CHAPTER 9

# BLACK EAGLE FEEDING HABITS - 2. COMPOSITION OF PREY SPECIES IN THE DIET

## INTRODUCTION

The diet of black eagles has been extensively researched by the collection of prey remains from under nesting cliffs in five major regions of southern Africa. Earlier work in two of these regions indicated that black eagles are highly specialized, almost obligate predators on rock hyrax (genus *Procavia* and *Heterohyrax*): this prey taxon comprised 98,2% of 1892 prey items collected beneath nest cliffs in the Matobo Hills, Zimbabwe (Gargett 1977); and 92,6% of 176 items collected in the Transvaal, South Africa (Tarboton & Allan 1984). These observations that rock hyrax make up over 90% of black eagle prey have been widely cited in the literature (e.g. Cramp & Simmons 1980; Brown, Urban & Newman 1982; Steyn 1982; Maclean 1985), but detailed analyses of recent extensive collections of prey remains from three major biomes in the Cape Province, South Africa by Boshoff *et al.* (1991), indicate that black eagles can be versatile predators: non-hyrax prey comprised 11,3% of 3623 items collected in the Karoo; 38,2% of 1370 items collected in eastern Cape grasslands; and 52,3% of 755 items collected in the Fynbos. Other prey taxa represented in these regions were lagomorphs (4,8 - 8,6% diet); small carnivores (1,8 - 5,2%); juvenile domestic bovids (2,3 - 7,3%); juvenile wild bovids (3,7 - 5,0%); birds (0,6 - 10,2%); reptiles (0,9 - 9,3%); rodents (0,1 - 10,5%); and primates (0 - 2,0%).

To date, these analyses of prey 'left-overs' represent the only extensive investigations of black eagle diet. Direct observations of the eagles with prey are very scant, but apart from one study (Jenkins 1984), most indicate a more catholic diet (e.g. Rowe 1947; Branfield 1990; Boshoff *et al.* 1991), with incidental observations of peculiar hunting behaviour such as dropping tortoises to the ground (Steyn 1984; Fraser 1985). Evidently black eagles can hunt opportunistically, and there is accumulating evidence that they may be able to successfully make use of alternate prey at sites where rock hyrax are scarce. This raises speculation that black eagles might not be rock hyrax specialists, but rather catch the most available prey species living in African mountainous regions.

The high representation of rock hyrax in collections of prey remains might also result, in part, from various biases inherent in using prey remains to determine diet (Boshoff & Palmer 1980; Brown 1988c; Brown & Plug 1990; Boshoff *et al.* 1990). The sturdy skulls of rock hyrax are likely to be more noticeable, more resistant to weathering and more easily identified than prey remains from lagomorphs, rodents, small carnivores and birds. Collopy (1983b) appraised collections of prey remains as a means of investigating golden eagle *Aquila chrysaetos* feeding habits, against direct observations of prey on the nests. He found no significant differences between species composition of diet as indicated by the two methods, but the prey remains in this case were collected directly off the nests of the eagles 43-45 times each nesting season. It is likely that most of the black eagle work referred to above was carried out by collecting remains from beneath the eyries on one or two visits.

It is clear that a comprehensive study of black eagle feeding habits involving extensive use of alternate methods would reveal any biases in the collection of prey remains, and would also provide insight to the degree of specialism of the black eagle as a predator. The latter requires detailed knowledge of the prey base which is provided in the present study (Chapters 4 & 5). Specialist predators, by pursuing their prey at low densities, may have a destabilising affect upon prey populations (e.g. Pearson 1966, 1971; Fitzgerald 1977; Henttonen 1985; Korpimäki, Norrdahl & Rinta-Jaskari 1991), so this may have an important bearing on the predator-prey system under investigation.

The amount of rock hyrax in the diet of the eagles coupled with the rate at which prey are captured (previous chapter), are important parameters which need to be accurately measured for the interpretation of the demographic influence of black eagle predation on rock hyrax. Dietary selection of the different components of rock hyrax populations is also very important in this regard and is treated in the next chapter. The dominance of rock hyrax among black eagle prey and the ratio of predator to prey biomass can also give an indication of the likelihood of co-evolution occurring in this system (Allen 1976).

By investigating variation in black eagle diet over time and at different localities, it may be possible to identify the ecological factors that affect dietary selection of prey species and age classes. Analyses of black eagle diet at farm sites can provide a measure of the beneficial versus the harmful effects of this predator with regard to small stock husbandry (this important aspect of black eagle predation on karoo farms is treated more fully in Chapter 11). Temporal and geographical variation in predator diet can also be a useful indicator of processes affecting ecological communities (Andrews 1990; Avery 1992).

Prey remains collected during 1986 and 1987 within the study area (n=2250 items) made up part of the karoo sample analysed by Boshoff *et al.* (1991). This chapter presents analyses of the full sample of black eagle prey remains collected in the study area to date (including a further 1573 items collected between 1988 and 1990). These collections are now housed at the South African Museum in Cape Town along with other material reviewed by Boshoff *et al.* (1991). The full collection at the museum now totals over 6000 items thought to have been fed upon by black eagles in the Cape, and so provides a substantial database which is extensively referred to in this and the following chapter.

Analyses of the KRNP prey remains collections are supplemented in this chapter with data on black eagle feeding habits derived from three alternate methods: time-lapse photography at nests; direct observations of prey leftovers on nests; and direct observations of hunting and feeding behaviour of the eagles. A detailed appraisal of the four methods is necessary for data interpretation. Overall black eagle diet is determined from an interpolation between these various methods and discussed in relation to prey availability to draw conclusions on the degree of specialisation shown by black eagles. The main factors influencing variation of diet in time and space are also considered. On account of the multiple topics treated in this chapter, the results and discussion sections have been merged.

## METHODS

*The collection of prey remains from eagle nest cliffs*

At the end of each black eagle nesting season (December/January) during the study period, an intensive search was made beneath the nest and roost cliffs of as many black eagle pairs as possible to look for the remains of any prey items. With experience, it became possible to predict exactly where to search for individual pairs, but some feeding sites were not discovered until the second or third collections. Despite intensive searching of all areas there was wide variation in the number of prey items per collection. Factors influencing this variation are discussed later. Attempts were made to remove all prey remains from the sites at each collection, but undoubtedly some remains were overlooked, so the season of collection does not necessarily reflect the year of capture (particularly for the first collections).

Screes and accessible krantzes (small cliffs) in the vicinity of nests yielded most material. Regular feeding spots, popularly known as 'butcher blocks' (Cowden 1969; Gargett 1990), were discovered for certain pairs. First collections at such sites could yield up to 300 prey items. Low compact growths of the shrub *Grewia robusta* were favoured, and the tops of these shrubs often appeared pruned to form a flat solid platform of twigs and leaves into which remains of past meals had become interwoven. These platforms presumably provided the eagles with a good grip while they dismembered their prey, free from dust and soil. Many remains were found under surrounding shrubs where they had become ensnared by the vegetation on the steep slope. At some sites there was evidence that the prey remains had been scavenged by small carnivores (possibly mongooses), and cached by these animals under boulders. Skeletal material in such micro-climates and buried under top soil were less decomposed than material exposed on the slopes. Besides the skeletal material, skin, feathers and regurgitated pellets were also collected. The age (since death) of all skeletal material collected was ranked as fresh, medium or old in accordance with the degree of decomposition (allowances were made for micro-climate - see detailed methodology in Chapter 10).

For each item collected, a subjective assessment had to be made as to whether it actually represented prey of the eagles. The possibility that other predators were using the same feeding stations as the eagles cannot be ruled out, but for the sake of consistency, all material found under obvious 'butcher blocks' was collected as eagle prey, even unlikely items such as Alpine swift *Apus melba*. Rock hyrax skulls collected at butcher blocks were often opened with characteristic triangular sections removed from the occipital region of the cranium, presumably to access the brain as observed by Gargett (1990). Similar signs were used to identify other eagle prey, but further from feeding and nesting sites the possibility that material represented non-violent mortality, or the work of another predator was considered. Rock hyrax carcasses discovered in thick vegetation or under boulders, the skin of which had been folded inside-out, were considered to be caracal prey (after P. Benadie & L.C. Moolman pers. comm.). Some rodent material was excluded as more likely killed by rock kestrels; while some bird material was thought to have been killed and fed on by resident peregrine falcons. Skeletal material of black eagles probably resulted from non-predatory mortality in the vicinity of the nest cliffs - complete skeletons were usually found. Cape vultures have been known to be killed by black eagles (e.g. Bowen 1970; Mundy *et al.* 1986), but bones of immature vultures collected beneath some very tall cliffs in the KRNP were thought more likely to indicate an extinct colony.

To decide whether skeletal material of very large animals found under nest cliffs represented prey that was killed or scavenged by the eagles, it was necessary to know likely upper limits on the size of animals that might be overpowered and carried by the eagles - these figures were derived from the literature. Golden eagles have been known to get airborne with dall sheep lambs *Ovis dalli dalli* weighing 10 - 12kg, but only when descending from windy slopes (Nette, Burles & Hoefs 1984). From observation of a captive bird, it seems unlikely that black eagles would be able to convey any prey larger than about six kilograms to their nests or feeding sites unless it was dismembered first. The largest prey delivered to black eagle nests being monitored by time-lapse cameras (previous chapter) was a klipspringer lamb, estimated to weigh approximately 3,6kg. Records of maximum prey size for large eagles are summarised in Table 26. Eagles are evidently capable of killing some enormous prey, but most of the very large

TABLE 26
MAXIMUM SIZE RECORDS FOR PREY KILLED BY EAGLES

| Source | Eagle | Prey | Size |
|---|---|---|---|
| Lehti (1947) | golden | pronghorn | 36,3kg |
| Letley (1962) | black | grey rhebok | 9 - 14kg |
| Cooper (1969) | golden | red deer | 20,5kg |
| Bruns (1970) | golden | pronghorn | 31,7kg |
| Skogland (1974) | golden | reindeer | 25kg |
| Svendsen (1980) | golden | domestic sheep | 25kg |
| Steyn (1982) | crowned | bushbuck | 30kg |
| O'Gara et al. (1983) | golden | domestic sheep | 20 - 25kg |
| Bergo (1987) | golden | red deer | 30 - 50kg |

items killed by golden eagles were weakened by harsh winter conditions. It is possible that some of the largest prey recorded for golden eagles may have been driven over cliffs (Bergo 1987). Brown *et al.* (1982) contend that black eagles can kill prey up to 10kg in weight. I chose 18kg as the cut off point for the maximum prey size that could be killed by black eagles, and assumed that anything above this would have had to be scavenged. This is about half the size of a full-grown domestic sheep. Assignment of estimated mass to prey items is discussed later. Intact skeletons of adult grey rhebok and domestic sheep or goats were excluded from the sample on the presumption that they died on the cliffs and were not dismembered by the eagles.

After these exclusions it is still not possible to be certain that the remaining material was fed on by the eagles. White-necked ravens may well have been partly responsible for an unusually large collection of greater padloper tortoise *Homopus femoralis* remains found beneath a black eagle nest cliff on the upper escarpment. It is also not possible to be sure about the separation of predated versus scavenged material, and it seems likely that a great many juvenile large bovids and adult small bovids would have been scavenged rather than killed and dismembered as assumed here.

Each collection was separated into hyrax and non-hyrax remains and then analysed separately. With a bit of practice, rock hyrax skeletal material is very readily identifiable from its sturdy and curvaceous nature. Limb and pelvic bones were separated for left and right and counted along with sacra, but highest counts of individuals were nearly always obtained from maxillae. These had often broken into left and right maxillae in very decomposed specimens. Only for small juveniles did I sometimes obtain a higher individual count using left and right mandibles. Vertebrae and ribs were not quantified. The high representation of rock hyrax by cranial and dental material is fortunate because it facilitated separation of nearly all individuals by sex and age class. The allocation of rock hyrax prey into separate components of the population on the basis of dental characteristics and the calculation of mass for rock hyrax prey is outlined in full and treated separately in Chapter 10.

Under the supervision of G. Avery, non-hyrax prey remains were identified by comparison with osteological material housed at the Archaeology Department of the South African Museum in Cape Town. Limb and pelvic bones were separated for left and right and counted along with sacra, sterna (in the case of birds), scutes (in the case of tortoises) and skull material to give a minimum number of individuals of each identifiable species for the collection. This minimum number was thus based on the most frequently counted body part. In contrast to the rock hyrax material, minimum numbers for other prey species were mostly obtained from limb and pelvic bones. Prey items were classified into three major age classes on the basis of the degree of epiphyseal fusion and dental eruption: adult (epiphyses fused); sub-adult (near adult size, epiphyses unfused or fusing); and juvenile (diaphyses and epiphyses still growing). The mass of each prey item was recorded by estimating the proportion of adult mass that the individual represented, and then multiplying this by a figure of mean adult mass. The latter were derived from Skinner & Smithers (1990) for mammals, from Maclean (1985) for birds, and from Branch (1988) for reptiles. An average mass was determined for each species from these estimates of individual mass.

In making separate analyses of each collection from the same site there was the risk that different remains of a single prey captured would be represented in more than one collection from the same site and thus over-represented. This was countered by pooling all remains by site at the end of the study and analysing again for minimum numbers. This was carried out for rock hyrax remains as well, since there was the same possibility of double counting fragments of the same maxillae. Very few pellets were collected beneath nest cliffs (perhaps because they decomposed rapidly), so pellet-analysis was not employed to supplement findings from prey remains.

<u>Time-lapse photography at eagles' nests</u> (see previous chapter: pages 147-148).

*Direct observations of prey on the nests*

Besides trips to change film in the time-lapse cameras, all active nests were normally visited once or twice each year to monitor breeding developments (and to ring chicks in 1987). During the course of the study, about 140 separate visits were made to active nests and most of these were whilst there was a chick in the nest. Each visit I recorded details of the species and estimated age and size of any prey items on the nest. This method could not provide the same volume of information as the time-lapse photography, but at least I could usually obtain a very clear view of the prey through 8,5x45 binoculars. Visits were generally more than ten days apart so the risk of counting the same prey item twice was negligible.

*Direct observations of hunting and feeding behaviour of the eagles*

This method included all sightings of kills (n=15) by eagles; all sightings of eagles carrying freshly-killed prey (n=5); all sightings of eagles delivering freshly-killed prey to nests (n=8); all observations of piracy (n=1); and all observations of eagles scavenging (n=5). These data were derived either during eight separate five-day periods (about 480h) of direct observations on the behaviour of the Lion's Head, Beagle Ravine, Kortkloof and Penberi study pairs; or during 131h of direct observations at active nests belonging to the Sloop and Gamka Dam pairs; or by incidental observation during other activities such as hyrax counts / collection of prey remains, which entailed approximately 567h spent in the veld. Methods employed in the course of direct observations of the behaviour of the study pairs in their territories were described in detail in Chapter 6 (pages 86-87). On two occasions when prey was killed far away, I pinpointed the exact locality of the kill and (with the help of an assistant) later discovered the remains of a karoo korhaan and a suricate at these sites. Some data on black eagle diet derived from direct observations of eagles and of prey on their nests were also obtained from other karoo sites outside the study area.

## RESULTS AND DISCUSSION

*Factors influencing the collections of prey remains*

Separate analyses of 71 collections of prey remains revealed a total of 3823 prey items identified, most of which were collected from lower escarpment sites (Table 27). Collections at lower escarpment sites were larger

TABLE 27
SIZE AND DISTRIBUTION OF ANNUAL COLLECTIONS OF PREY REMAINS

| | YEAR OF COLLECTION | | | | | |
|---|---|---|---|---|---|---|
| | 1986 | 1987 | 1988 | 1989 | 1990 | TOTAL |
| No. lower escarpment sites | 9 | 11 | 11 | 11 | 5 | 47 |
| No. upper escarpment sites | 3 | 7 | 7 | 7 | 0 | 24 |
| Total no. sites sampled | 12 | 18 | 18 | 18 | 5 | 71 |
| Total no. prey items collected | 881 | 1369 | 742 | 648 | 183 | 3823 |

(mean=63,7; s.d.=66,8; n=39) than collections from upper escarpment sites (mean=36,3; s.d.=27,6; n=24). This difference was statistically significant (Savage Scores Test: $X^2=4,2; p<0,01$). More prey items were found beneath the nests of birds which bred (mean=80,3; s.d.=73,6; n=30) than beneath the nests of non-breeders (mean=33,9; s.d.=37,0; n=39), and this difference (about 60% less for non-breeders) was highly significant (Kruskal-Wallis Test: $X^2=16,2; p<0,01$). There was also a significant decline in the number of prey items recovered on consecutive collections as old material was cleared out ($r_p=-0,28; p<0,05$), with first collections averaging nearly 90 items, dropping to nearly 40 items by the third collections (Figure 75). About 50 prey items can be expected to be delivered to nests during the 88d nestling period (previous chapter). If the average accumulation rate of prey items under nest cliffs is 40 p.a. then the large initial collections made at some sites (up to 341 items) might reflect diet over the previous seven years. The marked influence of breeding on size of collections is strongly suggestive that collections of prey remains are mostly comprised of prey captured during the nesting season, despite some observations of eagles carrying prey to nesting/feeding sites outside of the breeding season. It was very difficult to search for prey remains on the steep screes and cliffs of the upper escarpment where the eagles have many more rocks to choose from as feeding perches. But smaller samples from these localities might also be associated with the lower breeding rates of upper escarpment pairs (Chapter 6).

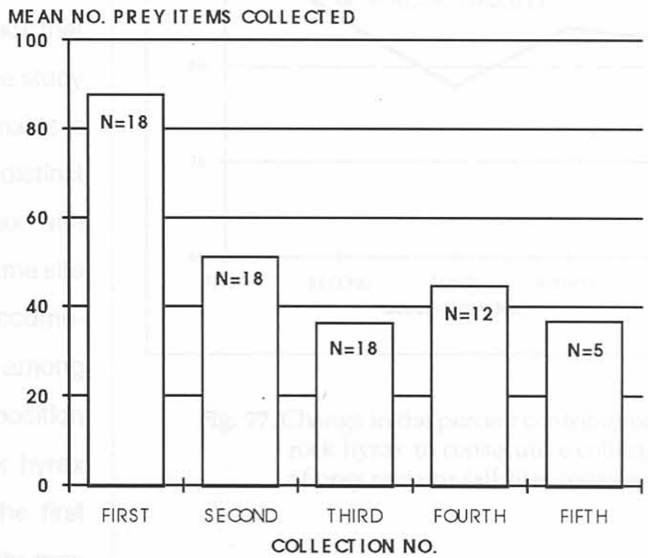


**Figure 75.** recovery of prey items on consecutive collections.

*Species composition of black eagle diet as indicated by prey remains - in terms of numbers*

The remains of about 40 different potential prey species were found beneath the nest cliffs of the black eagles in and around the KRNP (Table 28). Such a wide spectrum of prey is the product of a large sample size (n=3586 items). Larger collections generally revealed more species fed upon. This is illustrated in Figure 76 which suggests that a sample of about 75 items is needed from a site to give a good indication of the prey spectrum taken. By pooling the samples for each site at the end of the study and re-appraising to avoid the possibility of over-counting a single prey item (this is especially likely with the scutes of a tortoise for instance), sample size was slightly reduced but species composition was not significantly altered. Analyses of the pooled sample are thought to represent the more accurate interpretation of diet. There were minor discrepancies between the two treatments with some re-classifications within the pooled sample.

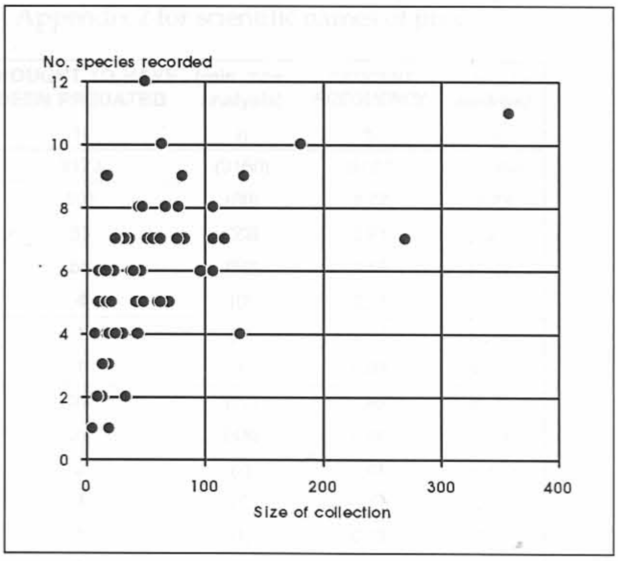


**Fig. 76.** Relationship between the size of the collection of prey remains, and the number of species represented.

Rock hyrax comprised 88% of black eagle prey by numbers. The predominance of rock hyrax in the diet of the study population of black eagles is close to that recorded for the Magaliesberg and the Transvaal (D.G. Allan *in litt.*; Jenkins 1984; Tarboton & Allan 1984), and falls between high levels of dominance in the Matobo Hills (Gargett 1977) and low levels of dominance in the eastern Cape grasslands and the Fynbos (Boshoff *et al.* 1991). I would conclude that the proportion of rock hyrax recorded in the diet of the study population of black eagles as indicated by prey remains is average to high, for this predator. There was a distinct decline however, in the proportion of rock hyrax with consecutive collections of prey remains from the same site (Figure 77). This is thought to be mainly due to accumulation of the large and noticeable rock hyrax skulls among prey remains with time - suggesting that real composition of black eagle diet might approximate 80% rock hyrax rather than 90% rock hyrax as suggested by the first collections. However, changes in prey availability may also have been responsible for the apparent change in dietary composition (discussed later).

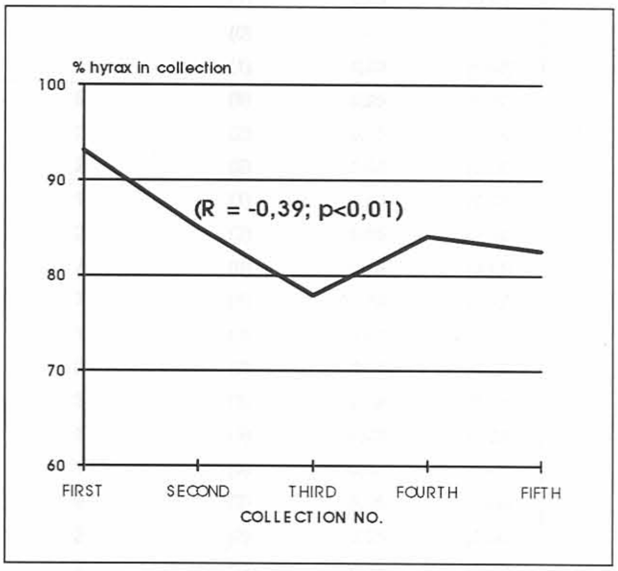


**Fig. 77.** Change in the percent contribution by rock hyrax to consecutive collections of prey remains (all sites considered).

# TABLE 28

## COMPOSITION OF THE ENTIRE COLLECTION OF PREY REMAINS COLLECTED BENEATH BLACK EAGLE NEST SITES IN AND AROUND THE KRNP

Any item larger than 18kg was considered scavenged rather than predated. Some prey individuals may have been represented twice (by different body parts) in collections from the same sites, so all collections were pooled by site and re-analysed at the end of the study (min. nos. analysis). Consult Appendix 2 for scientific names of prey.

| SPECIES/CATEGORY | CONSIDERED NOT EATEN | POSSIBLY SCAVENGED | (min. nos. analysis) | THOUGHT TO HAVE BEEN PREDATED | (min. nos. analysis) | PERCENT FREQUENCY | (min. nos. analysis) |
|---|---|---|---|---|---|---|---|
| | n | n | n | n | n | % | % |
| rock hyrax | | | | 3173 | (3150) | 87,07 | (87,84) |
| Smith's red rock rabbit | | | | 101 | (80) | 2,77 | (2,23) |
| Cape hare | | | | 33 | (23) | 0,91 | (0,64) |
| scrub hare | | | | 58 | (50) | 1,59 | (1,39) |
| unidentified lagomorph | | | | 4 | (0) | 0,11 | - |
| unidentified rodent | | | | 1 | (1) | 0,03 | (0,03) |
| Cape porcupine | | | | 1 | (1) | 0,03 | (0,03) |
| steenbok | | | | 23 | (27) | 0,63 | (0,75) |
| klipspringer | | | | 29 | (48) | 0,80 | (1,34) |
| springbok | | | | 2 | (2) | 0,05 | (0,06) |
| mountain reedbuck | | 1 | (1) | 4 | (7) | 0,11 | (0,20) |
| grey rhebok | | 3 | (7) | 1 | (1) | 0,03 | (0,03) |
| unidentified wild bovid | | | | 3 | (0) | 0,08 | - |
| unidentified domestic bovid | | 37 | (24) | 50 | (40) | 1,37 | (1,12) |
| unidentified bovid | | | | 2 | (0) | 0,05 | - |
| suricate | | | | 27 | (26) | 0,74 | (0,73) |
| small grey mongoose | | | | 11 | (10) | 0,30 | (0,28) |
| yellow mongoose | | | | 3 | (3) | 0,08 | (0,08) |
| water mongoose | | | | 1 | (1) | 0,03 | (0,03) |
| small-spotted genet | | | | 1 | (1) | 0,03 | (0,03) |
| zorilla (striped polecat) | | | | 2 | (2) | 0,05 | (0,06) |
| Cape wildcat | | | | 7 | (7) | 0,19 | (0,20) |
| bat-eared fox | | | | 1 | (1) | 0,03 | (0,03) |
| aardwolf | | 1 | (1) | | (0) | - | - |
| unidentified carnivore | | | | 1 | (1) | 0,03 | (0,03) |
| karoo korhaan | | | | 9 | (8) | 0,25 | (0,22) |
| helmeted guinea fowl | | | | 2 | (2) | 0,05 | (0,06) |
| greywing francolin | | | | 2 | (2) | 0,05 | (0,06) |
| African black duck | | | | 1 | (1) | 0,03 | (0,03) |
| red-eyed dove | | | | 2 | (2) | 0,05 | (0,06) |
| rock pigeon | | | | 7 | (9) | 0,19 | (0,25) |
| white-necked raven | | | | 7 | (6) | 0,19 | (0,17) |
| black-necked heron | | | | 1 | (0) | 0,03 | - |
| black stork | | | | 2 | (2) | 0,05 | (0,06) |
| rock kestrel | | | | 3 | (3) | 0,08 | (0,08) |
| large falcon | | | | 1 | (1) | 0,03 | (0,03) |
| spotted eagle owl | | | | 1 | (0) | 0,03 | - |
| Cape eagle owl | | | | 2 | (2) | 0,05 | (0,06) |
| Ludwig's bustard | | | | 2 | (2) | 0,05 | (0,06) |
| Alpine swift | | | | 1 | (1) | 0,03 | (0,03) |
| unidentified bird | | | | 2 | (1) | 0,05 | (0,03) |
| tent tortoise | | | | 4 | (2) | 0,11 | (0,06) |
| greater padloper | | | | 52 | (54) | 1,43 | (1,51) |
| leopard tortoise | | | | 3 | (5) | 0,08 | (0,14) |
| rock leguaan | | | | 1 | (1) | 0,03 | (0,03) |
| TOTAL | 7 | 42 | (33) | 3644 | (3586) | 100,00 | (100,00) |
| black eagle | 4 | | | | | | |
| Cape vulture | 3 | | | | | | |

Carrion comprised just under one percent of the collection if it is assumed that all prey items larger than 18kg were scavenged. If adult and near adult small antelope were also scavenged then carrion would have comprised 1,5% of the prey remains collection.

*Species composition of black eagle diet as indicated by prey remains - in terms of mass*

Average mass for black eagle prey, calculated from estimated mass (see methods) for 3589 prey items was 2565g. Average mass for 2931 rock hyrax taken was estimated to be 2582g (p. 211). Because of the similarity in these two estimates percent biomass of rock hyrax in black eagle diet was not dissimilar from percent frequency. The mean mass for 436 non-hyrax prey of the eagles was estimated to be 2440g. This is lower because small red rock rabbits, carnivores, birds and reptiles made up the majority of non-hyrax prey. It has to be borne in mind that large prey items are more likely to be represented in collections of prey remains than small prey items such as juvenile rock hyrax.

The prey remains suggested that black eagles were catching prey items ranging in size from 200g to 15000g (Figure 78). However 97,3% of prey items taken were estimated to fall into the size range of 500 - 4000g, in close agreement with the estimates of Boshoff *et al.* (1991). Most prey taken are thus smaller than the eagles themselves (mean body mass 3,82kg - see Chapter 8). Juveniles comprised 97% of bovid prey as well as the majority of large carnivores and birds fed upon by the eagles (Table 29).

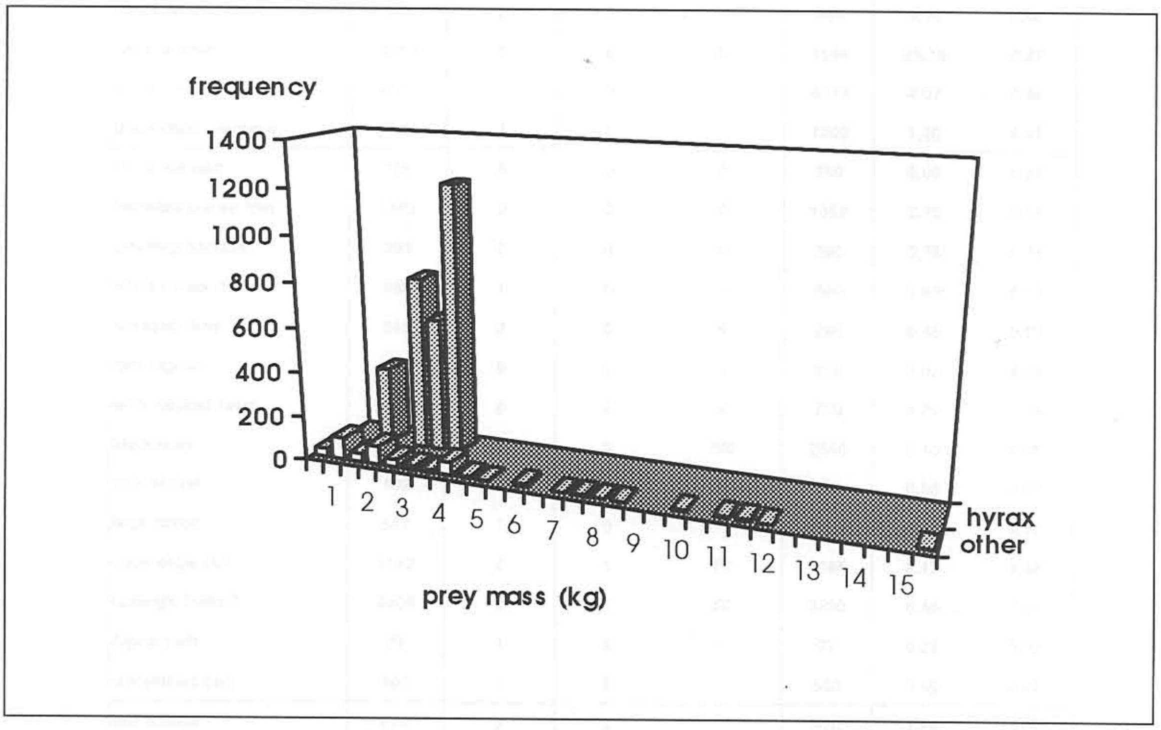


**Figure 78.** Frequency distribution of hyrax and other black eagle prey in accordance with size category, as indicated from 3589 prey remains.

# TABLE 29

## COMPOSITION OF BLACK EAGLE DIET IN TERMS OF MASS AND THE JUVENILE PREY COMPONENT, AS INDICATED BY PREY REMAINS

Immature prey items were separated on the basis of dental erruption and the degree of epiphyseal fusion. Average mass for each prey species was calculated from mass estimates for each individual (see methods). Consult Appendix 2 for scientific names of prey.

| SPECIES/CATEGORY | ADULT MASS | FREQUENCY | NO. IMMATURE | *(percent immature)* | AVERAGE MASS | BIOMASS | *(percent biomass)* |
|---|---|---|---|---|---|---|---|
| | g | n | n | % | g | kg | % |
| rock hyrax | 3200 | 3150 | 1211 | *38* | 2582 | 8133,30 | *88,43* |
| Smith's red rock rabbit | 1620 | 80 | 13 | *16* | 1541 | 123,28 | *1,34* |
| Cape hare | 2040 | 23 | 2 | *8* | 1983 | 45,61 | *0,50* |
| scrub hare | 3600 | 50 | 20 | *39* | 3268 | 163,40 | *1,78* |
| unidentified rodent | 75 | 1 | - | - | 75 | 0,08 | *0,00* |
| Cape porcupine | 11500 | 1 | 1 | - | 5750 | 5,75 | *0,06* |
| steenbok | 11095 | 27 | 25 | *93* | 4356 | 117,61 | *1,28* |
| klipspringer | 11900 | 48 | 46 | *96* | 5541 | 265,97 | *2,89* |
| springbok | 25000 | 2 | 2 | *100* | 3125 | 6,25 | *0,07* |
| mountain reedbuck | 29400 | 7 | 7 | *100* | 5250 | 36,75 | *0,40* |
| grey rhebok | 20000 | 1 | 1 | - | 2000 | 2,00 | *0,02* |
| unidentified domestic bovid | 38000 | 40 | 40 | *100* | 4180 | 167,20 | *1,82* |
| suricate | 734 | 26 | 1 | *4* | 731 | 19,01 | *0,21* |
| small grey mongoose | 797 | 10 | 0 | *0* | 797 | 7,97 | *0,09* |
| yellow mongoose | 830 | 3 | 0 | *0* | 830 | 2,49 | *0,03* |
| water mongoose | 3400 | 1 | 0 | - | 3400 | 3,40 | *0,04* |
| small-spotted genet | 1900 | 1 | 0 | - | 1900 | 1,90 | *0,02* |
| zorilla (striped polecat) | 843 | 2 | 0 | *0* | 843 | 1,69 | *0,02* |
| Cape wildcat | 4300 | 7 | 4 | *57* | 3594 | 25,16 | *0,27* |
| bat-eared fox | 4070 | 1 | 0 | - | 4070 | 4,07 | *0,04* |
| unidentified carnivore | 1500 | 1 | 1 | - | 1200 | 1,20 | *0,01* |
| karoo korhaan | 750 | 8 | 0 | *0* | 750 | 6,00 | *0,07* |
| helmeted guinea fowl | 1352 | 2 | 0 | *0* | 1352 | 2,70 | *0,03* |
| greywing francolin | 390 | 2 | 0 | *0* | 390 | 0,78 | *0,01* |
| African black duck | 880 | 1 | 0 | - | 880 | 0,88 | *0,01* |
| red-eyed dove | 240 | 2 | 0 | *0* | 240 | 0,48 | *0,01* |
| rock pigeon | 335 | 9 | 0 | *0* | 335 | 3,02 | *0,03* |
| white-necked raven | 700 | 6 | 0 | *0* | 700 | 4,20 | *0,05* |
| black stork | 3000 | 2 | 2 | *100* | 2550 | 5,10 | *0,06* |
| rock kestrel | 192 | 3 | 0 | *0* | 192 | 0,58 | *0,01* |
| large falcon | 587 | 1 | 0 | - | 587 | 0,59 | *0,01* |
| Cape eagle owl | 1142 | 2 | 1 | *50* | 1085 | 2,17 | *0,02* |
| Ludwig's bustard | 3400 | 2 | 1 | *50* | 3230 | 6,46 | *0,07* |
| Alpine swift | 77 | 1 | 0 | - | 77 | 0,08 | *0,00* |
| unidentified bird | 500 | 1 | 0 | - | 500 | 0,50 | *0,01* |
| tent tortoise | 570 | 2 | 0 | - | 570 | 1,14 | *0,01* |
| greater padloper | 510 | 54 | 21 | *39* | 402 | 21,71 | *0,24* |
| leopard tortoise | 12000 | 5 | 5 | *100* | 1080 | 5,40 | *0,06* |
| rock leguaan | 3000 | 1 | 1 | - | 2000 | 2,00 | *0,02* |
| AVERAGE | 5267 | | | | 2565 | | |
| TOTAL | | 3586 | 1405 | *39* | | 9197,88 | *100,00* |

The calculation of diet composition in terms of biomass is presented in Table 29. The entire collection of prey remains is thought to represent a total prey biomass of 9198kg captured/scavenged by the Nuweveldberg eagles. Comparisons of species composition of black eagle diet in terms of numbers and in terms of mass are summarised in Table 30, and illustrated in Figure 79. When considering diet in terms of biomass rather than frequency, the obvious differences are that large bovid prey take on added importance in fulfilling the food requirements of the eagles at the expense of the smaller carnivores, birds and reptiles. However it should be borne in mind that the product of frequency and mass for each prey species is a simplification of the importance of the prey as food, because eagles are known to consume differing proportions of different sized prey (Gargett 1982a; A.F. Boshoff pers. comm.).

TABLE 30

COMPOSITION OF THE PRINCIPAL PREY TAXA IN BLACK EAGLE DIET IN TERMS OF MASS AND NUMBERS, AS INDICATED BY PREY REMAINS

| PREY | FREQUENCY | percent | MEAN MASS | BIOMASS | percent |
|---|---|---|---|---|---|
| | n | % | g | kg | % |
| Hyrax | 3150 | *87,84* | 2582 | 8133,30 | *88,43* |
| Lagomorphs | 153 | *4,27* | 2172 | 332,29 | *3,61* |
| Rodents | 2 | *0,06* | 2915 | 5,83 | *0,06* |
| Bovids | 125 | *3,49* | 4766 | 595,78 | *6,48* |
| Carnivores | 52 | *1,45* | 1286 | 66,89 | *0,73* |
| Birds | 42 | *1,17* | 799 | 33,54 | *0,36* |
| Reptiles | 62 | *1,73* | 488 | 30,25 | *0,33* |
| **TOTAL** | 3586 | *100,00* | (2565) | 9197,88 | *100,00* |
| Carrion | (56) | | | | |

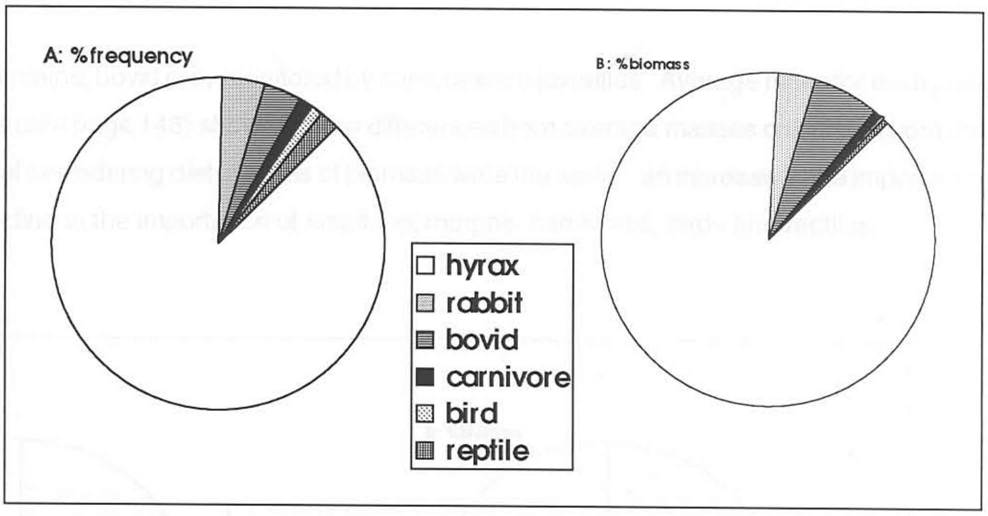


Fig. 79. Percent composition of the principal prey taxa in black eagle diet in terms of frequency (A) and biomass (B), as indicated by prey remains

Average mass calculated for prey items that were considered to have been scavenged by the eagles (i.e. >18kg) was 25,9kg. Taking the frequency of occurrence of carrion in prey remains to vary between 1 and 1,5%, and assuming that 50% of each carcass was monopolised by the eagles (it is actually unlikely that the eagles would consume most of a large ungulate carcass), the contribution of carrion as suggested by prey remains in meeting black eagle food requirements might vary between 4 and 8%. This may be under-estimated because most carrion would be fed on away from the nest cliffs (see later), but the assumption that 50% of each carcass fed on would be monopolised by the eagles is probably very generous. Frequency of scavenging is mentioned again under direct observations, but unfortunately it is not yet possible to be more precise on this aspect of black eagle feeding.

*Species composition of black eagle diet as indicated by time-lapse photography at nests*

The effectiveness of time-lapse photography as a tool for monitoring black eagle feeding habits was assessed in the previous chapter (page 151). Up to six nests were monitored by time-lapse photography each season over four years, yielding data (average 41d; s.d.=33d) on 17 separate nestling periods. The cameras were placed at the nests of the eagles for a total of 1050 days, during which time they were operational for 82% of the time (864 nest days). Excluding all days before hatching or after fledging, the cameras provided data on 701 days while the eagles were provisioning food to their chicks. A total of 62 films were exposed, which yielded data over an average of 13,5d (s.d.=5,1d) each. At the chosen interval of just over 3,5 min between frames, the films could however comfortably run for 16-17d if no problems were encountered. An average of 206 frames were exposed for each day of filming, and a total of 178000 frames were analysed to yield data on the feeding habits of the eagles.

During the 701 days while the eagles were monitored with chicks, a total of 389 prey deliveries were recorded from the films. Eighty five percent of these prey could be identified, representing 10 species and two unidentified categories, and the composition of black eagle diet that they suggest (in terms of both numbers and mass) is presented in Table 31 and Figure 80. The major prey taxa identified in the collections of prey remains (Table 30) were all represented in the monitored prey deliveries. But there were major differences (tested later) in the proportional representation of the prey by the two methods. Most noticeable was the high representation of red rock rabbits amongst the prey deliveries monitored by camera. Consequently, rock hyrax comprised a smaller fraction (68%) of black eagle diet as indicated by this method.

In accordance with the prey remains, bovid prey monitored by camera were juveniles. Average mass for each prey species delivered to the nests (see page 148) showed some differences from average masses calculated from the prey remains, but the effects of considering diet in terms of biomass were the same: an increase in the importance of large bovid prey, and a decline in the importance of small lagomorphs, carnivores, birds and reptiles.

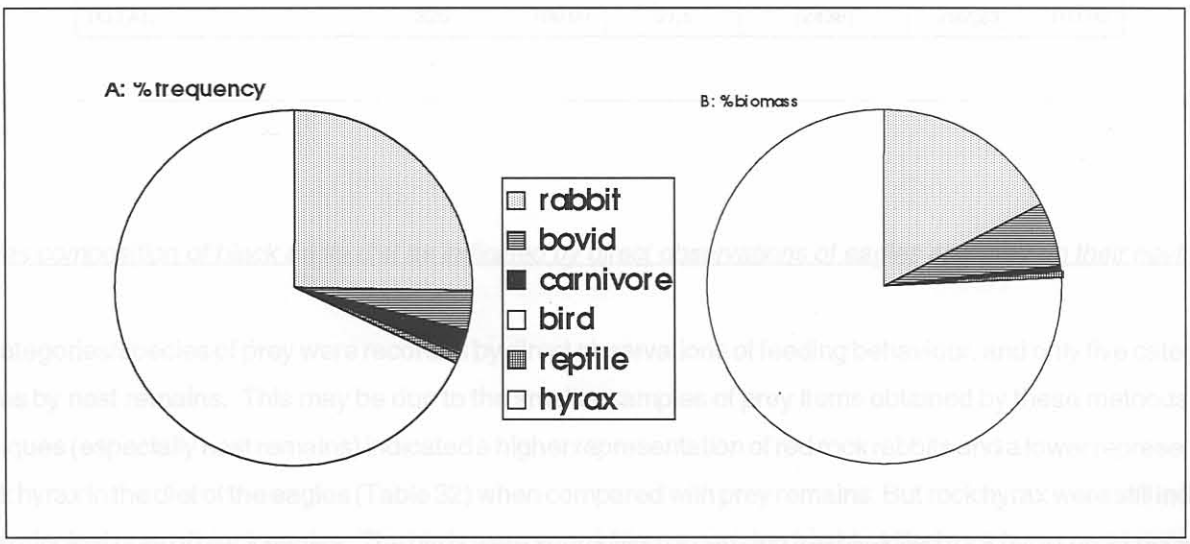


**Figure 80.** Percent composition of the principal prey taxa in black eagle diet in terms of frequency (A) and biomass (B), as indicated by time-lapse photography at nests

## TABLE 31

**COMPOSITION OF BLACK EAGLE DIET IN TERMS OF MASS AND NUMBERS AS INDICATED BY TIME-LAPSE PHOTOGRAPHY AT NESTS**

| PREY | FREQUENCY n | percent % | Percent juv. % | MEAN MASS g | BIOMASS kg | percent % |
|---|---|---|---|---|---|---|
| rock hyrax | 223 | 67,78 | 34,3 | 2691 | 600,09 | 75,75 |
| (unidentified non-hyrax) | (4) | | | | | |
| Smith's red rock rabbit | 67 | 21,16 | 12,5 | 1548 | 103,72 | 13,09 |
| Cape hare | 5 | 1,58 | 50,0 | 1836 | 9,18 | 1,16 |
| scrub hare | 6 | 1,90 | 0,0 | 3600 | 21,60 | 2,73 |
| unidentified lagomorph | 2 | 0,63 | 50,0 | 1133 | 2,27 | 0,29 |
| unidentified rodent | 1 | 0,32 | | 80 | 0,08 | 0,01 |
| steenbok | 2 | 0,63 | 100,0 | 1664 | 3,33 | 0,42 |
| klipspringer | 4 | 1,26 | 100,0 | 2231 | 8,92 | 1,13 |
| unidentified wild bovid | 1 | 0,32 | 100,0 | 1800 | 1,80 | 0,23 |
| domestic bovid | 5 | 1,58 | 100,0 | 6650 | 33,25 | 4,20 |
| small grey mongoose | 3 | 0,95 | | 744 | 2,23 | 0,28 |
| yellow mongoose | 2 | 0,63 | | 830 | 1,66 | 0,21 |
| unidentified viverrid | 1 | 0,32 | | 800 | 0,80 | 0,10 |
| unidentified bird | 1 | 0,32 | | 500 | 0,50 | 0,06 |
| rock leguaan | 2 | 0,63 | | 1400 | 2,80 | 0,35 |
| **SUMMARY:** | | | | | | |
| Hyrax | 223 | 67,78 | 34,3 | 2691 | 600,09 | 75,75 |
| Lagomorphs | 80 | 25,27 | 13,6 | 1710 | 136,76 | 17,26 |
| Rodents | 1 | 0,32 | 0,0 | 80 | 0,08 | 0,01 |
| Bovids | 12 | 3,79 | 100,0 | 3942 | 47,30 | 5,97 |
| Carnivores | 6 | 1,90 | 16,7 | 782 | 4,69 | 0,59 |
| Birds | 1 | 0,32 | 0,0 | 500 | 0,50 | 0,06 |
| Reptiles | 2 | 0,63 | 100,0 | 1400 | 2,80 | 0,35 |
| **TOTAL** | 325 | 100,00 | 31,5 | (2438) | 792,23 | 100,00 |

*Species composition of black eagle diet as indicated by direct observations of eagles and prey on their nests*

Ten categories/species of prey were recorded by direct observations of feeding behaviour, and only five categories/ species by nest remains. This may be due to the smaller samples of prey items obtained by these methods. Both techniques (especially nest remains) indicated a higher representation of red rock rabbits and a lower representation of rock hyrax in the diet of the eagles (Table 32) when compared with prey remains. But rock hyrax were still indicated as the principal prey of black eagles. The birds were seen killing or carrying freshly-killed rock hyrax on 21 occasions, and juveniles comprised six (29%) of these.

## TABLE 32
### COMPOSITION OF BLACK EAGLE DIET AS INDICATED BY DIRECT OBSERVATIONS AND NEST REMAINS

| PREY | DIRECT OBSERVATIONS OF PREY TAKEN | | | |
|---|---|---|---|---|
| | "Kills or freshly-killed" n | percent % | "Fresh remains on the nests" n | percent % |
| rock hyrax | 21 | *60,00* | 40 | *56,34* |
| Smith's red rock rabbit | 3 | *8,57* | 21 | *29,58* |
| Cape hare | 1 | *2,86* | - | - |
| scrub hare | 1 | *2,86* | 3 | *4,23* |
| unidentified lagomorph | - | - | 4 | *5,63* |
| steenbok | - | - | - | - |
| klipspringer | - | - | 1 | *1,41* |
| domestic bovid | - | - | 2 | *2,82* |
| suricate | 1 | *2,86* | - | - |
| unidentified viverrid/rodent | 1 | *2,86* | - | - |
| karoo korhaan | 1 | *2,86* | - | - |
| unidentified bird | 1 | *2,86* | - | - |
| rock leguaan | - | - | - | - |
| piracy | 1 | *2,86* | - | - |
| carrion | 4 | *11,43* | - | - |
| **SUMMARY:** | | | | |
| Hyrax | 21 | *60,00* | 40 | *56,34* |
| Lagomorphs | 5 | *14,29* | 28 | *29,58* |
| Rodents | - | - | - | - |
| Bovids | - | - | 3 | *4,23* |
| Carnivores | 2 | *5,71* | - | - |
| Birds | 2 | *5,71* | - | - |
| Reptiles | - | - | - | - |
| Piracy | 1 | *2,86* | - | - |
| Carrion | 4 | *11,43* | - | - |
| TOTAL | 35 | *100,00* | 71 | *100,00* |

Unfortunately, observations of feeding behaviour were rare (n=35 instances), but out of this small sample size, four observations of eagles feeding on carrion (one springbok; one grey rhebok; and two domestic sheep) is suggestive that scavenging may fulfil a notable amount of black eagle food requirements.

Circumstantial evidence indicated piracy on one occasion: a pair of eagles under observation repeatedly swooped on their neighbours who were perched on the ground out of sight, eventually driving them off; the observation pair then disappeared for 30 min, and when they emerged later the female had a full crop.

*Comparison of methods*

Annual clearance of prey remains from nest sites which were being monitored by time-lapse photography permitted direct comparison of the results from the two methods for 10 separate nestling periods (periods corresponding to the first collections of prey remains were excluded because these could represent diet before the cameras were operational). These results are presented in Figure 81. Similarity between the results from the two methods was confined to the relative proportions of the minor prey taxa (rodents, bovids and carnivores). It is possible that birds would be consumed rapidly and thus be under-represented by time-lapse photography (see previous chapter).

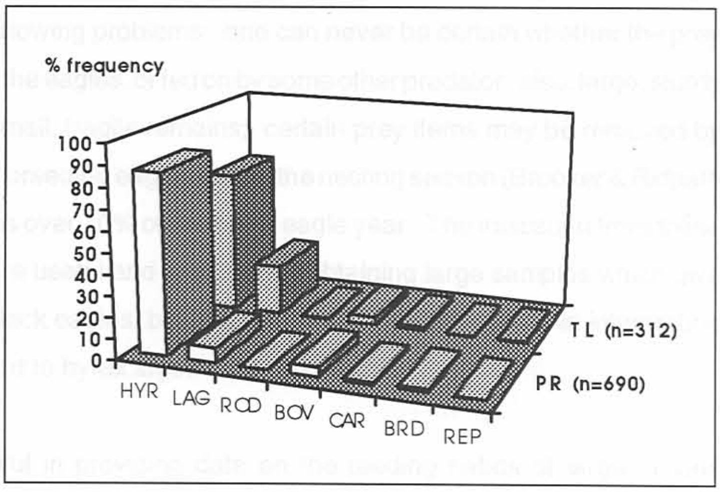


**Fig. 81.** direct comparison of diet composition as determined for ten separate nestling periods using two methods: time-lapse photography at nests (TL) and the subsequent collection of prey remains (PR). Sample sizes refer to the number of prey items observed. Legend: HYR = rock hyrax; LAG = lagomorphs; ROD = rodents; BOV = bovids; CAR = carnivores; BRD = birds; REP = reptiles.

Larger samples of prey items were recorded by the collection of prey remains for each nestling period, although some prey remains may have accumulated during the rest of the year. Prey species diversity was higher (mean=6,6 items) for the prey remains samples than for the time-lapse samples (mean=4,6 items). This difference was statistically significant (t-test for matched pairs: t=2,27; p<0,05). There was a statistically highly significant association between prey type and its representation as determined by the two methods of diet analysis ($X^2$=62,7; p<0,01). In particular, rock hyrax comprised a greater proportion of prey remains (86%) than time-lapse monitored deliveries (68%). These proportions were arcsine-transformed for use in a 2-tailed t-test for matched pairs, and the difference proved to be statistically highly significant (t=3,33; p<0,01). In the same way, there was a statistically highly significant difference between the proportions of red rock rabbits as determined by the two methods (t=3,33; 0<0,01). Red rock rabbits comprised 20% of the time-lapse monitored deliveries and only 3,3% of the prey remains.

Greater species diversity in the prey remains samples is probably due to larger sample size and the ability to accurately identify nearly every bone to species level. The differences in diet composition are considered to be mainly due to under-representation of red rock rabbits and other small prey items in the prey remains samples, rather than their over-representation on the time-lapse films for which no sensible reason could be put forward. Skeletal remains from red rock rabbits are small and fragile, often represented only by a small fragment of the maxilla, or a narrow bone from the hind limbs. These remains are far more likely to pass unnoticed than the obvious skulls left over from rock hyrax prey; and are also far more likely to decompose rapidly. This explanation for the observed differences is borne out by the relatively high representation of red rock rabbits in diet composition as determined by the two other methods: direct observations and observation of nest remains (Figure 82). These two alternate methods did not show the dominance of rock hyrax so characteristic of black eagle prey remains samples. Most prey items collected beneath nest cliffs should represent prey of the eagles and give a good indication of diet (Boshoff *et al.* 1990). In the present study this method gave the only comprehensive picture of the diversity of black eagle prey. But collections of prey remains present the following problems: one can never be certain whether the prey represented were killed by the eagles, scavenged by the eagles, or fed on by some other predator; also, large, sturdy prey remains are more likely to be collected than small, fragile remains; certain prey items may be removed by scavengers; and the collection mainly reflects diet of breeding eagles during the nesting season (Brooker & Ridpath 1980) - although this nesting season often comprises over 70% of the black eagle year. The indication from these comparisons of methodology is that prey remains are useful and practical for obtaining large samples which give a qualitative indication of prey spectrum taken by black eagles, but that one has to be very careful in interpreting their quantitative implications, particularly with regard to hyrax:lagomorph ratios.

Time-lapse photography at nests has proved useful in providing data on the feeding habits of large falcons (Enderson, Temple & Swartz 1972; Jenkins 1992) and golden eagles (Lockhart 1976); and can provide the following advantages over collections of prey remains: the method provides direct evidence of prey species fed on by the eagles and can yield useful sample sizes; although there maybe shortcomings with regard to very small prey items (as discussed on page 151), time-lapse photography should give fair representation to all medium and large-sized prey. For these reasons I feel that time-lapse photography gave the best indication of overall ratios between major prey taxa in this study. This method also provided much additional information on feeding habits, notably predation rate (previous chapter).

Composition of the major prey taxa in the diet of the eagles as indicated by all four methods of diet appraisal is illustrated in Figure 82. Occasional observations of prey remains on the nests of the eagles also provide direct evidence of prey species fed on (Collopy 1983b), but cannot give a comprehensive indication of diet composition because of under-representation of small prey items which are consumed rapidly. Observation of nest remains is labour-intensive and cannot provide the bulk of data afforded by the two former methods. Very high representation of red rock rabbits by this method is not easily explained, but may relate to more intensive use of this method in 1989 when rabbits were at peak abundance.

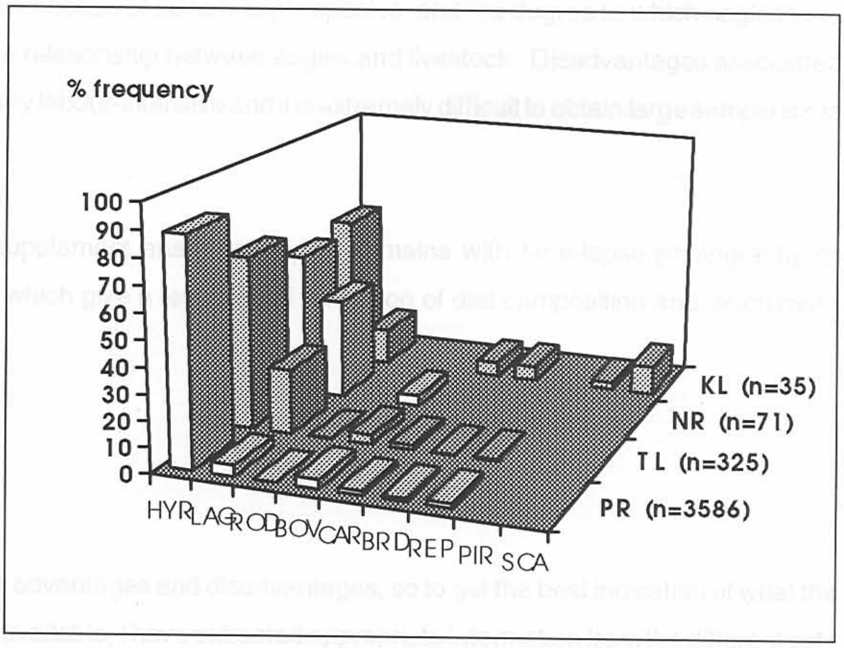


**Fig. 82.** direct comparison of diet composition as determined by four methods: collections of prey remains (PR); time-lapse photography at nests (TL); observation of prey on nests (NR); and kills and other direct observations of eagles feeding (KL). Sample sizes refer to the number of prey items observed. Legend: HYR = rock hyrax; LAG = lagomorphs; ROD = rodents; BOV = bovids; CAR = carnivores; BRD = birds; REP = reptiles; PIR = piracy; SCA = scavenging.

The three methods discussed so far are all based on the assumption that black eagle diet is accurately reflected in the prey that the birds convey to nesting or feeding sites. Observations of two pairs of eagles conducted over 10 days (116,2h) during the nestling phase indicated that 6 out of 8 prey items captured during this time were actually conveyed to nests. Transport of prey to the nests is necessary during breeding, but regular observations throughout the year of eagles carrying prey suggest that they do prefer to take food to their regular feeding sites. A possible reason for this is that the eagles are able to cache uneaten portions of large prey in safe places.

Intensive observations of the Penberi pair revealed that five meals were carried to such sites (four rock hyrax and one unknown), while three small or large meals were eaten away (karoo korhaan, suricate and springbok carrion). Most rock hyrax prey are small enough to be transported but large enough to last longer than one meal. High representation of adult rock hyrax in nest-based studies of diet may be encouraged by these characteristics. Scavenging from large ungulate carcasses is unlikely to be represented in nest-based studies of diet. Of four observed instances of black eagles scavenging, two of the food items weighed less than 18kg, and only one of these was considered likely to be conveyed to a feeding site. With regard to small prey, three juvenile rock hyrax were taken straight to the nest following capture. Whether small prey items were conveyed to the nest during the nestling period seemed to depend primarily on whether the captor was hungry or not.

The only method which can circumvent all these potential biases in nest-based studies of diet is intensive direct observation of the eagles themselves. This is the only method that can reliably indicate prey captured and eaten away from nest sites, and also the importance of scavenging and piracy in the diet of the eagles. Scavenging and piracy can fulfil a large proportion of the food needs of certain eagle species, and the degree to which eagles feed on carrion has an important bearing on the relationship between eagles and livestock. Disadvantages associated with direct observations are that they are very labour-intensive and it is extremely difficult to obtain large sample sizes of prey eaten.

Studies of eagle diet should evidently supplement analyses of prey remains with time-lapse photography or preferably extensive direct observations, which give a less biased indication of diet composition and much more information on general feeding habits.

*Interpolation of diet*

The four methods of diet appraisal all have advantages and disadvantages, so to get the best indication of what the eagles were eating in relation to what was available, I have extracted appropriate information from the different sets of results.

Time-lapse photography is considered to have given the most realistic indication of overall ratios of rock hyrax : lagomorphs : bovids : carnivores in black eagle prey (estimates of the proportion of rock hyrax in the diet of the eagles were close for all three alternate methods: 59-67%). Birds might be under-represented by this method though, so the ratio of carnivores : birds in the much larger sample of prey remains was used to indicate a likely amount for this taxon in the diet of the eagles. Reptiles were very infrequent in the time-lapse sample (n=2; 0,6%), while in the prey remains sample, high representation of this taxon (n=62; 1,7%) was caused mainly by a single nest site. An intermediate value for the amount of reptiles in the diet of the eagles was derived from both methods.

For separating relative abundances of individual prey species within these major prey taxa I used ratios indicated by the much larger prey remains sample. This is based on the assumption that the same bias should affect all lagomorphs, or all carnivores, or all bovids etc. within the prey remains sample. I also felt the prey remains gave a better indication of average prey mass for biomass calculations, because of the much larger samples of each prey species, and because of the opportunity for comparing these prey remains with skeletal material from adults to give a more considered estimate of individual mass.

Estimates for percent frequency and percent biomass in the diet of the eagles calculated in this way are presented for each prey species in Table 33, in order of descending frequency. This summary emphasises the importance of red rock rabbits as alternate prey. This species comprised one in five prey captured, but because of small body mass red rock rabbits fulfilled a reduced proportion of the eagle food needs. Hyrax and lagomorphs are evidently the major prey taxa: together they make up 92% of black eagle prey. I have not included categories for scavenging and piracy because this would be based on too small a sample of observations. However, it should be borne in mind that scavenging could afford the eagles with up to 11% of their food and that piracy can occur.

TABLE 33

PREY COMPOSITION OF BLACK EAGLE DIET IN TERMS OF MASS AND NUMBERS AS DETERMINED BY INTERPOLATION OF METHODS

| | % frequency | % biomass |
|---|---|---|
| rock hyrax | 66,73 | 72,64 |
| Smith's red rock rabbit | 21,33 | 13,86 |
| scrub hare | 2,40 | 3,30 |
| klipspringer | 1,43 | 3,34 |
| domestic bovids | 1,19 | 2,10 |
| Cape hare | 1,11 | 0,92 |
| greater padloper | 1,01 | 0,17 |
| suricate | 0,93 | 0,29 |
| steenbok | 0,80 | 1,48 |
| small grey mongoose | 0,36 | 0,12 |
| rock pigeon | 0,32 | 0,05 |
| large wild bovid lambs | 0,30 | 0,57 |
| karoo korhaan | 0,29 | 0,09 |
| Cape wildcat | 0,25 | 0,38 |
| white-necked raven | 0,21 | 0,06 |
| yellow mongoose | 0,11 | 0,04 |
| | | |
| HYRAX | 66,73 | 72,64 |
| LAGOMORPHS | 24,84 | 18,08 |
| RODENTS | 0,58 | 0,22 |
| BOVIDS | 3,72 | 7,49 |
| CARNIVORES | 1,86 | 0,95 |
| BIRDS | 1,11 | 0,42 |
| REPTILES | 1,16 | 0,20 |

<u>*Species composition of black eagle prey in relation to availability*</u>

The proportion of rock hyrax in the prey remains sample indicated that the dominance of this prey taxon was probably above average when compared to similar studies of diet in other regions. The karoo sample showed highest hyrax dominance for black eagle prey remains collected in the Cape (Boshoff *et al.* 1991). Lower dominance recorded for hyrax in Cape prey remains collections (Boshoff *et al.* 1991; the present study) than in previous studies could partly be due to more detailed analyses of bone fragments at the South African Museum in Cape Town. Only a negligible fraction of old and damaged bones could not be identified to species by comparison with the osteological material housed at the department of Archaeology. The extremely high dominance of rock hyrax (98,2%) in prey remains collected in the Matobo Hills (Gargett 1977) might be lowered somewhat if the large unidentified component of these collections (31%) could be classified in the same way as the Cape material. Over-representation of rock hyrax in collections of black eagle prey remains that may be due to classification bias is further exemplified by the under-representation of small, fragile prey items in these collections as revealed in the present study. One can conclude that most analyses of prey remains probably overestimate the proportion of rock hyrax in the diet of black eagles considerably. In the present study, proportion of hyrax in the diet as indicated by prey remains was 21% higher than that indicated by other, more reliable methods. This difference would have been greater had prey remains only been collected once from each site.

Despite this, rock hyrax made up the major part of black eagle prey as revealed by each of the four methods employed during the present study. As such, this prey taxon can certainly be considered the principal food (Petrides 1975) of black eagles in the karoo region, and makes up nearly three quarters of the biomass of live prey taken by the eagles in the Nuweveldberg. Predation of rock hyrax and other prey species by black eagles in relation to estimates of their availability and abundance are presented in Table 34. From this analysis rock hyrax appear to be taken roughly in proportion to their availability, with an average annual toll by the eagles equivalent to 11,4% of the standing crop.

Eagles apparently showed a higher preference rating for red rock rabbits and other lagomorphs than for hyrax (Table 34). In 1989, it is estimated that the eagles may have been removing as much as 11% of the red rock rabbit standing crop (Chapter 12). Heavy reliance on these prey was unexpected because all lagomorphs in the study area are nocturnal (Skinner & Smithers 1990) and were far less frequently encountered while walking transects than the diurnally active rock hyrax. The ratio at which I encountered rock hyrax to red rock rabbits was about 26 to one. I attributed much of this to the cryptic nature and short flushing distance of the red rock rabbit (Pepler 1990). However, the low profile maintained by red rock rabbits evidently did not protect them from successful predation by black eagles which managed to remove a substantial proportion of the rabbit population each year. Red rock rabbits may have been captured by the eagles while active in the mornings and evenings, or while moving rest sites (page 173). The relatively high toll taken of this nocturnal prey species by the eagles is suggestive that the eagles were hard-pressed to capture rock hyrax.

TABLE 34

PREY TAKEN BY BLACK EAGLES
IN RELATION TO ESTIMATES OF THEIR AVAILABILITY AND ABUNDANCE

Frequency of prey in eagle diet was determined by interpolation of methods (see text). Percent availability of prey was determined by transects walked through the veld (Chapter 5). Preference rating was calculated as % frequency in diet / % availability (Petrides 1975). Estimations of standing crop values for prey are explained in Chapters 4 & 5. The annual production of large wild bovid lambs was divided by 12 because these prey were only considered to be vulnerable for their first month. Prey capture rate from Chapter 8.

| | % frequency in eagle diet | % availability in the veld | Preference Rating | Estimated standing crop in a territory | Estimated take by resident pair of eagles | % standing crop removed by eagles |
|---|---|---|---|---|---|---|
| rock hyrax | 66,73 | 69,40 | 0,96 | 1013 | 115,4 | 11,4 |
| Smith's red rock rabbit | 21,33 | 2,68 | 7.96 | 441 | 36,9 | 8,4 |
| scrub hare | 2,40 | 0,38 | 6,32 | 34 | 4,2 | 12 |
| klipspringer | 1,43 | 16,26 | 0,09 | 85 | 2,5 | 3 |
| domestic bovids | 1,19 | - | - | - | 2,1 | - |
| Cape hare | 1,11 | 0,31 | 3,58 | 27 | 1,9 | 7 |
| greater padloper | 1,01 | - | - | - | - | - |
| suricate | 0,93 | 0 | - | - | 1,6 | - |
| steenbok | 0,80 | 2,38 | 0,34 | 12 | 1,4 | 11 |
| small grey mongoose | 0,36 | 1,07 | 0,34 | 16 | 0,6 | 4 |
| rock pigeon | 0,32 | - | - | - | - | - |
| large wild bovid lambs | 0,30 | 2,45 | 0,12 | (4) | 0,5 | 13 |
| karoo korhaan | 0,29 | - | - | - | - | - |
| Cape wildcat | 0,25 | 0,15 | - | 4 | 0,4 | 11 |
| white-necked raven | 0,21 | - | - | - | - | - |
| yellow mongoose | 0,11 | 0,08 | - | 1 | 0,2 | - |
| grey duiker | 0,00 | 0,31 | - | 2 | 0 | 0 |
| Cape fox | 0,00 | 0,15 | - | - | 0 | 0 |
| | | | | | | |
| LAGOMORPHS | 24,84 | 3,37 | 7,37 | 502 | 43,0 | 8,6 |
| BOVIDS | 3,72 | 21,39 | 0,17 | 103 | 6,4 | <6 |
| CARNIVORES | 1,86 | 1,46 | 1,27 | 21 | 2,4 | 11,4 |
| GAME BIRDS | 0,46 | 4,37 | 0,11 | - | - | - |

Black eagles can undoubtedly detect red rock rabbits better than I, but the high toll taken by the eagles is suggestive that once detected the rabbits were more susceptible to capture than rock hyrax. This is despite apparent territorial behaviour on the part of the rabbit to defend access to rocky shelters (Chapter 5). Evidently anti-predator adaptation for red rock rabbits was not much superior to that for rock hyrax during the circumstances of the present study. Reduced vulnerability of rock hyrax to their main predator is in agreement with theories of co-evolution which predict an evolutionary 'arms race' between predator and prey (Dawkins & Krebs 1979). Rock hyrax certainly do make use of a variety of predator-evasive behaviours notably an early warning system and remaining close to shelter (Chapter 4). When secure in their proximity to shelter, rock hyrax sit boldly on the rocks sometimes even in the presence of predators, so sighting rates of rock hyrax do not necessarily give a true representation of availability. The more obvious behaviour of this prey species probably led to unduly high estimates of its availability from the transect counts. However, if one uses the estimates of prey standing crop in Table 34, rock hyrax also comprise about 70% of the estimated abundance of prey animals.

The local rock hyrax population had just experienced a major decline (Chapters 1, 2 & 4), so the eagles may simply have been hard-pressed to remove more than 11% of the hyrax standing crop each year. Populations of the major alternate prey peaked conveniently in 1989 (see later). Capture of red rock rabbits by black eagles may be a more simple matter of detection, and a substantial removal of standing crop from the rabbit population may also have been facilitated if the rabbits showed a rapid recruitment in response to the 1989 rains.

High representation of red rock rabbits in the diet of black eagles is to be expected on account of the preference of this rabbit for the rocky habitats over which the eagles hunt (Chapter 6), but black eagles also showed an apparent dietary preference for the other lagomorphs in the park (Table 34). Scrub hares are found in tall vegetation throughout the park but their relatively high frequency of occurrence amongst the lagomorph prey might also be favoured by the persistence and noticeability of their large skeletal material in prey remains. Lower preference for Cape hares may be due to their restriction to the arid bottom plains, but the eagles were still apparently removing a significant portion of their population.

Many of the domestic bovid remains found under eagle nests in the KRNP appeared very old, suggesting they represented livestock captured or scavenged before the proclamation of the park (1979-1984). But two thirds of eagle pairs still had easy access to farmland, and time-lapse photography during the field study did not indicate fewer lambs in the diet of the eagles. The indicated toll taken by the eagles (two lambs per territory per year) is low. Black eagle predation of lambs on farms is treated later under geographical variation in diet, and in full detail in Chapter 11.

Wild bovids comprised a much smaller proportion of black eagle diet than lagomorphs or hyrax, but because of their greater size they met relatively more of the eagles' food requirements. Klipspringer were more frequent in the diet of the eagles than steenbok and this is consistent with their predominance in the rocky habitats (Table 13, page 80). But preference rating and the proportion of standing crop removed were much lower for klipspringer than steenbok. This suggests that the eagles were reluctant to attack the larger prey. In fact the eagles exhibited an avoidance for all bovids as prey. Adult klipspringer are particularly sturdy animals and can travel at great speed across dangerous rocky terrain. Risk of injury to the eagle must be high when attacking prey such as this, and a relatively minor injury could prove drastic to a predator which relies on great agility in flight. The predominance of juveniles in bovid prey suggests that this is near the upper limit of prey size that the eagles prefer to attack. Relatively low frequency of large wild bovid lambs (e.g. springbok) in eagle diet in comparison to apparent availability may be due to successful defence behaviour by their dams. Such lambs are more likely to be attacked by eagles when isolated or sickly (e.g. McEneany & Jenkins 1983; Bergo 1987; Mooring 1993).

Carnivores, birds, reptiles and rodents were all infrequent in the eagle diet, and because of their small size these prey fulfilled a small fraction of the food needs of the eagles. They do however indicate the versatility of black eagles as predators despite the reputation of this eagle as a specialist. While the population estimates of bovids and carnivores were not calculated rigorously, the relatively large estimates of the standing crop of hyrax, lagomorphs, steenbok and carnivores that are thought to be removed by the eagles each year (Table 34) suggests that this predator is taking advantage of the full range of prey available to it.

Of the carnivores, small grey mongooses were encountered in the veld far more regularly than suricates. Greater frequency of suricates in the diet of the eagles was therefore not expected and may indicate a greater vulnerability of suricates while foraging in groups away from shelter on the bottom plains (pers. obs.).

Pigeons and game birds made up most of the avian prey of black eagles. Capture of avian prey suggests that black eagles can be agile predators, as was observed when a pair of eagles captured a karoo korhaan in flight. The estimation of bird prey in eagle diet was however based mainly on the collections of prey remains, and it is probable that some of the pigeons, white-necked ravens and other birds had died on the cliffs for other reasons. Black eagles are not as manoeuvrable as smaller birds, and capture of avian prey probably depends on a high degree of speed and surprise. Low preference rating for game birds (Table 34), and generally low incidence of avian prey in black eagle diet are indicative that this does not happen very often.

No attempt was made to assess the availability of carrion, and the inferences on the importance of this food source to the eagles are based on questionable assumptions in the case of the prey remains, and small samples in the case of direct observations. Nevertheless the indications are that carrion could fulfil a noticeable portion of eagle food requirements. Scavenging has been recorded for black eagles in South Africa (Frere 1982; Steyn 1982) and both Brown (1988b) and Boshoff *et al.* (1991) report that black eagles readily come to traps baited with carrion. But this feeding behaviour was not observed in the Matobo Hills despite intense work by Gargett (1990) and a team of observers. I think this indicates again that black eagles can adapt to other food sources where these are readily available, and where hyrax may not be.

<u>*Temporal variation in black eagle diet*</u>

Annual change in the relative contributions of rock hyrax, red rock rabbits and other prey to black eagle diet is shown in Figure 83. An obvious decline in the rock hyrax component of diet was revealed by collections of prey remains between December 1987 and December 1988, and by the time-lapse cameras between 1988 and 1989. Counts at hyrax colonies indicated a significant decline in group size during 1988 (Chapter 4). The change in diet indicated by prey remains tallies with this. However, a decline in the rock hyrax component of prey remains is to be expected with consecutive collections from the same site (first collections made up a significant component of both the 1986 and 1987 samples). It is possible that the observed decline from 91% hyrax to 79% hyrax in the prey remains, was due to both these effects. Summer rainfall at the end of 1987 and at the end of 1988 was below average for both seasons. This undoubtedly hampered recovery of the vegetation following the intense drought of the early 1980's, and is considered responsible for high mortality and low recruitment of hyrax in those years (Chapter 4).

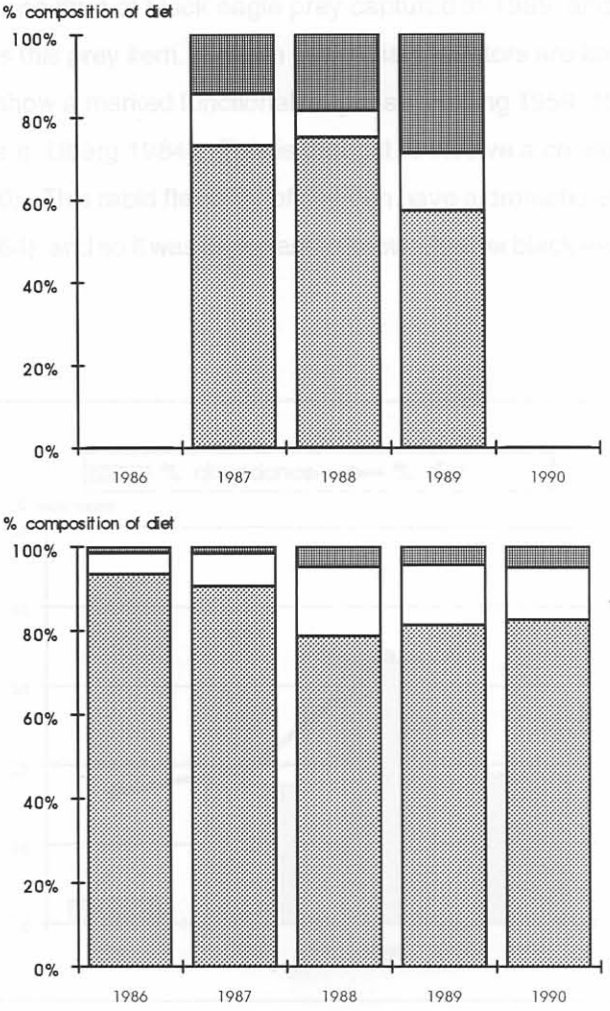


**Fig. 83.** Change in percentage composition of black eagle diet over the study period as indicated by time-lapse photography (top) and collections of prey remains (bottom). (rock hyrax = pale grey; red rock rabbit = dark grey; other prey = white)

Differences in the patterns revealed by the two methods may also result from the inclusion of more food-stressed (see later) upper escarpment eagle pairs in the prey remains collections. The hyrax prey base of these upper escarpment pairs was not monitored and may have been behaving differently from the hyrax populations in the lower escarpment territories. In contrast to the indications from the prey remains, time-lapse photography revealed that the proportion of hyrax in the diet as well as prey capture rate (Chapter 8) were both highest in 1988 for the three years of monitoring . The dry conditions during 1988 may have increased the vulnerability of foraging hyrax, and black eagle predation certainly contributed to the observed decline (Chapter 12), which in turn was reflected in lowest delivery rates of rock hyrax to nests in 1989. Given the limitations of prey remains analyses in representing non-hyrax prey, I think the time-lapse photography (although restricted to lower escarpment nests) gives a more real indication of changes in feeding habits.

Over the three years of monitoring by time-lapse photography, red rock rabbits became increasingly prevalent as black eagle prey (Fig. 83). This complied with observed increases in the rabbit population which peaked in 1989 (Fig. 40b, page 81). Red rock rabbits comprised nearly one third of black eagle prey captured in 1989, and the noticeable change in diet might indicate a 'switch' towards this prey item. Certain generalist predators are known to subsist on a variety of alternate prey species and can show a marked functional response (Holling 1959, 1965) to feed mostly on one prey when it becomes abundant (e.g. Liberg 1984). This is thought to involve a change in the specific search image of the predator (Tinbergen 1960). This rapid flexibility of diet can have a dramatic effect on predator-prey relationships (e.g. Erlinge *et al.* 1983, 1984), and so it was important to know whether black eagles could be behaving in this way.

Changes in the proportional abundance and proportional predation of red rock rabbits over the study period are shown in Figure 84. If black eagles were showing 'switching' behaviour, one might expect that the change in rabbit abundance would not be as great as the corresponding increase in their contribution to eagle diet. It is clear from Figure 84 however, that this was not the case and it is concluded that the increased predation of red rock rabbits by black eagles did not represent any 'switching' behaviour. After the decline of the hyrax population in 1988, the increase in the red rock rabbits was timely, but the response of the eagles can be described as opportunistic predation that was in proportion to growth of an alternate prey population. The rabbit population was never greater than the hyrax population, so it may be that the increase in rabbits was not sufficient to trigger a switch response.

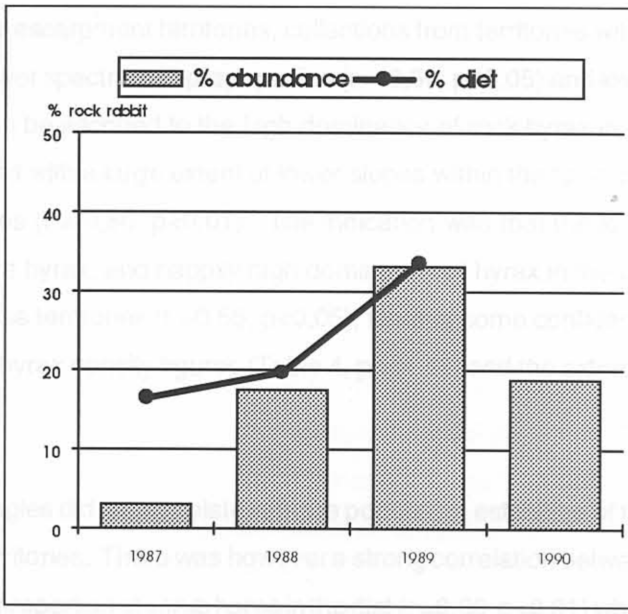


**Figure 84.** Changes in the percentage contribution of red rock rabbits to prey abundance and to eagle diet over the study period. As I was only concerned with ratios of the two main prey species, other prey are excluded from this analysis

In the shorter term, it has been proposed that eagle diet can vary in and out of the nesting period (Boshoff *et al.* 1990). It has been suggested that this can lead to bias in nest-based studies of diet (Brooker & Ridpath 1980). The only reliable indication of black eagle diet during the non-breeding part of the year (February - June), is a small sample of direct observations. These data were compared with direct observations of eagle feeding behaviour during the nesting season (July - January) when I knew the birds were breeding: rock hyrax comprised 14 out of 22 meals (64%) when the birds were nesting, and three out of eight meals (38%) when they were not. This suggestion that the eagles took a wider spectrum of prey when not breeding was not statistically significant. If the eagles chose a different diet when they were obliged to carry food to nestlings, then this should be reflected in a comparison of prey remains collected beneath the nests of birds that bred and beneath the nests of birds that didn't make any breeding effort in respective years. All first collections of prey remains, and all collections when breeding attempts failed were excluded from this analysis. Rock hyrax comprised 85,3% of prey items collected beneath the nests of breeders, and 88,2% of prey items collected beneath the nesting and feeding sites of non-breeders. No significant differences in the diet of breeding and non-breeding eagles could be detected.

*Geographical variation in black eagle diet*

Correlation analyses were employed to identify relationships between diet of 17 eagle pairs (as indicated by prey remains) and various characteristics of their territories. Although collections of prey remains were larger under the small cliffs ($r = -0,49$; $p<0,05$) of the lower escarpment territories, collections from territories with a large amount of lower escarpment revealed a narrower spectrum of prey species ($r=-0,50$; $p<0,05$) and lower indices of prey diversity ($r=-0,54$; $p<0,05$). This can be ascribed to the high dominance of rock hyrax in the diet of the lower escarpment eagles which correlated with a large extent of lower slopes within the territories ($r=0,80$; $p<0,01$) and a small extent of upper slopes ($r=-0,80$; $p<0,01$). The indication was that the lower escarpment territories actually accommodated more hyrax, and happily high dominance of hyrax in the diet correlated with population estimates of hyrax in these territories ($r=0,55$; $p<0,05$), lending some confidence to these estimates which had been calculated from hyrax density figures (Table 4, page 48) and the extent of the major topographical habitats in each territory.

The proportion of red rock rabbits in the diet of the eagles did not correlate with the population estimates of this prey derived in a similar fashion for the respective territories. There was however a strong correlation between estimates of red rock rabbits in the territories and the proportion of scrub hares in the diet ($r=0,66$; $p<0,01$) which warrants explaining. The estimates of red rock rabbits were derived from midden densities, so this raises the speculation of whether scrub hare middens could have been mistaken for red rock rabbit middens. Incidental sightings of animals indicated that red rock rabbits outnumbered scrub hares seven to one (Chapter 5). While Smith's red rock rabbits are renowned to make extensive use of middens, scrub hares are not (Skinner & Smithers 1990). So it is very unlikely that scrub hares could have been responsible for many of the middens encountered. Furthermore, the compressed shape of red rock rabbit faecal pellets is diagnostic (Skinner & Smithers 1990) and was checked for during the midden counts. So it is likely that the correlation was spurious. Scrub hares are known to avoid the open plains and prefer tall vegetation (Smithers 1971). The proportion of scrub hare in the diet of the eagles correlated negatively with the extent of the bottom plains in their respective territories ($r=-0,49$; $p<0,05$) and positively with the extent of middle plateau ($r=0,48$; $p=0,05$) and upper slopes ($r=0,49$; $p<0,05$). Tall vegetation in the KRNP grows on the rocky habitats favoured by red rock rabbits. While both lagomorphs might prefer the same broad habitats, only the scrub hares are likely to be fairly represented in collections of prey remains. A similar but opposite association to that with scrub hares was evident between low population estimates of red rock rabbits in eagle territories and high representation of karoo korhaans in eagle diet ($r=-0,49$; $p<0,05$). This correlation reflects the diametrically-opposed preferences of these prey species for the bottom plains habitat.

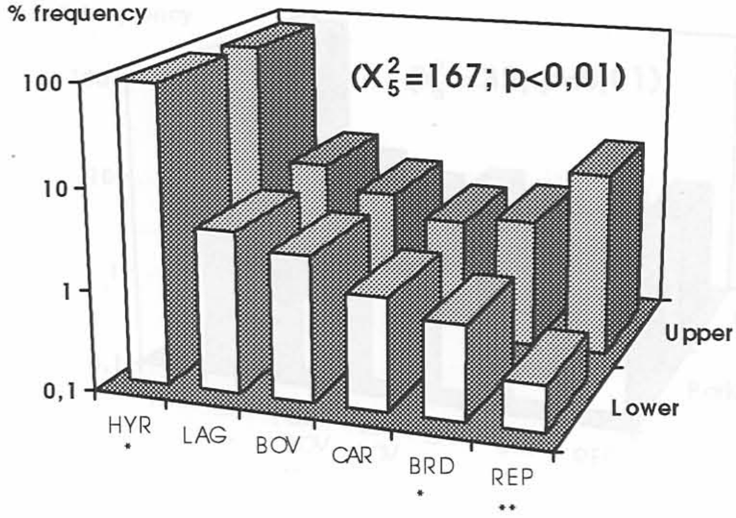


**Figure 85.** Differences in the composition of the major prey taxa represented in collections of prey remains from beneath upper escarpment and lower escarpment black eagle nests sites. Vertical scaling is logarithmic. Asterixes denote differences between the samples that were statistically significant for a Chi-square test (*<0,05; **<0,01).

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A direct comparison of the diet of upper escarpment and lower escarpment eagle pairs showed a statistically highly significant difference in the representation of the major prey taxa (Figure 85). Birds, especially rock pigeons, featured highly in prey remains collected beneath the tall cliffs (r =0,76; p<0,01) of the upper escarpment, and in territories with a large extent of upper plateau (r =0,82; p<0,01). The proportion of greater padloper tortoise in the diet showed a similar pattern, and was greatest in territories with more upper escarpment (r =0,81; p<0,01). Both these prey species were undoubtedly more available to eagles nesting on the upper escarpment, but it is possible that factors other than eagles were partly responsible for collection of their remains beneath the cliffs. The investigation of black eagle diet in the Cape Province revealed great geographical variation in the importance of birds and reptiles as eagle food, with fynbos eagles taking the greatest quantities of these two taxa (nearly 20% of their diet), and karoo eagles taking the lowest proportions of these taxa in their diet (Boshoff *et al.* 1991).

Another prey species associated with the upper plateau (r =0,80; p<0,01) was Cape wildcat. This may reflect the preference of this predator for high altitude mountains, which was also characteristic of two other small/medium size, generalist predators: jackal buzzards and Cape eagle owls (page 137). By contrast, high representation of small grey mongoose in eagle diet was associated with a large extent of middle plateau in the respective eagle territories (r =0,63; p<0,01). An interesting relationship exists between black eagles and small grey mongooses. This small predator was considered to be responsible for most scavenging beneath eagle nests, and was found responsible for failure rate of eagles nesting on the accessible lower escarpment cliffs through nestling predation (Chapter 6). Predation of red rock rabbits by upper escarpment and lower escarpment pairs was not different and this would comply with an even distribution of this prey through the mountainous habitats, as indicated by the midden counts (Table 10, page 76).

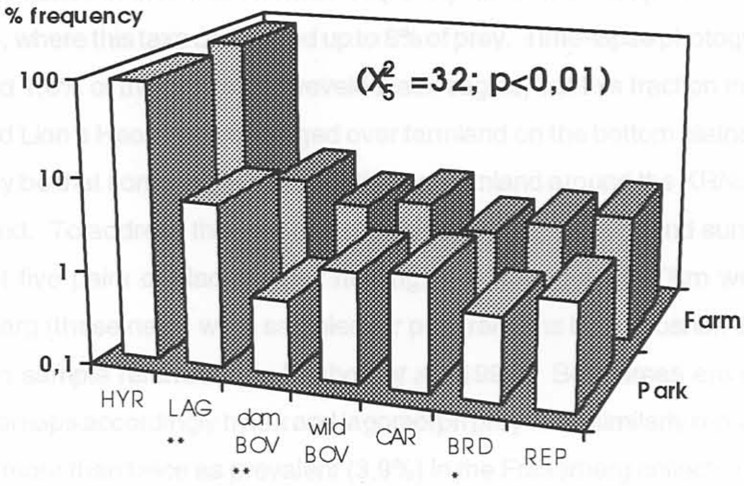


**Figure 86.** Differences in the composition of the major prey taxa represented in collections of prey remains from beneath black eagle nests sites on farm and parkland. Vertical scaling is logarithmic. Asterixes denote differences between the samples that were statistically significant for a Chi-square test (*<0,05; **<0,01).

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There were differences between the diets of eagles hunting mainly over farmland and those hunting mainly in the park (Figure 86). Farm birds ate relatively more domestic lambs ($X^2$=7,1; p<0,01), more birds ($X^2$=4,0; p<0,05), and less lagomorphs ($X^2$=14,8; p<0,01). Significant correlations were obtained between the extent of farmland in the eagles' territories and the proportions of domestic lamb (r =0,61; p<0,01) and klipspringer (r =0,49; p<0,05) in their respective diet. Most farmland in the study area was situated on the bottom plains frequented by karoo korhaans, or on the upper plateau frequented by rock pigeons. This may explain higher representation of bird prey in farm diet. Red rock rabbits and scrub hares however, mainly occur in the mountainous terrain, and this would explain their predominance in the diet of park birds.

Greater representation of klipspringer in farm diet is puzzling because this species prefers the rocky mountainous habitats. Although a preference for bovid prey amongst farm birds might account for this, it has to be conceded that separation of some juvenile klipspringer material from juvenile domestic bovid material is difficult because the bones of very small juveniles are very similar in shape, so some errors may have arisen here. However, the low frequencies of klipspringer in the diets of both park and farm birds indicate that any under-estimation of domestic lambs in the diet of farm birds through any erroneous classification of material is likely to be by less than 0,76% (of total diet).

There was no indication from diet composition that rock hyrax were less available on farmland. If this is true then farm birds are unlikely to be food-stressed and the abundance of domestic lambs forms an additional, timely food source which can bring the eagles into condition for early breeding (Chapter 6). Approximately 20% of lambs die before weaning, mostly to non-violent causes of death (Chapter 11). So much of this extra food supply may take the form of carrion, and it is likely that farm birds scavenge more than park birds.

The proportion of domestic lambs in the diet of farm birds (1,6%) was low in comparison with other regions of the Cape (Boshoff *et al.* 1991), where this taxa comprised up to 8% of prey. Time-lapse photography also indicated that domestic lambs comprised 1,6% of the prey of Nuweveld black eagles, but this fraction increased to 3,4% for two eagle pairs (Bakenkop and Lion's Head) which foraged over farmland on the bottom plains and had less access to mountainous areas. It may be that some eagle pairs nesting on farmland around the KRNP were still influenced by the accessibility of parkland. To address this, the diet of eagles nesting on farmland surrounding the KRNP was compared with the diet of five pairs of black eagles nesting in a farmed area 80km west along the Nuweveld escarpment near Fraserberg (these nests were sampled for prey remains by A. Boshoff & G Palmer in 1986, and make up part of the karoo sample referred to in Boshoff *et al.*, 1991). Both areas are characterised by similar escarpment terrain, and perhaps accordingly hyrax and lagomorph prey were similarly represented in the two areas. But domestic lambs were more than twice as prevalent (3,9%) in the Fraserberg collections, suggesting that black eagles may indeed be eating fewer lambs in the vicinity of the KRNP. Unfortunately collections of prey remains do not permit a fuller interpretation of black eagles as stock predators and stock scavengers. These aspects will be taken further in Chapter 11.

<u>*The black eagle as a specialist predator*</u>

An indication of the degree to which black eagles can be considered specialist predators can be obtained by comparing their feeding habits with those of other predators in the same region. Martial eagles occur in the Karoo, often alongside black eagles as was the case in the KRNP. Martial eagles are similar in size and rapaciousness to black eagles, but they are more usually found in flat country. Fortunately extensive work has been done on the diet of both these eagles in the karoo region (Boshoff & Palmer 1980; Boshoff *et al.* 1990; Boshoff *et al.* 1991). The two species took a similar spectrum of prey: 32 prey species were represented in 25 collections of prey remains (n=910) from beneath martial eagle nests in the Karoo (Boshoff *et al.* 1990); while 30 prey species were represented in 31 collections of prey remains (n=3337) from beneath black eagle nests in the Karoo (Boshoff *et al.* 1991). However, individual collections of prey remains from martial eagle sites contained a wider array of species (mean

*Martial eagle attacking helmeted guineafowl*

8,2; s.d.=2,9) than collections from black eagle sites (mean 6,7; s.d.=2,6). This difference was statistically highly significant (Kruskal Wallis test: $X^2$=14,3; p<0,01), despite the fact that collections at martial eagle sites were usually smaller (mean 36,4 items; s.d.=29,1) than collections from black eagle sites (mean 107,6 items; s.d.=91,8) (Kruskal Wallis test: $X^2$=3,8; p=0,052). To examine intraspecific variation in the diet of both eagles, Boshoff and workers calculated the Shannon-Wiener index of general diversity (Odum 1971: 144) for each site with an adequate sample size. I compared these indices for the two eagle species using a Kruskal-Wallis test and found that collections of prey from martial eagle sites had higher diversity indices (mean 1,64; s.d.=0,27) than collections of prey from black eagle sites (mean 0,57; s.d.=0,37). This difference was statistically highly significant ($X^2$=25,3; p<0,01). While these differences do indicate greater prey-specificity on the part of the black eagle, there are no comparable data for the diversity of prey species available to these eagles, so it is not known whether the differences are caused primarily by the behaviour of the eagles or by variation in relative abundances of the prey. However, hyrax comprised only 52% of prey remains beneath the nest of a pair of martial eagles which had access to the same prey (available to black eagles) in mountainous habitat within the KRNP.

Present findings on black eagle feeding habits suggest that most studies of diet have over-emphasized the importance of rock hyrax. Furthermore, comparisons of predation with prey availability did not indicate a positive preference rating for rock hyrax in the diet of the eagles. In fact the eagles may have been removing equal portions of other prey populations. These observations suggest that black eagles are not obligate predators of rock hyrax, but rather catch the most available prey in mountainous regions.

In apparent contraposition to this, I would argue that these findings still do not refute the notion that black eagles are specialist predators of rock hyrax. At the time of study, local hyrax populations had just experienced a major population decline. The reduced population was probably well protected within the carrying capacity set by the extent of rocky habitat (Chapter 12). Despite this, rock hyrax comprised the major component of black eagle diet in the present study. It is relevant to note that rock hyrax were not represented at all in an analysis of 100 caracal scats collected in the KRNP during the present study (Chapter 7), whereas Palmer & Fairall (1988) found hair of rock hyrax in 22% of caracal scats collected three years previously in the same study area, and this prey is thought to comprise over half of caracal food elsewhere in the Karoo (Grobler 1981; Moolman 1984, 1986a). I think this indicates that, unlike the generalist caracals subsisting on alternate prey, black eagles in the present study were behaving like true specialist predators by pursuing their prey at low density (Pearson 1966, 1971; Fitzgerald 1977; Hansson 1984; Korpimäki *et al.* 1991). Predation by the eagles was almost the sole mortality agent acting on adult hyrax age classes at this time (Chapter 10).

As specialists, black eagles are evidently highly successful at predating rock hyrax when compared with other predators, but the morphological and behavioural adaptations that enable this (Chapter 6) do not preclude the black eagle from opportune and successful exploitation of other food sources, and this was evident in the high level of predation on an alternative prey species in this study. These observations add to the growing body of literature which shows a high degree of opportunism in black eagle feeding habits when the staple prey is not readily available.