kg meat (wet weight) per day or 31373kg per annum. In terms of the average black eagle territory (24km^2), this would correspond to an annual food consumption by resident caracals in the territory of 2282kg meat (or 1798kg if Grobler's predictions on food consumption are used). During the present study, resident black eagles only consumed about 268kg meat per territory per annum (Chapter 8). Caracals probably consume at least six times as much food as black eagles even when the eagles are catching more prey under more 'normal' conditions. In this regard, caracals can be considered more important predators overall, in this karoo environment. Caracal food consumption in a black eagle territory might vary from 1106kg if caracal numbers were as low as in the S W Cape, to 3444kg if caracal numbers were as high as in the MZNP.

<u>The potential impact of generalist predators on hyrax numbers</u>

Mean mass of hyrax in the KRNP varies from 1650g just after the birth pulse to 2430g just before it, and probably approaches 2040g overall (Chapter 4). Grobler (1981) found from feeding trials that caracals are able to consume 55% of a hyrax carcass by mass. So a 2040g hyrax carcass should yield 1122g of meat (wet weight). If, under normal circumstances, hyrax make up 20% of caracal food, then it follows from the above arguments that a standard population of caracals in the KRNP may kill up to 5600 hyrax each year. The estimated population size for hyrax in the KRNP during the study period was 13365 animals (Chapter 4) - this is after the population had declined by perhaps a factor of four (N. Fairall *in litt.*), and the population was considered to be at 60% of the local carrying capacity (Chapter 12).

Palmer & Fairall (1988) estimated that caracal were consuming 420 - 460 hyrax p.a. in their study area of 120km^2. This would correspond to a figure of about 1210 hyrax for the present extent of the KRNP (330km^2). This study was carried out during a major hyrax decline and so does not refer to normal conditions. Energy requirements of caracals may also have been underestimated in this calculation. Grobler (1981) estimated that caracals in the MZNP (65,4km^2) took an annual toll of 2995 hyrax, which would correspond to a figure of over 15000 hyrax for an area the size of the KRNP. High caracal densities and a high proportion of hyrax in the diet give rise to such a high estimate of impact which refers to a situation where hyrax probably occur at much higher density (Fourie 1983). Estimates of potential impact of caracals on hyrax populations in the Karoo are evidently variable. Predictions on caracal impact under normal conditions in this study are intermediate between other estimates of caracal impact on hyrax populations in the Karoo. Accuracy of the current assessment of impact under normal circumstances depends on three main parameters: estimated caracal density; estimated contribution of hyrax to caracal diet; and predictions of caracal food requirements. Biological field data on caracals were used in the calculation of the two former parameters but I suspect the predicted food requirements of caracals from Nagy's (1987) equation may be somewhat over-estimated, as were predicted food requirements of black eagles by this method (Chapter 8).

For comparative purposes, the consumption of hyrax by caracals in the KRNP given above would correspond to 407 hyrax killed by caracals in each black eagle territory per annum. However this scenario only portrays the impact that caracals may have on hyrax under more 'normal' conditions. During the present study hyrax numbers had declined to 1026 animals per eagle territory, caracal numbers may have been depressed, and the diet investigation indicated that they were not killing hyrax at all. It is likely though that a few were still being killed by caracals but this was undetected. Black eagles meanwhile were killing about 117 hyrax in their territories each year (Chapter 12). Under optimal conditions, caracals might conceivably increase to densities comparable to the MZNP, and they may take as much as 50% hyrax in their diet when this prey becomes super-abundant. Under such conditions, caracals have the potential to remove over 1500 hyrax from an average black eagle territory in a year. It is very unlikely that black eagles would be able to remove more than 350 hyrax from their territory in ideal conditions (Chapter 8). If the preceding assumptions and predictions are realistic, then it is apparent that caracals may play a far more important role than black eagles as hyrax predators when these prey become super-abundant.

Paucity of data on the feeding habits of the smaller generalist predators precludes such specific predictions about their impact on juvenile hyrax. Within a black eagle territory, about 417 juvenile hyrax were produced each year during the study period. About 250 of these were dying in their first year, and the variable nature of this high level of juvenile mortality was held responsible by Swart *et al.* (1986) for most change in hyrax numbers in the MZNP. These authors considered that the effects of predation were secondary in importance to this one parameter. However, hyrax are at their most vulnerable to predation in their first year of life. Just to present some perspective on this: a black eagle territory in the KRNP probably accommodates 2,2 black eagles, 3,6 adult caracals, 2,4 juvenile caracals, 2,4 adult wildcats, 1,6 juvenile wildcats, 1,6 small generalist avian predators, and an unknown number of Cape cobras. Black eagles are known to catch at least 16 juvenile hyrax in their territory every year and this is probably under-estimated due to biases inherent in analyses of prey remains collections (Chapter 10). If we assume there are about six small secondary predators per black eagle territory and that each one of these is able to catch 14 juvenile hyrax per annum, then this would amount to 84 juvenile hyrax killed. This scenario excludes any potential predation of juveniles by caracals yet it still suggests that predation may be responsible for at least 40% of the juvenile mortality referred to by Swart *et al.* (1986). This just indicates that predation should not be treated separately from juvenile mortality in population models for hyrax.

CONCLUSION

Analyses of caracal scats collected from the KRNP in 1987 suggest that this predator was behaving as a true generalist by not pursuing hyrax prey at low availability (unlike black eagles which are presumed to be more efficient, specialist predators on hyrax). Differences between this food study and those of other researchers can be explained in terms of changes in prey availability. Various indications suggest that caracals may pose a threat to hyrax in all habitats of the park, but especially along the escarpments and in the riparian thickets. Radio-tracking of caracals in the park was unsuccessful, but trapping success indicated densities intermediate between those in the MZNP and in the S W Cape, in keeping with intermediate rainfall. These densities were nearly three times greater than those of black eagles, and caracals may consume six times as much food as black eagles in the park. A high degree of variation in the numbers of caracals killed on karoo farmland related to rainfall patterns rather than persecution level, and suggested that caracals can show an effective numeric response (with some time-lag) to changes in prey density. While black eagles appear to be the most important hyrax predators under the current conditions of low hyrax availability, diet studies and metabolic predictions indicate that caracals have a far greater potential for removing hyrax when these prey exceed their carrying capacity as defined by the rocky habitats. Seven species of smaller, secondary predators (five avian, one carnivore, and one reptile) are also numerous in the KRNP, and along with black eagles and caracals, are probably directly responsible for a substantial component of the mortality of juvenile hyrax which has been shown to play a major role in hyrax population dynamics in the Karoo.