CHAPTER 10

BLACK EAGLE FEEDING HABITS -

3. COMPOSITION OF HYRAX POPULATION CLASSES IN THE DIET

INTRODUCTION

Numerous studies on predation have shown that particular components of prey populations are more heavily preyed upon than others (e.g. Kruuk 1970, 1972a; Hornocker 1970; Mech 1970; Rudnai 1974; Beacham 1979; Southern & Lowe 1982; Korpimäki 1985b; Donázar & Ceballos 1989; FitzGibbon & Fanshawe 1989; FitzGibbon 1990; Sinclair, Olsen & Redhead 1990). Some theorists have argued that patterns of disproportionate predation of the different prey population components have evolved to harvest the prey population in an optimal way (Slobodkin 1968). More often, there are behavioural traits which explain greater vulnerability and predation of certain population classes (see discussion). Heavier predation (through inferior flight response) can also be expected for any population classes which are less able to maintain a satisfactory body condition, and are thus more likely to become sickly. Smaller prey individuals may suffer heavier overall rates of predation because they are vulnerable to a wider range of predators (Chapter 7). There is little field evidence to suggest that predators actively choose their prey in accordance with an optimal harvest strategy, but there is evidence that predators tend to choose more profitable prey sizes when these are available (Curio 1976).

Different age and sex classes of populations vary with regard to their potential contribution to population growth. Usually young females carry a high potential for reproducing, while old (post-breeding) individuals and surplus males carry low potential. Whether predators actively 'choose' their prey or simply catch the most vulnerable individuals, their demographic influence on the prey is going to vary with the emphasis of their predation in terms of prey population classes. Predators which remove more 'reproductively-valuable' individuals can be expected to exert more demographic and evolutionary influence on their prey than predators which remove more 'reproductively-expendable' individuals. Anti-predator adaptation is only likely to spread amongst the prey population, if it contributes in some way to the likelihood of successful reproduction by a prey individual.

So to fully appreciate the influence of black eagle predation on rock hyrax (involving population modelling - Chapter 12), it was necessary to assess the level of this predation to the resolution of different sex and age classes of the hyrax. Fortunately, accumulations of hyrax cranial and dental material beneath black eagle feeding sites (Chapter 9) permits such detailed analyses. In this chapter, representation of age classes of male and female hyrax in these samples are compared with estimates of their availability among the prey population, and explanations are sought for any patterns of disproportionate predation. The extensive collection of prey remains housed at the South African Museum in Cape Town is used to expand the investigation of temporal and geographical variation in this aspect of black eagle diet. No previous studies on age/sex-specific predation by black eagles have been carried out in any detail.

METHODS

Techniques employed in the collection of prey remains from beneath black eagle nesting and feeding sites were described in Chapter 9. Minimum counts of individual hyrax were nearly always obtained from maxillary remains, except in the case of young juveniles in a few samples where mandibles were more numerous. Fourie (1983) recommends that patterns of tooth eruption and tooth wear on maxillae be used for age-determination of hyrax. The high representation of hyrax in prey remains by maxillae was fortunate because it facilitated separation of most individuals by sex and age class. Convenient separation of hyrax skulls or maxillae by sex was facilitated by the high degree of sexual dimorphism evident in the morphology of their upper incisors. These are used by females for feeding, and by males for fighting (Fourie 1983). Males have large, sharply-pointed incisors which are triangular and symmetrical in cross section; whereas females have small converging incisors which are flatter and asymmetric in cross section, with their tips less pointed (Figure 87). Even if these teeth have fallen out, the incisor apertures normally clearly reflect the cross-section of these teeth. This dimorphism is not clear for juvenile animals (Fourie 1983) and so no attempts were made to separate the sexes in the age class 0-1y. Independent observers were employed to check (from incisor/aperture morphology) the sex of 31 skulls of immature and adult hyrax from 'known-sex' animals which had been shot. Ninety seven percent of their predictions tallied with known sex of individuals, with one immature (1-2y old) erroneously classified.

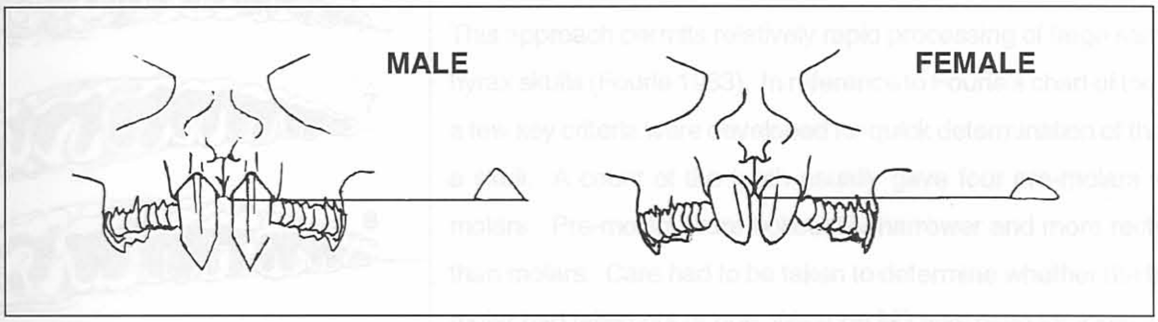


Figure 87. Sexual dimorphism for the upper incisors of adult rock hyrax - a head-on view of skulls.

Hyrax maxillae were allocated to annual age classes on the basis of tooth eruption and tooth wear. Adult rock hyrax have four premolars and three molars on each side of the maxilla and the mandibles (Fourie 1983). A certain amount of agreement could be found between three studies on the age-determination of *Procavia capensis* with regard to eruption of these teeth (the following analysis refers to teeth of the maxilla): For rock hyrax at one year old, Fairall (1980), Steyn & Hanks (1983) and Fourie (1983) all agree that incisors have become permanent; that M1 is in wear; and that M3 has not yet appeared. There was some inconsistency between the studies regarding the status of M2 with both Fairall and Steyn & Hanks observing that M2 was visible/erupting, but Fourie noting no sign of M2. I concluded that rock hyrax at one year old showed the following dentition pattern: M1 fully emerged and in wear; M2 may be visible but not in wear; M3 not visible. For rock hyrax at two years of age, all studies reported that both M1 and M2 were emerged and in wear; and all concurred that M3 was in the process of erupting.

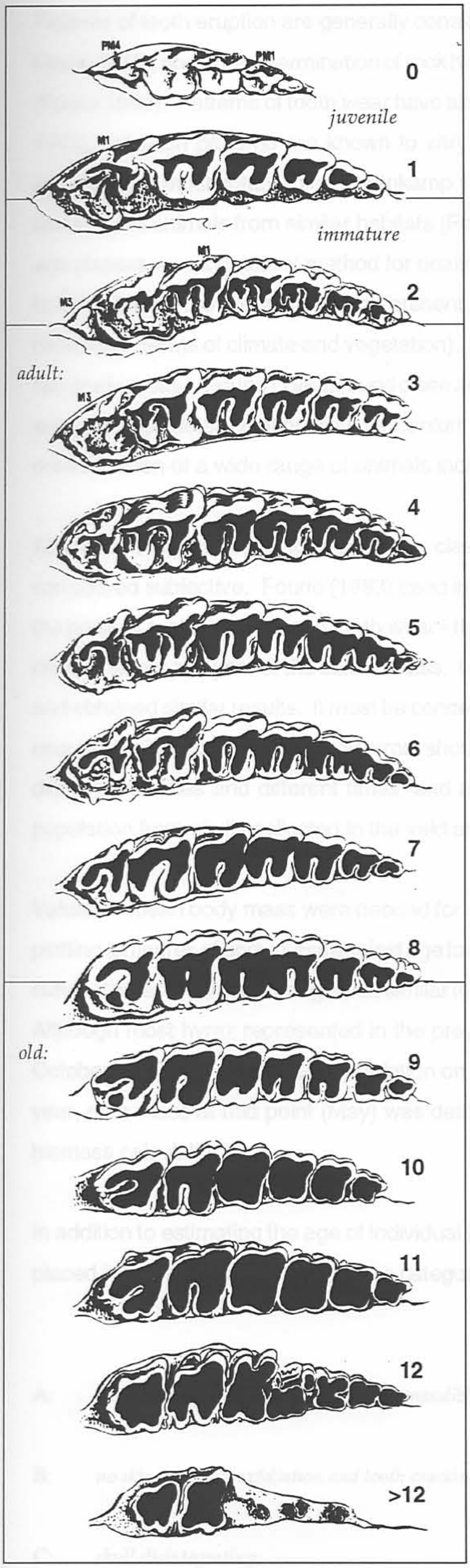


Figure 88. Age-specific patterns of tooth wear for rock hyrax maxillae, from Fourie (1983: Fig. 35). Values to the right of each pattern denote age class in years.

In summary, separation of the first two annual age classes was carried out according to the following criteria: if M2 was not yet emerged and beginning to show signs of wear, the animal was placed in an age class of 0-1y old. If M2 was in wear and M3 was not yet 60% emerged, the animal was placed in an age class of 1-2y old. If M3 had emerged by 60% or more, the individual was considered to be older than two years of age and adult. Subsequent separation of adult hyrax into annual age classes was based mainly on tooth wear patterns observed by Fourie (1983), except that Fourie only recorded wear on M3 at year four whereas the other studies recorded M3 as permanent by 36 months (Fairall 1980), or in wear from 28 months old (Steyn & Hanks 1983). If M3 appeared to be mostly emerged but showed little or no wear and the cusps of all molars appeared very angular and unworn, the individual was classified as 2-3y old. If wear was clearly noticeable on M3, the animal was classified as older than three years and I referred to Fourie's chart of tooth wear (reproduced here as Figure 88) for subsequent separation of the older age classes. Tooth eruption and wear patterns were assumed to be the same for both sexes.

This approach permits relatively rapid processing of large samples of hyrax skulls (Fourie 1983). In reference to Fourie's chart of tooth wear a few key criteria were developed for quick determination of the age of a skull. A count of the teeth usually gave four pre-molars and 1-3 molars. Pre-molars were noticeably narrower and more rectangular than molars. Care had to be taken to determine whether the first pre-molar had fallen out or not. Wear on M3 was used as a key indicator of age, except for young animals as discussed, and for some cases where abnormal jaw structure led to a markedly differential wear pattern on pre-molars and molars - in these cases a compromise was reached between age indicated by wear on molars and age indicated by wear on pre-molars. A good indication of the degree of wear on cusps could be obtained by running a pencil down the central axis of the row of teeth. In accordance with Fourie (1983), the age at which the cusps on these teeth start to merge into a smooth central surface was taken at eight years. From this age on, dental attrition might be associated with senescence so adults were separated from old individuals at this point. Another useful criterion for separating very old animals was the indication from the chart that the 'cutting' ridge on the outside of the teeth was lost at about ten years of age.

Patterns of tooth eruption are generally considered to give a good indication of an animal's age (Spinage 1973; Hall-Martin 1976), and age-determination of rock hyrax up to three years old by this method is considered to be very accurate (Fourie 1983). Patterns of tooth wear have also been widely used for age-determination in wildlife research (Spinage 1973), but such patterns are known to vary with certain characteristics of the individual being examined and its environment, most notably diet (Steenkamp 1975). So it is recommended that comparisons within species should be restricted to animals from similar habitats (Fourie 1983). Using tooth wear to indicate separation of adult (>3 y old) age classes was a practical method for dealing with large volumes of material in the present study, and its use here is defended on the grounds that the present study, and that of Fourie (1983) were both conducted in similar karoo habitats (in terms of climate and vegetation). One might expect the feeding habits of rock hyrax to be similar in these two study areas. Fourie (1983) found close agreement between age-determination of rock hyrax from tooth eruption/wear and age-determination from *cementum annuli* in the teeth. The latter is considered a reliable method for age-determination of a wide range of animals including rock hyrax (Grue & Jensen 1979; Fairall 1980).

Allocation of hyrax skulls to annual age classes on the basis of comparison with a chart of tooth wear might be considered subjective. Fourie (1983) used independent, experienced observers to allocate skulls to age classes on the basis of tooth eruption and tooth wear - they placed 70% of skulls in the correct class, and 100% of skulls in age classes within one year of the correct class. I employed observers to independently check my allocations of 25 skulls and obtained similar results. It must be conceded that some discrepancies in age-determination of adults might have occurred using tooth wear, but any errors should have been applied consistently for all collections of prey remains from different localities and different times, and also to estimates of the availability of the different age classes in the population from skulls collected in the veld and from the shot sample (Chapter 4).

Values of mean body mass were needed for each hyrax age class for various calculations. These were obtained by plotting all figures of body mass against age for 59 individuals shot (data summary in Table 6 on page 50). The resultant curve of mass increase with age was similar to that derived in other studies of hyrax growth (Fairall 1980; Fourie 1983). Although most hyrax represented in the prey remains were probably captured during the nestling period (August-October), a similar emphasis of predation on the different hyrax population classes probably applies throughout the year, so a mass at mid point (May) was determined from the growth curve for each hyrax age class to be used in biomass calculations.

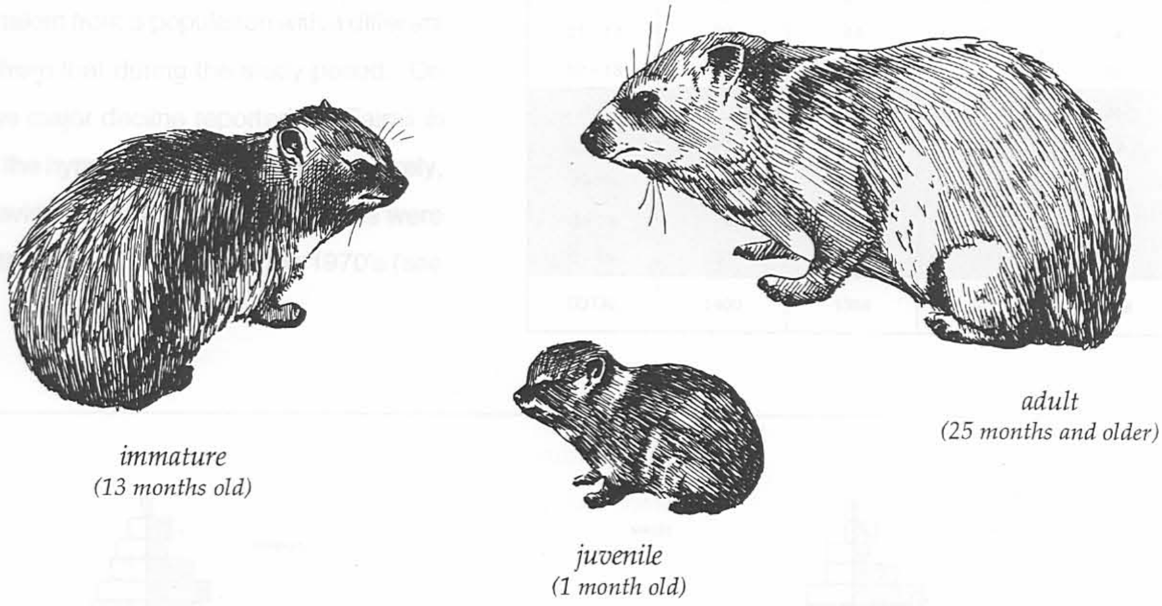
In addition to estimating the age of individual hyrax represented in the prey remains (when captured), each skull was placed into one of the following three categories for estimated time since death:

A: *some skin still attached; maxillae and mandibles often still linked; little tooth cracking; no exfoliation of cranium.*

B: *no skin attached; exfoliation and tooth cracking evident but skull structure still solid.*

C: *skull disintegrating.*

The object of this exercise was to separate freshly-killed specimens from old material in which larger, stronger skulls may have persisted. From regular observation of hyrax skulls left to decompose in cages (to exclude scavengers), it became clear that nearly all skulls placed in the first category would represent animals killed within the year preceding the collection. Care was taken not to place skulls which were thought to have been well preserved for longer than a year in a micro climate of soil or vegetation into category A. Some allowance was also made for faster decomposition of the more fragile juvenile skulls. Most flesh and skin disappeared from the experimental carcasses by about six months depending on the action of invertebrates. Exfoliation and cracking of the cranium and teeth could begin within a year of death if the skull was exposed to direct sunlight. Disintegration of adult skulls was thought to commence after about two years in exposed conditions. Additional information recorded for each skull was whether the cranium had been opened by the eagles (in the occipital region) or not, or whether this was indeterminable (e.g. disintegrating skulls). Hyrax teeth were checked for any plant material lodged between the cusps which might indicate that these individuals had been foraging when captured. Gargett (1990) noted such evidence for a hyrax delivered to a Matobo eagle nest. However, very few skulls examined in the present study showed any such evidence, and no real conclusions could be drawn from these examinations because it is likely that most plant material would have disintegrated or washed away prior to collection.



RESULTS AND DISCUSSION

Overall composition of rock hyrax captured

Between 1986 and 1991 a total of 3359 hyrax skulls or maxillae were collected beneath black eagle nesting and feeding sites in the KRNP. Sexual dimorphism was evident for 87,5% of the sample excluding juveniles. Allocation to annual age classes was possible for 91,6% of the sample. The overall composition of this sample is presented in Table 35 and Figure 89.

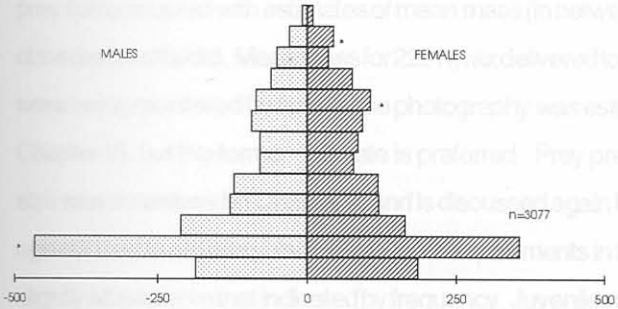
Despite suspicions that large hyrax skulls would be over-represented amongst the older material collected, the composition of only the freshly-killed material (category A) was not very different (Figure 90). However it is not known whether the older material was taken from a population with a different composition from that during the study period. On account of the major decline reported (N. Fairall *in litt.*, 1991) for the hyrax population, this seems likely, and there is evidence that Cape black eagles were catching relatively more juveniles in the 1970's (see later).

TABLE 35

COMPOSITION OF ALL HYRAX SKULLS/MAXILLAE COLLECTED BENEATH BLACK EAGLE NESTING SITES IN AND AROUND THE KRNP DURING THE STUDY PERIOD

Skulls/maxillae of indeterminable sex are placed in the 'unknown' column. Disintegrating skulls could not always be allocated to annual age classes but could usually be placed in a larger age grouping (shaded rows).

AGE CLASS (y)	MALES	FEMALES	UNKNOWN	TOTAL
0 - 1	-	-	372	372
1 - 2	418	322	81	821
2 - 3	198	155	23	376
3 - 4	121	113	15	249
4 - 5	111	109	21	241
5 - 6	73	72	12	157
6 - 7	72	79	14	165
7 - 8	89	90	7	186
8 - 9	81	102	8	191
9 - 10	58	73	6	137
10 - 11	48	34	5	87
11 - 12	29	44	1	74
12 - 13	8	10	-	18
< 2	1	4	20	25
2 - 8	31	29	58	118
2 - 13	5	10	30	45
8 - 13	10	11	8	29
0 - 13	2	2	61	65
TOTAL	1400	1398	561	3359



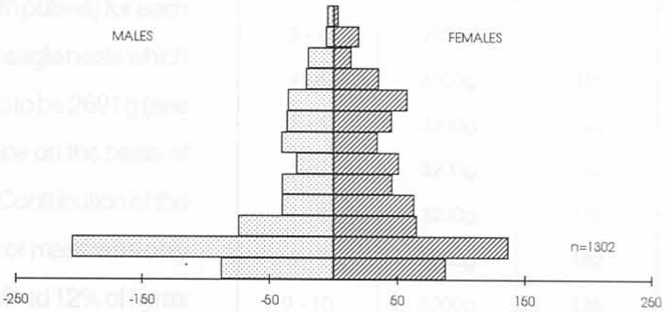


Fig. 89. Population structure of all classifiable hyrax skulls/ maxillae (n=3077) collected beneath black eagle nests in and around the KRNP during the study period. Asterixes denote age classes where sex ratio differed significantly (p<0,05) from parity. (youngest age class at the bottom)

Fig. 90. Population structure of all fresh (category A) classifiable hyrax skulls/maxillae (n=1302) collected beneath black eagle nests in and around the KRNP during the study period.

A direct comparison of freshly-killed (category A) and older (categories B + C) skulls collected at the end of 1987 (this was the largest collection, and contained many 'first-time' collections from nesting sites), only provided a slight indication that skulls of the very oldest individuals might be more prevalent amongst the more ancient material (Figure 91); and there was certainly no suggestion that juveniles were under-represented amongst the older material. However, the dynamic nature of hyrax population structure (Chapter 4), may well preclude such comparisons from portraying such bias in the methodology.

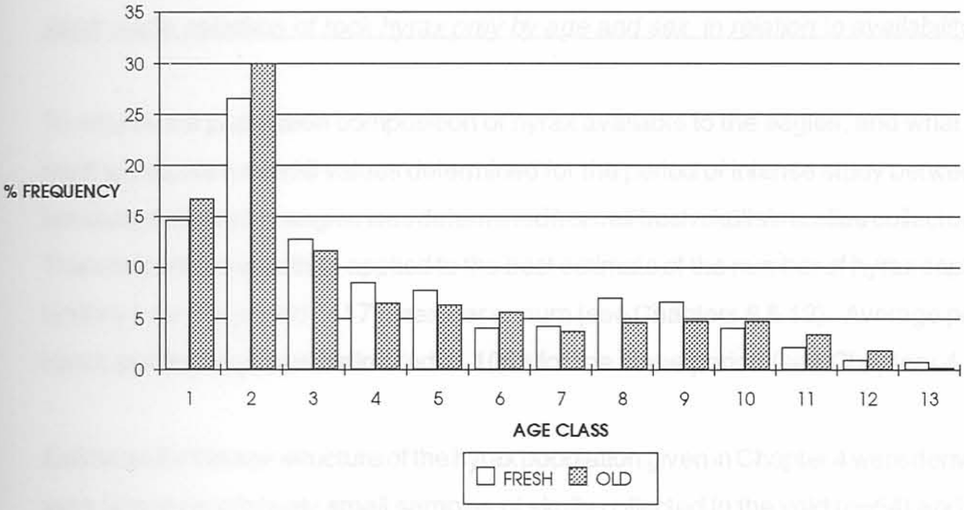


Fig. 91. Percent frequency representation of the annual age classes by fresh (category A) and older (categories B & C) hyrax skulls/maxillae from one large collection of prey remains from black eagle nesting sites in and around the KRNP at the end of 1987.

Whether considering only freshly-killed material or the entire sample, the general pattern of composition was the same. Immature hyrax (1-2y old) comprised 27% of the entire collection of skulls, and greatly outnumbered juveniles or any other age class in eagle diet. There was a general trend for younger age classes to be represented more frequently in the sample, but 7-9y olds outnumbered 5-7y olds.

TABLE 36

MEAN MASS AND FREQUENCY OF THE HYRAX AGE CLASSES REPRESENTED IN THE PREY REMAINS

AGE CLASS (y)	MEAN MASS (in May)	FREQUENCY
0 - 1	1100g	348
1 - 2	2150g	779
2 - 3	2700g	362
3 - 4	2950g	237
4 - 5	3100g	235
5 - 6	3200g	149
6 - 7	3200g	158
7 - 8	3200g	175
8 - 9	3200g	182
9 - 10	3200g	135
10 - 11	3200g	86
11 - 12	3200g	71
12 +	3200g	14
	mean 2582g	total 2931

In Table 36 a mean mass of 2582g is derived from the age structure of 2931 hyrax prey items coupled with estimates of mean mass (in between birth pulses) for each class (see methods). Mean mass for 223 hyrax delivered to black eagle nests which were being monitored by time-lapse photography was estimated to be 2691g (see Chapter 9), but the former estimate is preferred. Prey preference on the basis of size was considered in Chapter 9, and is discussed again later. Contribution of the age classes to meeting black eagle food requirements in terms of mass was only slightly altered from that indicated by frequency. Juveniles comprised 12% of hyrax captured but they only comprised 5% of the hyrax biomass consumed. It should be borne in mind that juvenile maxillae might be under-represented in the collections of prey remains. The relative contribution by immatures was slightly reduced in terms of mass, while that of adult and old age classes was slightly increased.

Overall sex ratio for the entire sample was extremely close to parity (Table 35). The entire collection of skulls was used for comparisons of each age class by sex, on the basis that freshly-killed material did not present a noticeably different picture, and assuming that male and female skulls belonging to the same age class decompose at the same rate. There was a statistically significant association with sex for certain age classes $(K_{11}^2 = 24,0; p < 0,05)$. In particular, males were more predominant in the immature class $(K_1^2 = 5,7; p < 0,05)$, while females comprised significantly more 8-9y olds $(K_1^2 = 4,2; p < 0,05)$, and significantly more 11-12y olds $(K_1^2 = 4,0; p < 0,05)$.

Black eagle selection of rock hyrax prey by age and sex, in relation to availability

To assess the population composition of hyrax available to the eagles, and what they were taking from it, I used the most appropriate overall values determined for the period of intense study between 1987 and 1990. Composition of hyrax captured by the eagles was determined from all fresh skulls/maxillae collected at the end of 1988, 1989 and 1990. This composition was then applied to the best estimate of the number of hyrax captured by black eagles in an average territory over this period - 117 hyrax per annum (see Chapters 8 & 12). Average post-reproductive population size for hyrax, per territory, was estimated at 1062 for the same period (see Chapters 4 & 12).

Estimates for the age structure of the hyrax population given in Chapter 4 were derived from life table calculations which were based on relatively small samples of skulls collected in the veld (n=54) and of animals shot (n=52). Estimates for the composition of the toll taken by the eagles were derived from a much larger sample (n=955). The skulls collected in the veld (away from known black eagle feeding sites) were thought to represent mortality other than that attributable to black eagles. Constructing an age structure for the population from these skulls proved inappropriate when it was discovered that black eagles accounted for the majority of adult and old hyrax that died (see later). This problem became manifest when I found that for a few older female age classes, the estimated toll taken by the eagles (which I have more confidence in) exceeded the estimated total mortality of that class, which had been calculated from the life tables (effects of a declining hyrax population had been taken into consideration when constructing the life tables).

These discrepancies were dealt with in the following manner: a simulated stable hyrax population was created on a computer spreadsheet (MICROSOFT EXCEL 4.0). Initially, overall mortality rates described in Chapter 4 were used for both males and females, but these were then adjusted in order to satisfy conditions that were observed. These conditions, the source of observations on which they were based, and the extent to which they could be satisfied in the model are presented in Table 37. The initial cohort and subsequent sex-specific mortality rates were manipulated to give a best fit for the model in meeting the observed conditions. I was not able to satisfy all conditions exactly. For instance, it was difficult to reconcile observed mortality rates with estimates of composition. This was probably caused by the variety of sources of observation, some of which represented the population at slightly different times. Also, the simulated population represents a population where the numbers dying in any age class conform to a fixed composition of age classes, and this composition remained stable over at least 50 birth pulses. In reality, recruitment and mortality varied dramatically on an annual basis (Chapter 4). This led to a noticeable decline in the hyrax population during 1988 and a partial recovery thereafter. So the spreadsheet simulation can only be regarded as a simplified

TABLE 37

PRE-DISPOSING CONDITIONS FOR THE SIMULATION OF AN ARTIFICIAL ROCK HYRAX POPULATION - THE SOURCE OF THEIR OBSERVATION, AND THE DEGREE TO WHICH THEY COULD BE SATISFIED IN THE MODEL

PRE-DISPOSING CONDITIONS	SOURCE	MODEL
Total population should approach 1062 individuals	Counts and colony plots (chapter 4)	1061,7
Juveniles should comprise @35% pop.	Counts at colonies (juveniles might have been slightly underestimated)	40,6%
One-year olds should comprise @18%	Counts at colonies	16,2%
Two-year olds should comprise @12%	Life tables from veld skulls and shot sample	9,9%
3-7 year olds should comprise @29%	Life tables from veld skulls and shot sample	27,7%
Old individuals (8-13y olds) should comprise @6%	Life tables from veld skulls and shot sample	5,7%
Adult sex ratio should approach 1male:1,2 females due to heavier male mortality between one and three years old	Shot sample & Fourie (1983)	1:1,20
Mean litter size should approach @2,53	Shot sample, Millar (1971), Fourie (1983)	2,44
About 79% of females should be pregnant	Shot sample	78,5
Juvenile mortality rate should approach @0,55	Counts at colonies & Fourie (1983)	0,60
Overall adult + Immature mortality rate should approach @0,30	Counts at colonies	0,27
Age specific mortality rates for adult and old ahyrax were based on those derived from life tables, but a few were adjusted to accomodate black eagle depredations (more reliable data)		
Age specific fecundity rates were derived from Fairall et al. (1986) & Fourie (1983), and adjusted to conform with observations on litter size and pregnancy rate (see above).		

---

caricature of this situation but it is my best estimate of overall hyrax population composition and mortality rates across the study period. It certainly provides a more comprehensive indication of population composition and process than that presented in Chapter 4.

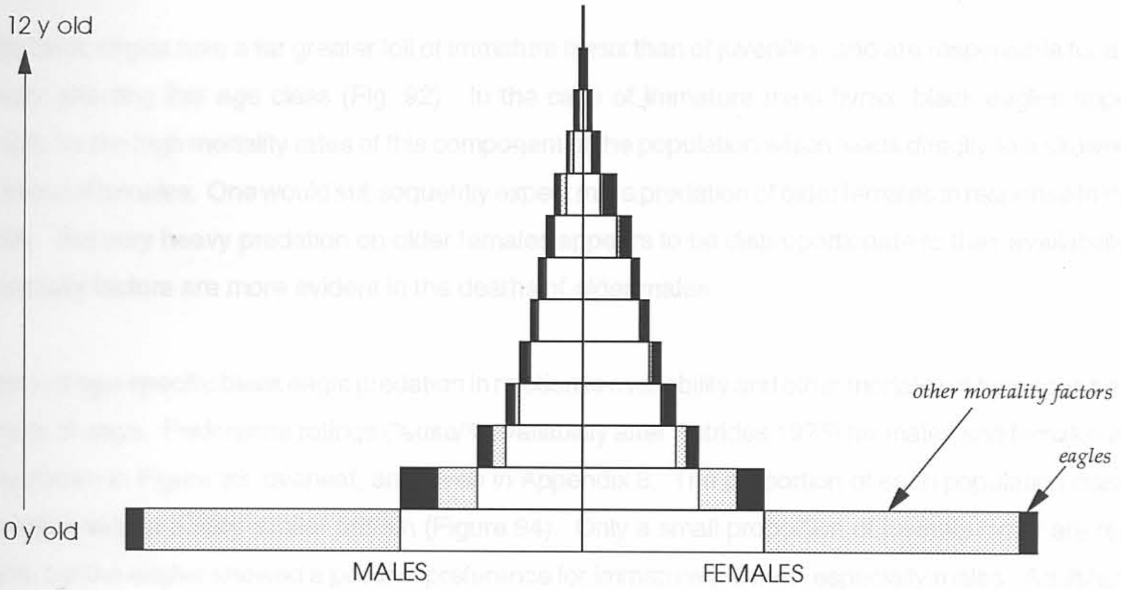


Figure 92. A diagramatic summary of age- and sex-specific predation by black eagles in relation to the availability and the annual mortality of the hyrax population classes. This summary was derived by computer simulation of a stable hyrax population which best represents the population under study - see text for method.

The model is summarised diagrammatically in Figure 92, showing age and sex-specific predation by black eagles in relation to the availability and mortality of hyrax population classes. This summary really represents an annual 'snapshot' of the hyrax population during the period of study. The diagram emphasises that black eagles are not an important mortality agent for juvenile rock hyrax. By use of a hyrax population model, Swart *et al.* (1986) emphasised that juvenile mortality was the most important parameter affecting rock hyrax population dynamics in the MZNP, but the highest values for juvenile mortality (84%) that were used in their model were not observed in nature. Starvation and disease were considered to be the main factors causing this juvenile mortality, but it has been shown in Chapter 7 that predation of this age class should not be ignored. Predators normally take a high toll of juvenile prey (e.g. Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990), probably because juveniles often react in a naive fashion to predators (Fourie 1983; pers. obs.) and may not be able to flee as effectively as older animals.

The toll of juvenile hyrax taken by black eagles in the present study may have been under-estimated if this age class was under-represented in collections of prey remains. Skulls of small juveniles may be entirely consumed by the eagles, so this seems likely. Direct observations of eagles hunting or feeding on hyrax suggested that the proportion of juveniles amongst hyrax captured (29%) might be twice that indicated by the collections of prey remains (12-15%). But this is based on a very small sample (n=21) of observations (Chapter 9). Time-lapse photography actually indicated that only 13% of all hyrax delivered to black eagle nests (n=223) were estimated to weigh less than or half adult mass when intact (this would correspond to the size of the first age class). Even if black eagles were capturing twice as many juveniles as indicated by the prey remains, this would still only represent a minor part of the juvenile mortality. The juvenile age class might be somewhat under-represented in calculations of age structure of the prey remains sample, but this should not unduly affect estimates of the toll taken from the older age classes because the juvenile component may also have been slightly under-estimated in the investigations of prey capture rate based on time-lapse photography (Chapter 8).

Evidently black eagles take a far greater toll of immature hyrax than of juveniles, and are responsible for a major part of mortality affecting this age class (Fig. 92). In the case of immature male hyrax, black eagles appear largely responsible for the high mortality rates of this component of the population which leads directly to a skewed adult sex ratio in favour of females. One would subsequently expect more predation of older females in response to their greater availability. But very heavy predation on older females appears to be disproportionate to their availability (Fig. 92). Other mortality factors are more evident in the deaths of older males.

The pattern of age-specific black eagle predation in relation to availability and other mortality of hyrax can be presented in a number of ways. Preference ratings (%use/%availability after Petrides 1975) for males and females in each age class are shown in Figure 93, overleaf, and given in Appendix 8. The proportion of each population class removed by the eagles reveals a very similar pattern (Figure 94). Only a small proportion of juvenile hyrax are removed, as discussed, but the eagles showed a positive preference for immature animals, especially males. Adult hyrax appear to be taken roughly in proportion to their availability with no obvious preference for either sex (just over 10% of these classes are removed by the eagles each year). But animals older than 7y are evidently heavily preyed upon. Just under one third (32%) of all old hyrax in the population were removed by the eagles each year. Eagles showed the highest preference ratings for these older prey animals, especially females.

The high preference ratings for females indicates that heavy predation of these classes is not just a response to greater availability. Females were noticeably preferred by the eagles in each of the older age classes except the 10-11y olds. Unfortunately, hyrax of this age only comprise a tiny fraction of the population, so the shift might be an artefact caused by small sample sizes. But most 10-11y old hyrax captured by the eagles between 1987 and 1989 would have been born around 1978. A relationship between sex and rainfall during the estimated birth year is described later and in Chapter 4. Greater availability of males born or recruited in the dry year of 1978 conforms to this relationship. A shift in the availability of the sexes amongst 10-11y olds may well have been lost in the calculations of population structure. Estimates of selection by the eagles were not modified or smoothed in any way, so the shift in preference towards male 10-11y olds might reflect errors in the estimates of availability.

Black eagles were a major mortality agent for all age classes except juveniles. Eagles accounted for 45,2% of the immature hyrax that died each year; 67,1% of the adult hyrax that died; and 64,6% of old animals that died (Figure 95). Between ages 7 to 10y old, other mortality factors appear to affect males, while black eagles were mostly responsible for female deaths in these age classes.

Black eagles were evidently responsible for most post-juvenile mortality of the hyrax population. It is conceivable that such 'hard' selection pressure would encourage co-evolution between prey and predator. But the present study represented a hyrax population at low density being pursued by a specialist predator (Chapter 9). These conditions may be associated with the maximum pressure that predators can exert upon their prey (Pearson 1966, 1971; Fitzgerald 1977). So extrapolating to the level of historic species interaction can only be speculative. In other regions such as the Mountain Zebra National Park, black eagles may be nest-site limited, and other predators may have more influence on rock hyrax populations (Swart *et al.* 1986).

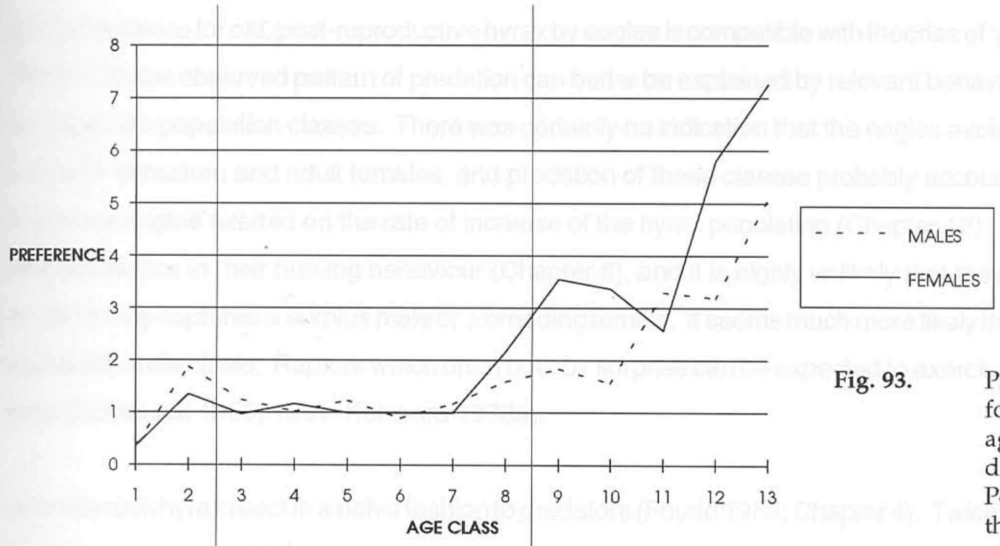


Fig. 93. Preference ratings by black eagles for male and female rock hyrax age classes - calculated as percent diet/percent availability, after Petrides (1975). Vertical lines down the page separate immature, adult and old age classes. Consult Appendix 8 for values.

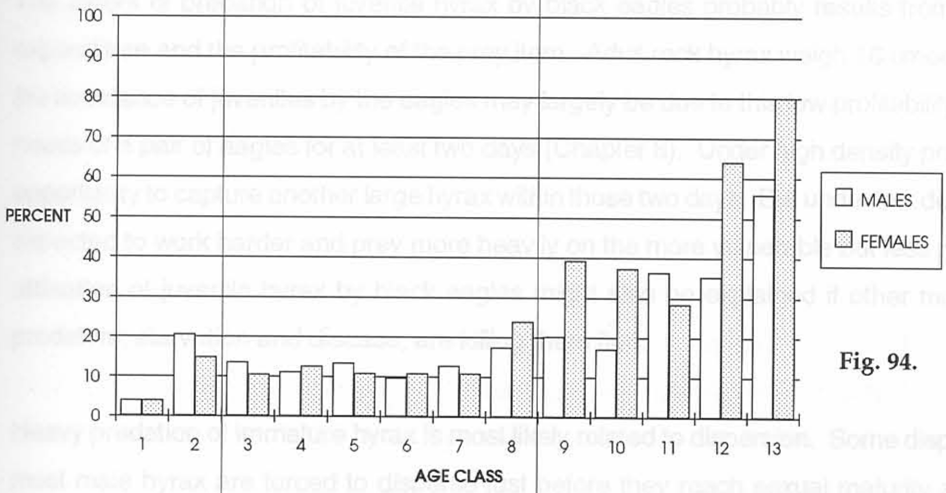


Fig. 94. The estimated proportion of each hyrax population class removed annually by black eagles.

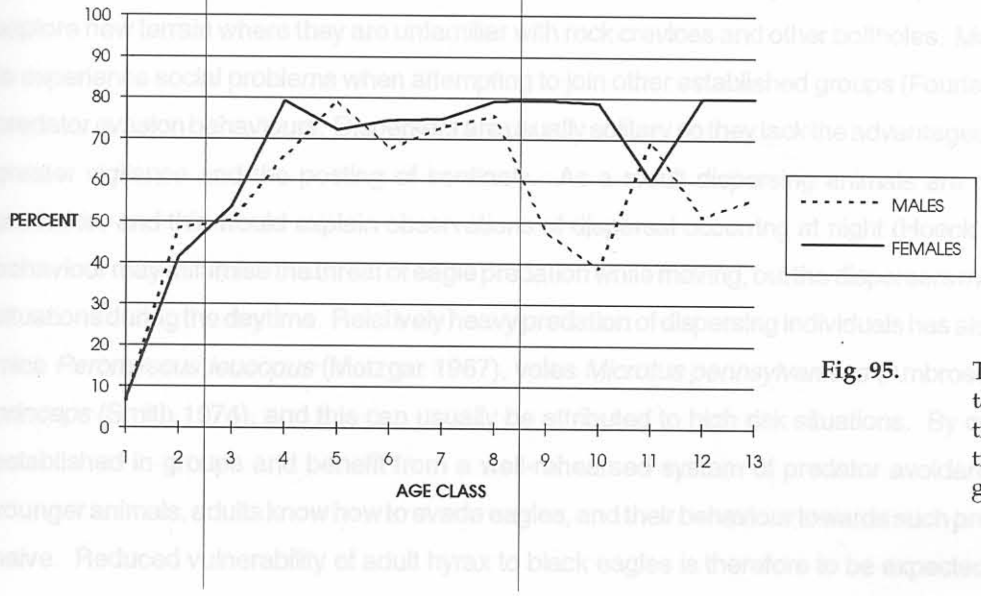


Fig. 95. The estimated proportion of mortality affecting each hyrax population class annually, that can be attributed to predation by black eagles.

High preference for old, post-reproductive hyrax by eagles is compatible with theories of 'prudent' predation (Slobodkin 1968). But the observed pattern of predation can better be explained by relevant behaviour affecting the vulnerability of respective population classes. There was certainly no indication that the eagles avoided the more 'reproductively-valuable' immature and adult females, and predation of these classes probably accounted for most of the influence that black eagles exerted on the rate of increase of the hyrax population (Chapter 12). Black eagles usually employ surprise tactics in their hunting behaviour (Chapter 6), and it is highly unlikely that they would exercise control over whether they captured a surplus male or a breeding female. It seems much more likely that they simply catch the most vulnerable individuals. Raptors which often hunt by surprise can be expected to exercise less selective effect on their prey (Rudebeck 1950, 1951; Kenward 1978a).

Juvenile rock hyrax react in a naive fashion to predators (Fourie 1983; Chapter 4). Twice, black eagles were observed to capture juveniles which took refuge in bushes instead of crevices when the sentinel sounded the alarm. Juveniles are probably easier to catch than older hyrax, but they are highly precocious at birth and very agile at escaping over rocks, so their capture does not necessarily incur much less energy expenditure on the part of the eagles, per strike. The extent of predation of juvenile hyrax by black eagles probably results from a trade-off between this energy expenditure and the profitability of the prey item. Adult rock hyrax weigh 16 times the mass of young juveniles. So the avoidance of juveniles by the eagles may largely be due to this low profitability. A large hyrax can fulfil the food needs of a pair of eagles for at least two days (Chapter 8). Under high density prey conditions there may be ample opportunity to capture another large hyrax within those two days. But under low density conditions the eagles can be expected to work harder and prey more heavily on the more vulnerable but less profitable juveniles. Relatively low utilisation of juvenile hyrax by black eagles might also be explained if other mortality factors such as generalist predators, starvation and disease, are killing them first.

Heavy predation of immature hyrax is most likely related to dispersion. Some dispersion occurs in the first year, but most male hyrax are forced to disperse just before they reach sexual maturity at their second rut (Fourie 1983). Although under low density conditions some adult, non-territorial males may be tolerated within a social group in a sexually quiescent state (Hoeck *et al.* 1982; Van der Merwe & Skinner 1982; Chapter 4). Dispersion of females is less frequent and less obligatory and mostly occurs after the second rut (Fourie 1983). Dispersing animals are forced to explore new terrain where they are unfamiliar with rock crevices and other boltholes. Males especially are more likely to experience social problems when attempting to join other established groups (Fourie 1983) and this may influence predator evasion behaviours. Dispersers are usually solitary so they lack the advantages of group-living, which include greater vigilance and the posting of sentinels. As a result dispersing animals are probably highly vulnerable to predation, and this would explain observations of dispersal occurring at night (Hoeck 1982; pers. obs.). Nocturnal behaviour may minimise the threat of eagle predation while moving, but the dispersers may still find themselves in risky situations during the daytime. Relatively heavy predation of dispersing individuals has also been noted for white-footed mice *Peromyscus leucopus* (Metzgar 1967), voles *Microtus pennsylvanicus* (Ambrose 1972), and pikas *Ochotona princeps* (Smith 1974), and this can usually be attributed to high risk situations. By contrast, most adult hyrax are established in groups and benefit from a well-rehearsed system of predator avoidance and daily routine. Unlike younger animals, adults know how to evade eagles, and their behaviour towards such predators cannot be considered naive. Reduced vulnerability of adult hyrax to black eagles is therefore to be expected.

It is generally accepted that old animals become less alert to danger and less able to escape predators. Deterioration in these behaviours may be directly caused by senescence. But these effects are likely to be aggravated by loss of body condition in association with dental attrition, which in rock hyrax occurs after eight years (Fourie 1983). Dental attrition may necessitate changes in foraging behaviour which result in more time spent away from shelter. These explanations are offered to account for the very high preference for old hyrax shown by black eagles in the present study. Relatively heavy predation of old animals is often reported in predation studies of higher vertebrates (Hornocker 1970; Kruuk 1970, 1972a; Mech 1970).

The disproportionately high predation of old female hyrax in comparison with old males may be due to a tendency amongst older females to accept high-risk sentinel behaviour (Chapter 4). Sentinels were clearly highly vulnerable to predation while running to catch up with foraging groups, usually when the groups had disappeared into riverine scrub. At this stage the sentinel did not have the advantage of others looking out for it, and usually ran the whole length down to the river, rather than pausing at temporary shelters as the others had done. But relatively less predation of older males may also be due to greater involvement of other factors in the deaths of old males. Intra-specific aggression is more often recorded for male rock hyrax than for females (Fourie 1983). This aggression can take the form of vicious contests over territory or harem ownership, and the wounds inflicted can lead to the deaths of the individuals involved (Fourie 1983). Territorial male hyrax may be most susceptible to this mortality in late adulthood when they are displaced.

Hoeck *et al.* (1982) and Fourie (1983) suggested that non-breeding 'peripheral' adult male hyrax which are loosely associated with harem groups may suffer heavier rates of predation and act as a buffer to the breeding colony. A similar role is suggested for sub-ordinate, non-breeding individuals among springbok *Antidorcas marsupialis* (Bigalke 1970), and among red grouse *Lagopus scoticus* (Jenkins *et al.* 1964). In most social organisations, males are more likely to be forced into such situations than females, and this probably explains why many studies indicate disproportionately heavier predation of males (e.g. Rudnai 1974; Beacham 1979; Korpimäki 1985b; Sinclair *et al.* 1990). In the case of hyrax, it would appear that heavier predation of males is confined to the immature age class.

Much of the age and sex-specific vulnerability of hyrax can be expected to peak at particular times of the year. It is thus possible to predict when particular prey categories should become more important in the diet of the eagles. For instance, juveniles might be more heavily predated between November and March when they are more abundant and show more naive behaviour towards predators. Immature males should be more heavily preyed upon when dispersing before the rut in February and March; while immature females should be more heavily preyed upon after the rut in winter. One would expect adult hyrax to suffer greater predation at those times of year when body condition is at its worst for their respective sex. For males, this occurs during the rut (April); while for females this occurs during lactation in November and December (Fourie 1983). Such effects are likely to be influenced by rainfall patterns and the food supply. Annual collections of prey remains may be slightly biased by these variations in vulnerability, and they do not permit any testing of these predictions. However, they do allow other investigations of variation in the selection of different hyrax population components by black eagles over longer time periods.

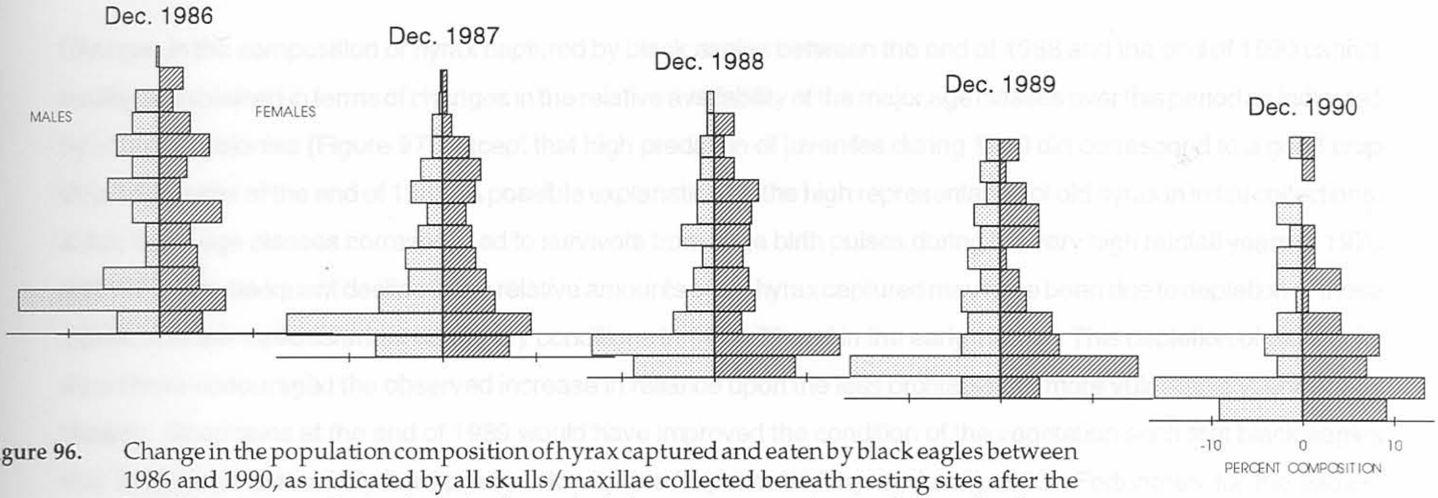


Figure 96. Change in the population composition of hyrax captured and eaten by black eagles between 1986 and 1990, as indicated by all skulls/maxillae collected beneath nesting sites after the breeding season in December. (males to the left, youngest age class at the base line)

Annual variation in the age and sex composition of rock hyrax captured by black eagles

The composition of hyrax preyed upon by black eagles over the five annual collections is shown diagrammatically in Figure 96. Trends in the selection and availability of four major age classes during the study period are summarised in Figure 97, and were tested for any change. There was a statistically highly significant change in the crude age composition of hyrax taken by black eagles over the study period ($K^2_{12} = 26{,}9; p < 0{,}01$). In particular, juveniles showed a significant ($K^2_4 = 10{,}7; P < 0{,}05$), erratic change which resulted in an overall increase during the study period; whilst old animals showed an opposite trend ($K^2_4 = 11{,}3; p < 0{,}05$). Representation of immatures in collections of prey remains showed a steady increase but none of this change was statistically significant. Adults comprised the most consistent portion of hyrax age classes in prey remains over the study period. Mean age of hyrax captured by black eagles in 1986 was 4,8y; by 1990 this had dropped to 3,4y.

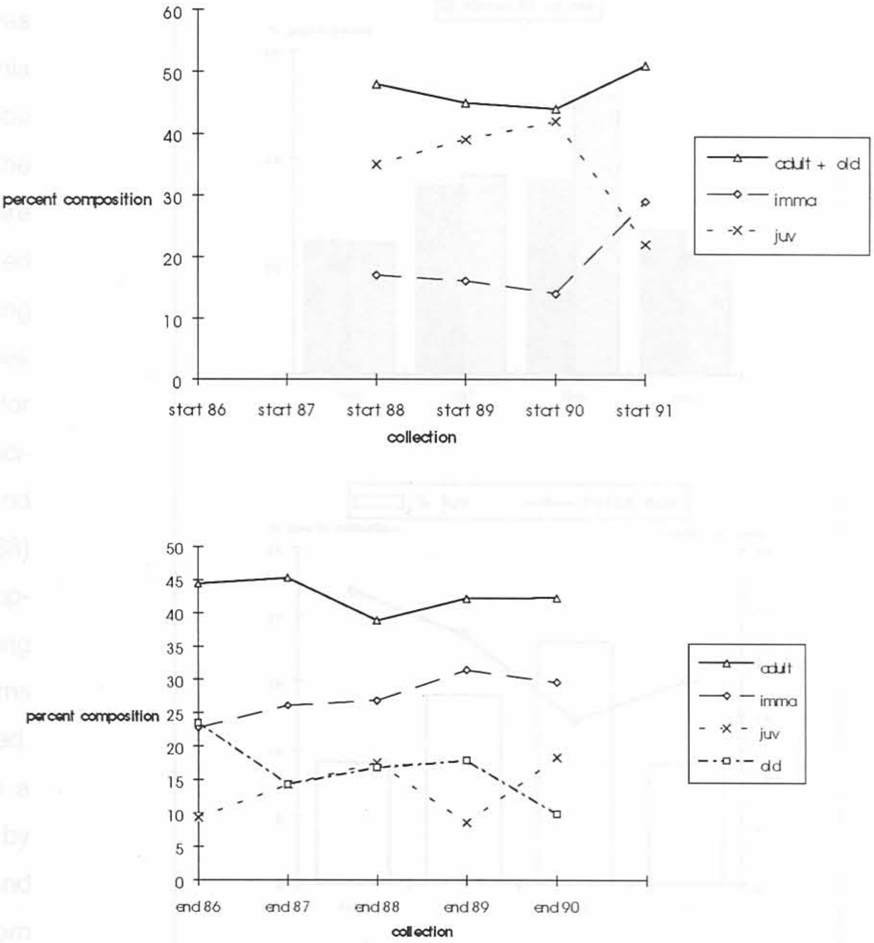


Figure 97. Year to year changes in the composition of the major hyrax population components available to the eagles (above - from colony counts) and taken by the eagles (below - from prey remains), over the study period.

Changes in the composition of hyrax captured by black eagles between the end of 1988 and the end of 1990 cannot readily be explained in terms of changes in the relative availability of the major age classes over this period as indicated by counts at colonies (Figure 97); except that high predation of juveniles during 1990 did correspond to a good crop of juvenile hyrax at the end of 1989. A possible explanation for the high representation of old hyrax in initial collections, is that these age classes corresponded to survivors from large birth pulses during the very high rainfall years of 1976 and 1977. A subsequent decline in the relative amounts of old hyrax captured may have been due to depletion of these stocks, and low replenishment during dry conditions in 1978-79 and in the early 1980's. This depletion of old stocks would have encouraged the observed increase in reliance upon the less profitable but more vulnerable younger age classes. Good rains at the end of 1989 would have improved the condition of the vegetation such that black eagles may have been particularly hard-pressed to capture 'experienced' hyrax during 1990. Fortunately for the eagles, alternative prey species were more available by this time, so the eagles were able to partly compensate for this by capturing a greater portion of other prey species (Chapter 9).

The pattern of increase in the juvenile component of hyrax captured by black eagles was closely mirrored by the amount of hyrax crania opened by the eagles (Figure 98). It may be that this correlation results merely from the fragile nature of juvenile skulls (which are easier to open). But the association indicated between opening of crania and eagle breeding (Chapter 6) suggests that this habit in itself might indicate food stress (more evidence for this is provided later). Increases in the incidence of both opening of hyrax crania and capture of juvenile hyrax (especially in 1988) suggest that the eagles may have been coping with a decline in their main prey by taking a greater portion of less profitable prey items and reducing wastage of any prey captured. Hyrax colony counts did in fact indicate a significant overall decline in hyrax numbers by about one third between the end of 1987 and the end of 1990; whilst sightings of hyrax from transects walked through the veld indicated that this decline was evident during 1986 and may have reduced the hyrax population by half (Chapters 4 & 5).

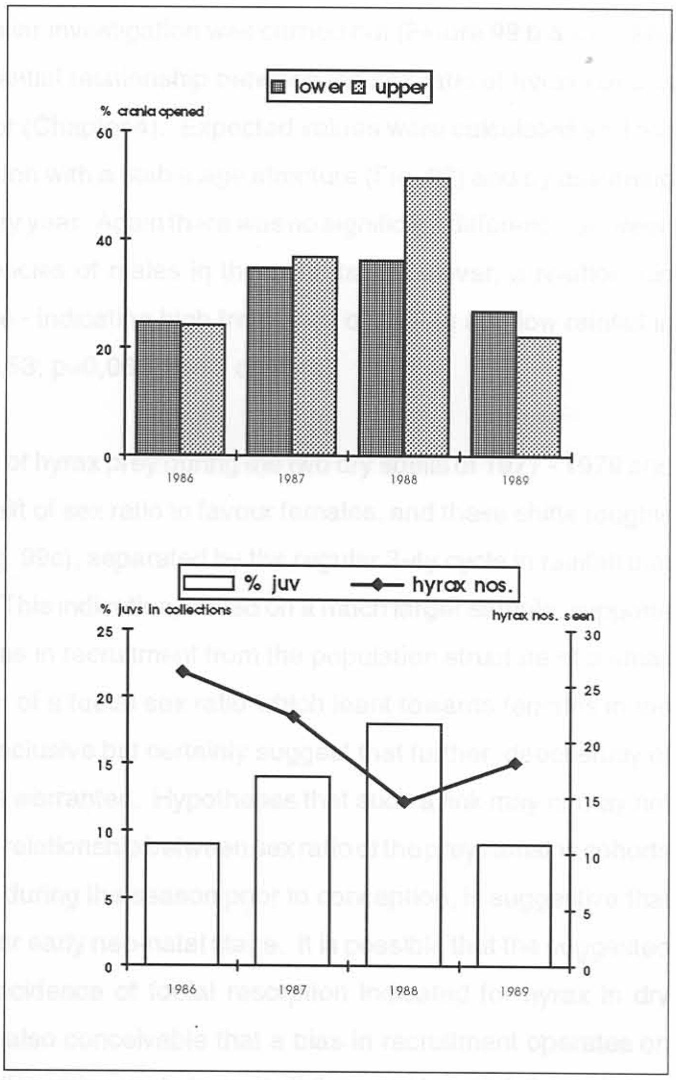


Figure 98. Annual change in the percentage of hyrax crania opened by upper and lower escarpment eagles (above), and concurrent change in the juvenile component of hyrax captured (below). Eagles caught more juveniles and opened more crania when colony counts indicated that hyrax numbers were lowest in 1988 (below).

In order to investigate whether large hyrax birth pulses during wet years led to subsequent high capture frequencies for these cohorts by black eagles, the year of birth was predicted for all fresh skulls collected. Observed frequencies of hyrax captured from each cohort were then compared with expected values had the eagles been preying upon a stable age structure with regular recruitment (as determined earlier in this chapter - see Fig. 92). Observed and expected numbers of hyrax removed from each cohort are plotted in Figure 99a. There was no statistically significant difference between these two distributions overall. However, when residual proportions were calculated for each cohort as: (observed-expected)/expected, these residuals (n=17) showed a significant, positive correlation with rainfall in the previous summer season, prior to conception of the respective cohorts (r=0,61; p<0,01). This pattern among hyrax prey of black eagles confirm that the prey population age structure is indeed influenced by relayed effects of variable recruitment, as observed by Fourie (1983) and in the present study (Chapter 4).

Prompted by the observation that high predominance of males amongst immature hyrax captured during 1986 and 1987 did not persist beyond that (Figure 96), a similar investigation was carried out (Figure 99 b & c) to see whether the hyrax prey of black eagles reflected a potential relationship between the sex ratio of hyrax cohorts and rainfall at the time of their birth as suggested earlier (Chapter 4). Expected values were calculated as if the eagles were continually capturing hyrax from a population with a stable age structure (Fig. 92) and by assuming that equal numbers of males and females were born every year. Again there was no significant difference between the overall patterns of observed and expected frequencies of males in the cohorts. However, a relationship between high values for residuals (calculated as before - indicating high frequency of males) and low rainfall in the summer season of their birth was suggested (r=-0,53; p=0,066; n=13 cohorts).

There appeared to be a build-up in the male component of hyrax prey during the two dry spells of 1977 - 1979 and 1983 - 1984 (Fig. 99b). Both culminated in a sudden shift of sex ratio to favour females, and these shifts roughly coincided with peaks in the summer rainfall pattern (Fig. 99c), separated by the regular 3-4y cycle in rainfall that is characteristic of the Beaufort West area (Chapter 2). This indication, based on a much larger sample, supports previous statistical evidence of a rainfall-related sex-bias in recruitment from the population structure of a small sample of shot hyrax (page 51), and direct observation of a foetal sex ratio which leant towards females in the wet year of 1989 (page 52). These data are not yet conclusive but certainly suggest that further, direct study of this aspect of hyrax population biology in arid regions is warranted. Hypotheses that such a link may or may not be adaptive were discussed on page 62. The suggested relationship between sex ratio of the prey remains cohorts and rainfall during the season of their birth, rather than during the season prior to conception, is suggestive that any sex-bias in recruitment occurs at the late pre-natal or early neo-natal stage. It is possible that the suggested sex-biased recruitment might be linked with a high incidence of foetal resorption indicated for hyrax in dry conditions (Chapter 4; Millar 1971; Fourie 1983). It is also conceivable that a bias in recruitment operates on immature animals if the filter of predation that acts on dispersing male hyrax is influenced by rainfall one or two years previously, but there were no indications to support this idea.

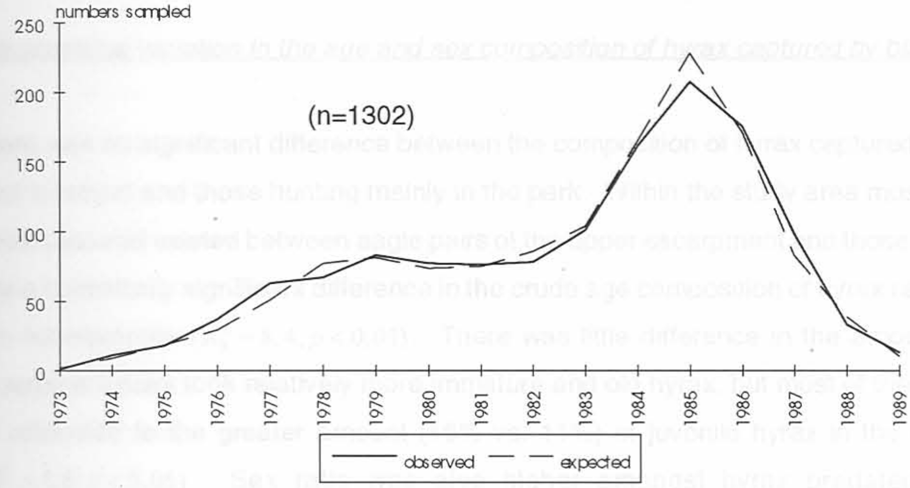


Fig. 99a. The birth dates of all hyrax represented by fresh skulls/maxillae in the prey remains were estimated to plot these observed frequencies of cohorts born between 1973 and 1989, among black eagle prey. Expected frequencies were calculated for each cohort as if the eagles had been predating a stable hyrax population with constant rates of recruitment and mortality.

Fig. 99b. Observed and expected contribution of males to hyrax cohorts. Observed values were determined from all fresh skulls/maxillae in the prey remains collections. Expected values were calculated for eagles predating a stable hyrax population with a constant and equal production of male and female juveniles each birth pulse.

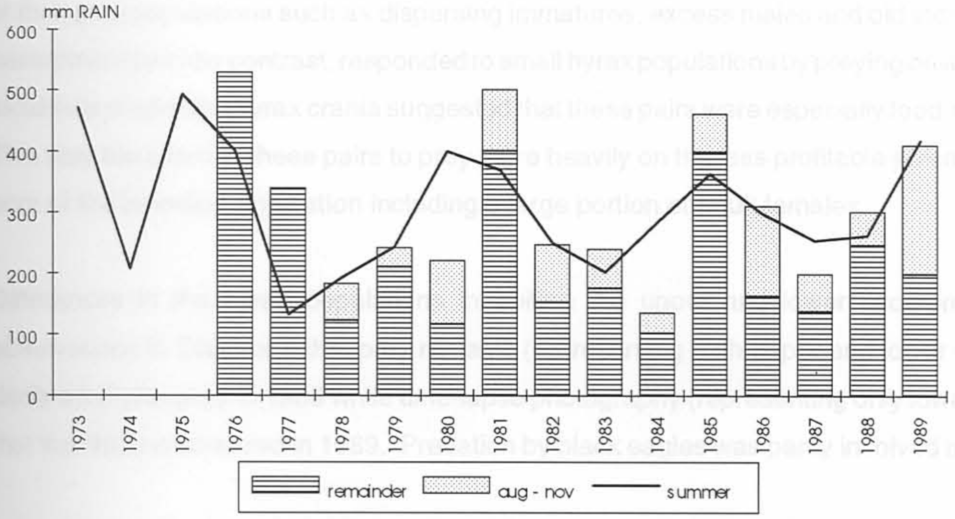


Fig. 99c. Rainfall patterns over the years in which the hyrax cohorts represented in the prey remains were born. January to December rainfall is represented as columns (rainfall during late hyrax gestation is lightly shaded); July to June rainfall is plotted as a line.

Geographical variation in the age and sex composition of hyrax captured by black eagles within the study area

There was no significant difference between the composition of hyrax captured by black eagles hunting mainly over farmland and those hunting mainly in the park. Within the study area most variation in the composition of hyrax captured existed between eagle pairs of the upper escarpment and those of the lower escarpment. There was a statistically significant difference in the crude age composition of hyrax captured by eagles nesting on the two escarpments $(K_3^2 = 8,4; p < 0,01)$. There was little difference in the amounts of adult hyrax killed; lower escarpment pairs took relatively more immature and old hyrax; but most of the difference in composition could be attributed to the greater amount (15% vs. 11%) of juvenile hyrax in the diet of upper escarpment pairs $(K_1^2 = 5,6; p < 0,05)$. Sex ratio was also higher amongst hyrax predated by upper escarpment pairs $(\overline{x} = 1,53\,females\,/\,male)$, than amongst those predated by lower escarpment pairs $(\overline{x} = 0,98\,females\,/\,male)$. This difference was statistically significant $(K_1^2 = 4,5; p < 0,05)$.

General correlation analyses on various characteristics of eagle territories and diet of the respective pairs revealed the following: juvenile hyrax were more prevalent in the diet of eagle pairs which took a wider prey spectrum $(r_p = 0,58; p < 0,01)$, and which defended more upper plateau $(r_p = 0,59; p < 0,01)$ and less middle plateau $(r_p = 0,50; p < 0,05)$ in their territories; immature hyrax were more prevalent in the diet of eagle pairs which took a narrower range of prey species $(r_p = -0,76; p < 0,01)$; old hyrax were more prevalent in the diet of eagle pairs which had more hyrax available in their territories $(r_p = 0,50; p < 0,05)$; male hyrax were more prevalent in the diet of eagle pairs which defended less upper plateau in their territories $(r_p = -0,67; p < 0,01)$.

The majority of these differences and relationships stem from fundamental differences between lower and upper escarpment territories. Lower escarpment territories were larger, contained more mountain slopes and thus accommodated larger hyrax populations than upper escarpment territories (Chapter 6). Eagle pairs nesting on the lower escarpment took a greater portion of hyrax in their diet (Chapter 9). It is likely that these pairs were less hard-pressed to capture hyrax and accordingly could prey on the more vulnerable and superfluous components of their prey populations such as dispersing immatures, excess males and old individuals in senescence. Upper escarpment pairs by contrast, responded to small hyrax populations by preying on a wider species spectrum. High incidence of opening hyrax crania suggested that these pairs were especially food-stressed during 1988 (Fig. 98). This may have forced these pairs to prey more heavily on the less profitable juvenile age class, and on the main core of the breeding population including a large portion of adult females.

Differences in the hyrax populations inhabiting the upper and lower escarpments might also explain the observations in Chapter 9 that prey remains (representing both upper and lower escarpment pairs) indicated a decline in hyrax prey in 1988 while time-lapse photography (representing only lower escarpment pairs) indicated that this decline occurred in 1989. Predation by black eagles was partly involved in these declines (Chapter 12).

Regional variation in the age and sex composition of rock hyrax captured by black eagles

Age and sex-determination of all rock hyrax skulls housed at the S. A. Museum which had been collected by Boshoff *et al.* (1991) from beneath black eagle eyries in the Cape Province, permitted investigation of wide-scale geographic variation. Population structure diagrams for rock hyrax remains collected in seven principal regions of the Cape Province are presented in Figure 100. For two of these regions, population structure could be contrasted for collections made in the early 1970's and in the late 1980's. Data on rock hyrax captured by black eagles in the Mountain Zebra National Park in the early 1980's were accessed from Fourie (1983).

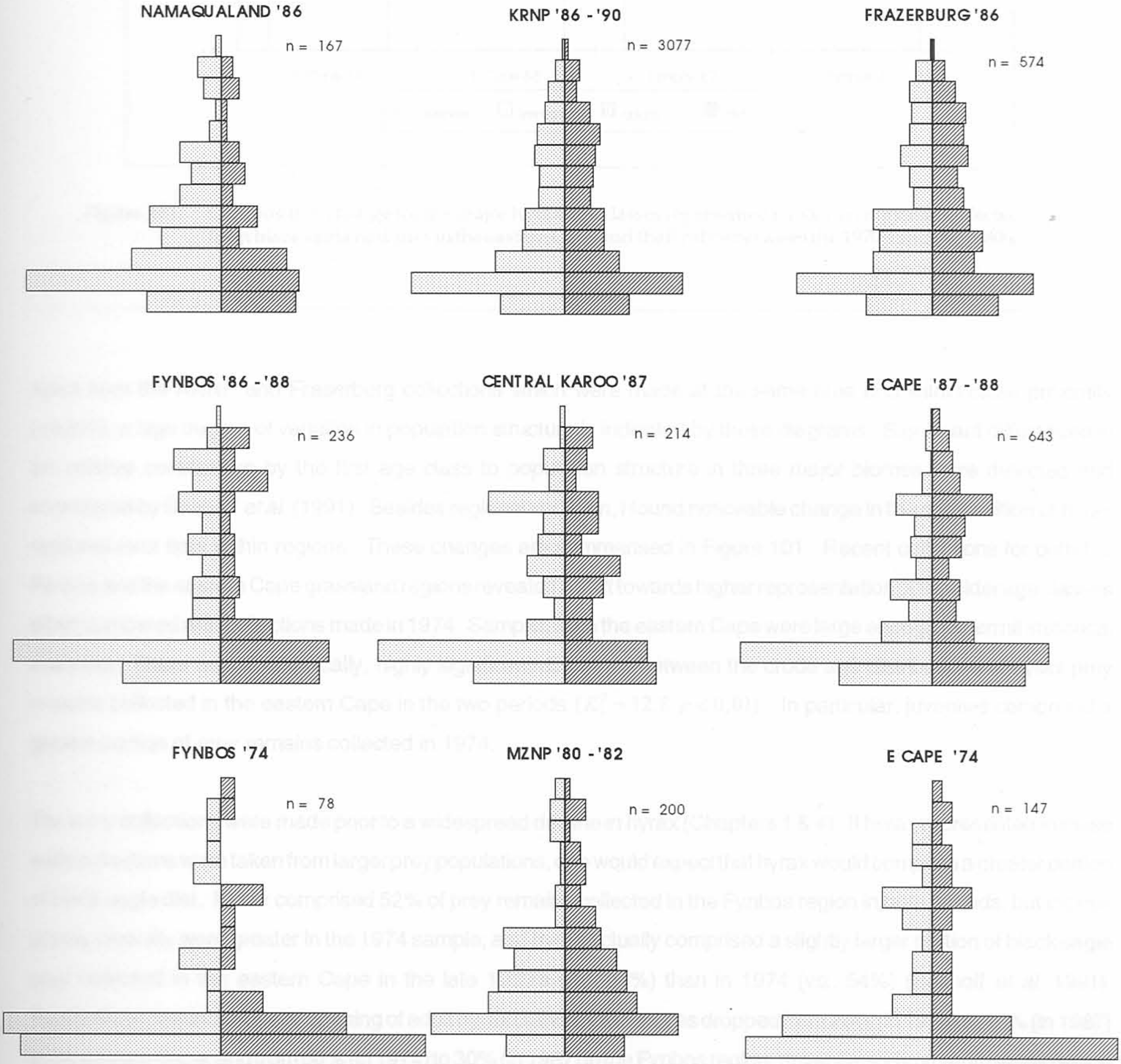


Figure 100. Population structure diagrams derived from hyrax skulls/maxillae collected beneath black eagle nesting sites for Namaqualand, the eastern Cape, Fynbos and four areas of the Karoo during the 1980's; and for the eastern Cape and Fynbos during the 1970's. These diagrams were determined from material collected by Boshoff et al. (1991), except for the KRNP (present study) and the MZNP (referenced from Fourie 1983). Males are shown to the left of the axes, females to the right; juvenile age classes at the base-line. Sample sizes are provided.

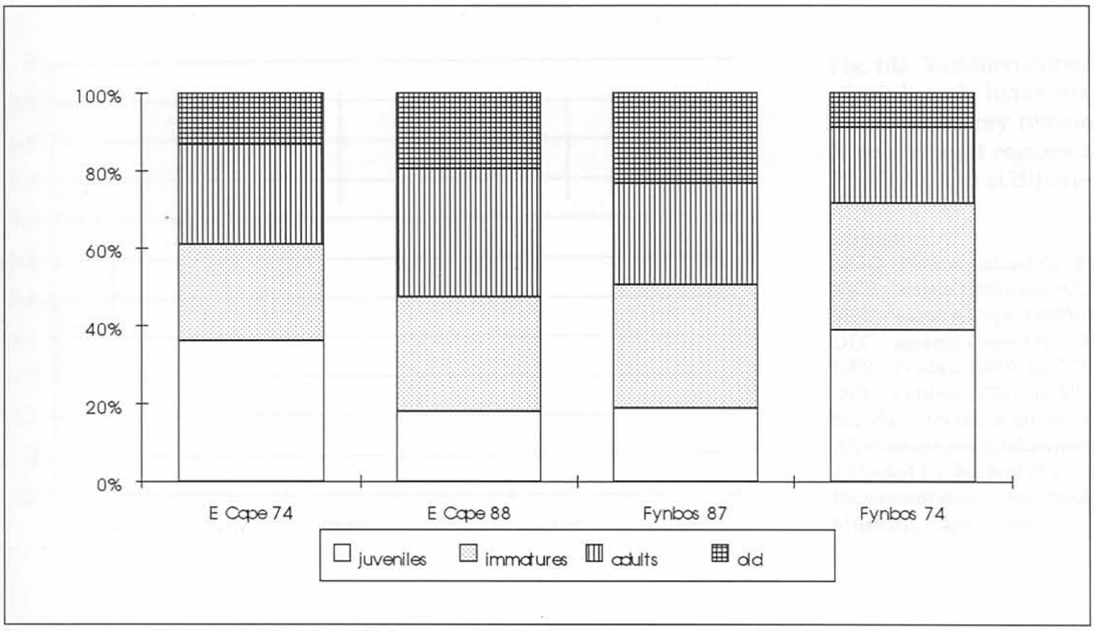


Figure 101. Composition change for the major hyrax age classes represented by skulls/maxillae collected from black eagle nest sites in the eastern Cape and the Fynbos between the 1970's and the 1980's.

Apart from the KRNP and Fraserberg collections which were made at the same time and within close proximity (<80km), a high degree of variation in population structure is indicated by these diagrams. Significant differences in the relative contribution by the first age class to population structure in three major biomes were detected and considered by Boshoff *et al.* (1991). Besides regional variation, I found noticeable change in the composition of hyrax captured over time within regions. These changes are summarised in Figure 101. Recent collections for both the Fynbos and the eastern Cape grassland regions revealed a shift towards higher representation of the older age classes when compared with collections made in 1974. Samples from the eastern Cape were large enough to permit statistical analyses. There was a statistically, highly significant difference between the crude age distributions of hyrax prey remains collected in the eastern Cape in the two periods $(K_3^2 = 12{,}8; p < 0{,}01)$. In particular, juveniles comprised a greater portion of prey remains collected in 1974.

The early collections were made prior to a widespread decline in hyrax (Chapters 1 & 4). If hyrax represented in these early collections were taken from larger prey populations, one would expect that hyrax would comprise a greater portion of black eagle diet. Hyrax comprised 52% of prey remains collected in the Fynbos region in both periods, but indices of prey diversity were greater in the 1974 sample; and hyrax actually comprised a slightly larger portion of black eagle prey collected in the eastern Cape in the late 1980's (viz. 64%) than in 1974 (viz. 54%) (Boshoff *et al.* 1991). Furthermore, the incidence of opening of adult hyrax crania by the eagles dropped from 20% (in 1974) to 15% (in 1987) in the eastern Cape; and from 50% (in 1974) to 30% (in 1987) in the Fynbos region. Juvenile and immature skulls (which are easier to open) were excluded from this analysis, so it appears that the eagles may have been more food-stressed up until 1974.

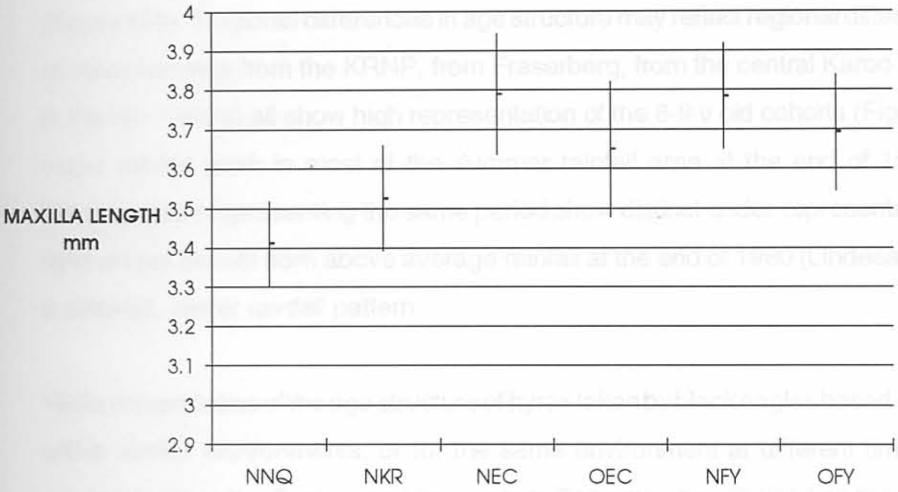


Fig. 102. Variation in the size (length) of adult male hyrax maxillae from black eagle prey remains collected from different regions of the Cape Province, and at different times.

Legend:
NNQ - Namaqualand (n=41);
NKR - Karoo 1980's (n=50);
NEC - eastern Cape 1980's (n=50);
OEC - eastern Cape 1970's (n=50);
NFY - Fynbos 1980's (n=37);
OFY - Fynbos 1970's (n=10).
Standard deviation on the mean is shown.
All measurements taken from hyrax skulls collected by Boshoff *et al.* (1991), and in the present study - now housed at the S.A. Museum, Cape Town.

Low representation of adult and old hyrax age classes from the early collections in both regions corresponds to a period of drought in the summer rainfall area of southern Africa during the 1960's at the time of birth of those cohorts (Tyson 1986 - Fig 1.11). Whereas high representation of older age classes in the late 1980's collections corresponds to good rains during the late 1970's. It appears that the 1960's drought may have caused reduced recruitment of hyrax cohorts and also reduced individual growth. Skull dimensions of adult male hyrax were larger for the 1987 collections than for the 1974 collections in both regions (Figure 102), although this difference was only significant for the larger samples of adult males collected in the eastern Cape (for length of maxillae: t=3,41; p<0,01; for width of maxillae: t=4,1; p<0,01). From scaling, linear differences suggest that the mass of rock hyrax could have been 12,5% and 6,5% larger for the recent collections in the eastern Cape and Fynbos respectively.

It has been suggested that body mass in *P. capensis* is related to temperature (Yom Tov in press) or perhaps vegetation type (R.G. Klein *in litt.*). The present observations indicate that body mass in rock hyrax maybe more closely related to precipitation and consequent food availability. From scaling, linear differences (Figure 102) indicated that mean hyrax mass in the very dry Namaqualand might be 12% less than mean hyrax mass in the Karoo (2040g: Chapter 4); and that mean hyrax mass in the wetter eastern Cape and Fynbos regions might be >20% larger than mean hyrax mass in the Karoo. The variation in the linear dimensions of adult male hyrax skulls was certainly significant across the various regions ($F_{3,174} = 86,9; p < 0,01$).

Differences in the age structure of hyrax captured during the two decades suggest that the prey population was in different stages of growth at those times. The high representation of younger animals in the 1974 collections suggest that the eagles were preying on less accessible prey populations (smaller?) which were possibly growing. The high representation of older animals and reduced evidence of food stress in the late 1980's collections suggest that the eagles were preying on more available prey populations (larger?) which may have been declining. The degree of representation of cohorts in other regions and at other times can also be explained in terms of the expected effects of rainfall on recruitment and growth of the population. The sudden increase in representation of cohorts younger than

6 y in the MZNP collection (Fourie 1983) also suggests that this population began increasing in earnest from 1974 on (Figure 100). Regional differences in age structure may reflect regional differences in rainfall. For instance collections of hyrax remains from the KRNP, from Fraserberg, from the central Karoo and from the eastern Cape (all collected in the late 1980's) all show high representation of the 8-9 y old cohorts (Figure 100) which probably correspond to a major rainfall peak in most of the summer rainfall area at the end of 1980 (Lindesay 1984). Collections from Namaqualand representing the same period show distinct under-representation of the 8-10y old cohorts. Namaqualand did not benefit from above average rainfall at the end of 1980 (Lindesay 1984). The Fynbos region is subject to a different, winter rainfall pattern.

While comparisons of the age structure of hyrax taken by black eagles based on tooth eruption and wear are acceptable within similar environments, or for the same environment at different times, comparisons across widely-differing regions such as the Fynbos and the eastern Cape may be criticised on the grounds that hyrax diet and tooth wear is likely to vary between such regions. Some bias may have been introduced by differential tooth wear but it is considered unlikely that this bias would mask the observed, major differences between the samples. Correlation between the age structure of the various samples and rainfall patterns for the respective regions would appear to indicate that the methods are widely applicable.

The age distributions of hyrax captured by black eagles at different times (Figures 100 & 101) supply good evidence for the notion that hyrax populations showed a widespread increase during the late 1970's and a widespread decline in the early 1980's. This is in keeping with many hearsay reports (Chapters 1 & 4). One might expect a long-term synchrony between growth and decline phases of hyrax populations and the nine year wet and nine year dry cycle observed by Tyson (1986: Fig. 1.11) for the summer rainfall areas of southern Africa. In which case, regular cycles of rock hyrax abundance would be generated by regular climatic effects. Climate is not considered to be the cause of cyclicity for small mammals in the far northern hemisphere (see Chapter 12).

The patterns of variation suggest that most of the differences in composition of hyrax taken by black eagles might be explained in terms of differences in the availability of the different prey population components. However, predominance of juvenile hyrax in collections of prey remains appears to be a regular feature of eagles which are thought to be preying on smaller hyrax populations and perhaps suffering from food stress. This was evident for comparisons of the upper and lower escarpment territories, and for comparisons of annual collections in the present study where changes in the composition of hyrax captured did not clearly correspond to changes in the relative availability of the population components. The same trend was evident in comparisons of hyrax captured in 1974 and in the late 1980's. Boshoff *et al.* (1991) ascribed the heavy reliance upon juvenile hyrax age classes by fynbos black eagles to growing prey populations. But again, the Fynbos eagles took the least hyrax in their diet (52%) and showed most evidence of food-stress (30-50% adult crania opened). It appears that black eagle diet varies along a continuum from one extreme where they take a large component of hyrax in their diet made up mostly of males and older age classes, to another extreme where they take a wide variety of alternate prey and the smaller hyrax component is made up mostly of younger age classes and females. Heavy predation of breeding females has been associated with predators exerting a strong limiting influence on their prey (Korpimäki 1985b; Sinclair *et al.* 1990).

A similar variation involving spotted hyenas *Crocuta crocuta* and blue wildebeest *Connochaetes taurinus* was observed by Kruuk (1970, 1972a) in two regions of East Africa: hyenas killed relatively more surplus components (old and weak individuals) from large prey populations in the Serengeti, and relatively more healthy adults from relatively small prey populations in Ngorongoro. It would appear that reliance on surplus elements of mainly one prey population is a luxury enjoyed by predators experiencing a high ratio of prey to predator, such as hyenas inhabiting the Serengeti in Kruuk's studies and the black eagles inhabiting the lower escarpment in the present study. Correlation analyses performed on a database of the prey remains collected at 53 different sites (samples <20 excluded) around the Cape Province revealed that high representation of juvenile hyrax was indeed associated with high prey diversity in diet $(r_p = 0{,}38; p < 0{,}01)$, and with an adult sex ratio that favoured females $(r_p = 0{,}27; p < 0{,}05)$; whilst high representation of adult age classes was associated with a greater proportion of hyrax in the diet $(r_p = 0{,}47; p < 0{,}01)$. There was a slight tendency for the incidence of opening of adult hyrax crania to be high where hyrax proportion in the diet was low, but this could not be demonstrated significantly $(r_p = -0{,}31; p = 0{,}08)$.

As suggested earlier, black eagles may be forced to reduce wastage, to prey more heavily on alternate prey species and on the less profitable younger age classes when their main prey is less available (low prey:predator ratio). These dietary traits may be used to indicate the state of availability of hyrax populations in black eagle territories. Hyrax populations may be naturally sparse due to low density of suitable rock outcrops. This is probably the case for the Cape Fold mountains (Fynbos). Large eagle territories in such terrain are likely to support a greater number of alternate prey which are more likely to be encountered by the wide-ranging, hunting eagles. The Nuweveldberg and the Matobo Hills probably represent the other extreme where high hyrax densities permit black eagles to nest very close together (Chapter 6). The smaller territories maintained by these eagles would support fewer alternate prey and these eagles must subsist predominantly on the large hyrax populations. Consequently these eagles should be more susceptible to fluctuations in their hyrax prey base, and this would appear to be borne out by recent rather dramatic changes in black eagle territories in the Matobo Hills (Gargett 1993 unpubl.). Against these constraints on hyrax populations imposed by the nature of the rocky habitats, variation in rainfall and plant production can lead to major long-term changes in the abundance of hyrax which are reflected in the composition of eagle diet.

Most of the variation in the species composition of black eagle diet and in the age and sex composition of hyrax caught by black eagles must be caused by these major influences. The great variability in the age and sex composition of hyrax taken by black eagles evident in Figure 100 must surely be an indication of the dynamic nature of the structure of rock hyrax populations. But on top of these effects it appears that the eagles can alter the emphasis of their selective predation, most notably by taking more juveniles when conditions get hard. In the case of the black eagle-rock hyrax system in the water-limited karoo environment, droughts and rainfall events probably lead to sudden changes in hyrax vulnerability and consequent predation by eagles, perhaps without significant change in absolute hyrax abundance. One would expect that high representation of naive younger age classes in eagle diet would be characteristic of hyrax populations which are well protected within their habitat and are able to grow in the absence of heavy predation pressure; whereas high representation of the more experienced older age classes in eagle diet would be characteristic of hyrax populations which are in great excess to their carrying capacity and are declining. So the degree to which hyrax populations are in balance with their carrying capacity set by the vegetation within the safe confines of the rocky habitat is also likely to be a major influence on the emphasis of age and sex-specific predation by black eagles.