PREDATOR-PREY INTERACTION

CHAPTER 8

BLACK EAGLE FEEDING HABITS -

1. PREY CAPTURE RATE

INTRODUCTION

To interpret predator-prey interactions, a simple and fundamental requirement is to know how many prey the predators are catching. A variety of methods can be used to assess prey capture rate by eagles. Many researchers have looked at the consumption of prey by hand-fed eagles (e.g. Fevhold & Craighead 1958; Brown & Watson 1964; Love 1979; Collopy 1980, 1986; Gargett 1982a; Stalmaster & Gessaman 1982). Gargett (1982a) made predictions on the number of prey taken by black eagles in the Matobo Hills from food consumption trials involving a hand-reared eagle, and provided useful data on the proportion of hyrax carcasses consumed by the eagles. Eagles are known to abstain from breeding when food is scarce (Chapter 6). So feeding studies such as these can give a useful indication of the extra cost to a resident pair of eagles for raising offspring, and to what extent hunting eagles must increase their prey capture rate during the nesting season in order to ensure successful breeding. However, food consumption rates of captive eagles will usually be lower than those of wild birds, and metabolic predictions can be used to estimate the greater food requirements in the wild (e.g. Sapsford 1984; Nagy 1987). Field studies of prey capture rate by eagles (usually derived from observations of nests or prey on nests) are less frequent (e.g. McGahan 1967; Gargett 1972; Lockhart 1976; Collopy 1980, 1983b, 1986). This is probably due to the difficulties experienced in obtaining sufficient, accurate data on prey capture rate by eagles in the field, especially when they are not breeding. The least biased method of assessing prey capture rate is undoubtedly direct observation of the hunting eagles, but as discussed later (Chapter 9), it is very difficult to obtain adequate sample sizes with this method.

Direct or indirect observations of prey deliveries to nests, potentially afford the most data on prey capture rate by raptors in the field. Such data can be used to investigate how prey capture rate varies: across years; with chick age (e.g. Geer 1981); with pairs and characteristics of their territories; with daily climatic conditions which may favour predator or prey; and with the time of day and activity rhythms. These relationships may provide additional insight to the predator-prey interaction.

In this chapter I combine information from indirect monitoring of eagle nests, from direct observations of hunting eagles, from food consumption trials of hand-fed eagles, and from metabolic predictions in order to assess the number of prey captured by black eagles and the factors that affect this prey capture rate. The findings are contrasted with other similar studies. Comprehensive and precise determination of prey capture rate was essential for assessment of the numeric impact of eagles on hyrax in Chapter 12, and realistic minimum and maximum values for prey capture rate were also needed for modelling purposes.

METHODS

Time-lapse photography

Eleven super-8 mm cine cameras were purchased and modified to take single frames at periodic intervals after Temple (1972). Six of these cameras (4x 6v Canon 814E; 1x9v Chinon; 1x6v Minolta) had an electronic single-frame facility which greatly facilitated the modification. The cameras which consistently gave reliable results were the Canon 814E models. These cameras are also equipped with powerful zoom lenses. The single frame facility on the remaining five cameras (1x3v Canon 310XL; 1x9v Eumig Viennette 8; 1x6v Chinon 38 Pacific; 1x6v Yashika; 1x6v Sankyo) was a manual cable release and solenoids were manufactured to operate these. Agfa 100 super-8 cine film was used throughout and developed in Germany. Each film was 50 feet (15,2m) long with a normal running time of five min. Approximately 3600 frames were available on each film.

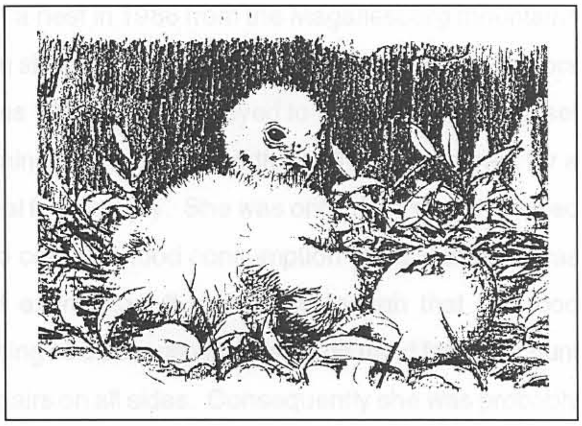
The time-lapse circuit was designed by K. Musgrave (Diginet Systems, Pretoria), and is shown diagrammatically in Appendix 5. A photo-resistor was used to switch the unit off at night. The interval between frames could be adjusted using a variable resistor. A linear regression was obtained between time interval and resistance (Appendix 5). The system was tested at a time interval of two min for 10d at a nest in 1986. But when it was observed that most prey items could remain on the nest for a few days, I decided to increase the time interval to just over 3,5 min and increase the battery amp hours to eleven. This meant that films could be changed every 17 d instead of every 10 d.

Weather-proof housing for each camera was manufactured from 5l oil cans. The top of the cans (front) was replaced with a permanently sealed piece of transparent perspex into which I cut an aperture for the camera lens and protected this with a lens hood. It was important that the photo-resistor should press against the transparent perspex in the front and not be obscured from the light. The bottom of the cans (back) was replaced with a removable piece of perspex which I sealed off with masking tape to prevent light entering through the viewfinder. This back section could be tightened against a rubber seal with wing nuts. Cameras and circuits were positioned and orientated within these containers using foam rubber and stones, and connected by wiring to motorcycle batteries outside. The electronic circuit was bound in insulation tape to prevent short-circuiting against the metal casing. I surrounded the metal cans with 14 mm softboard to insulate them from the heat of direct sunlight, and hoped that this would make the boxes less obvious to the eagles.

This system proved sufficiently weather-proof, even through heavy rain storms for the cameras with the electronic single frame facility. However, the solenoids powering the cable releases on the other cameras used far more power and were adversely affected by the position of the box (they only functioned efficiently if vertical), and by moisture entering past the lens. This system proved unreliable and mostly unsuccessful and I abandoned the use of these cameras after 1987.

Units were attached to rocks or bushes overlooking the eagle nests at distances varying from 2 - 30m. The powerful zoom lenses of the Canon 814E cameras proved very useful, but focusing through the viewfinder did not prove accurate enough especially for wide aperture conditions, and I resorted to actual measurement of the distance from the nest to the lens. The lens could then be taped firmly at the correct focal distance and zoom setting for the duration of the nesting season. Aperture was automatically controlled by the cameras. The camera box could usually be attached pointing directly at the nest by wiring it firmly to masonry nails embedded in crevices and to large rocks which I placed around the housing. The anchoring had to be very secure to withstand buffeting by winds of up to 150kph, and re-arrangements deemed necessary by the local troops of baboons. A system of using mirrors on extendable tripod legs to peer over cliff edges did not prove successful because of the high winds. Suitable viewpoints for the cameras were available at nine of the ten lower escarpment nest sites, but time-lapse photography was not feasible at upper escarpment nests because of the large cliffs (80-120m) and overhangs.

Time spent checking the cameras and changing films was minimized by synchronizing the different cameras to the same renewal dates every 17 d. While replacing film and battery I recorded age of the chick, any prey on the nest and exact time of disconnection and reconnection. The camera was run at 16 frames/second mode for a short while before removing each film so that the last frames were not over-exposed. Thorough checks of all working components were necessary at each visit.



Where possible, time-lapse photography was initiated during incubation and terminated after fledging. This provided for accurate timings of hatching and fledging, but it soon became evident that the cameras only gave a comprehensive picture of feeding habits while there was a chick in the nest. Besides diet and prey capture rate, the films could also be analysed for factors affecting the timing of prey deliveries, for nest attendancy by the adults and for development of behaviour in the chick. They also provided very useful data on eagle mortalities.

Films were analysed on an 8mm viewer to provide summarized information by film; by day; by site; and by season. Detailed, frame by frame analyses for coverages of certain nestling periods were computerized by C. Wessels. For quantification of prey deliveries, prey items were identified to species if possible, and then size of the food item was estimated by two parameters: the proportion of adult mass that the individual was thought to represent (when intact); and the uneaten proportion of that individual that was delivered. Despite the tiny format of super-8 film, the images were clear enough to derive a large amount of this information. Timing of events were calculated either by running the film through a projector and making measurements with a stopwatch, or by comparing frame numbers for the events with total frames from dawn to dusk for the respective days. Cameras commenced filming approximately 35 min before sunrise and switched off about 35 min after sunset, depending on situation and weather. Exact timings of sunrise and sunset for each day of the year were obtained for the Beaufort West weather station.

The efficiency of this system at monitoring events at eagle nests was tested by conducting direct observations of nests (135 h) or of the adult pair of eagles (61 h) concurrent with time-lapse photography, and then comparing results. Three nesting pairs were observed for a total of 196h spanning 21 d while the cameras were running (see p. 187).

Direct observations

The hunting behaviour of four resident pairs of black eagles was directly observed for eight five-day sessions during the study period. The methodology of these observations was described in detail in Chapter 6. Several days were also spent watching the nests of two other pairs during the nestling stage. Although hunting eagles were not in sight all of the time and only a portion of kills were actually witnessed, unseen kills could usually be inferred when eagles appeared with obvious, bulging crops indicating that they had just fed. This must be the least biased method for field determination of prey capture rate, and provided the only field indication of prey capture rate by black eagles outside of the nesting season.

Food requirements of a hand-fed eagle

Precise data on the food requirements of a black eagle were obtained by monitoring the food consumption of a hand-raised female eagle, Samburu, who was kept in captivity and under semi-natural conditions from 5d old until she attained adult plumage at three years. Samburu was taken from a nest in 1986 from the Magaliesberg mountains near Pretoria where two chicks had hatched and were engaged in siblicide (Gargett 1990). She was raised indoors using a black eagle puppet for feeding to avoid 'imprinting' (Jones 1981), and conveyed to the KRNP at the onset of fieldwork in 1986. After fledging she was mostly kept unrestrained, 'at hack' (Woodford 1970), in the park for a period of two years during which she was still reliant on an artificial food supply. She was only observed or inferred to kill for herself on a couple of occasions. So it was possible to compare food consumption while Samburu was aviary-bound with food consumption while she flew free and exercised. It is unlikely though that her food requirements would have attained those of a wild, territorial breeding bird because there was no need for her to hunt and her movements were restricted by the presence of resident pairs on all sides. Consequently she was probably inactive for a much greater portion of her time than wild eagles normally are. Samburu was very uninhibited towards humans and her freedom was temporarily curtailed after two years when she developed a habit for chasing tourists around the park. She was eventually released in the Drakensberg in 1990.

Through the nestling stage, Samburu was fed on rodents (laboratory rats and gerbils) which were initially skinned and put through a mincer. Fur and skin were introduced to the diet at age 27d to induce pellet formation and clear the crop. From age 36d Samburu was encouraged to feed herself from whole laboratory rats. This is the age at which wild eaglets begin to feed themselves (Ellis 1979; Collopy 1980, 1984; Gargett 1990). Four to five meals were provided daily to begin with and these were steadily decreased to two meals per day towards the end of the nestling period, and to one meal per day or less thereafter. Food containers were weighed before and after each meal to assess the amount of food consumed. All pellets egested by Samburu were collected and weighed. Samburu was weighed daily before meals, and a detailed diary was kept of the ontogeny of behaviours, feathering etc.. After the nestling stage, she was fed mainly on sheep heart (with and without fat attached) and to a lesser extent on day-old chicks and rock hyrax. The food consumption of a wild-caught adult black eagle was also measured over 38d while this bird was held captive before translocation.

The energetic cost of raising Samburu was assessed through the nestling period. Samples of cleaned rat, gerbil, rat skin and pellets were prepared and oven-dried at 65^{0}C for 24h to assess dry matter concentration. They were then combusted in a bomb calorimeter to determine energy content. This enabled assessment of the amount of energy ingested (and regurgitated as pellets) throughout the nestling stage. To determine assimilation efficiency, energy excreted in the faeces was assessed by collecting all excreta during three feeding trials conducted at ages 17d (for 3d), 21d (for 3d) and 48d (for 2d). Excreta were collected on pre-weighed silver foil surrounding the artificial nest. After each trial the entire foil was oven-dried, weighed and samples of excreta prepared for bomb calorimetry. The weight-gain of Samburu was also determined for each trial. Oxygen consumption of Samburu at rest was determined in a metabolic chamber during three experiments at ages 18d, 37d and 47d, but the equipment proved unreliable.

Samburu

Metabolic predictions

The energy/food needs of animals are known to be related to body mass in a predictable fashion (Kleiber 1961, 1975; Kirkwood 1981; Nagy 1987). Previously, predictions on feeding rate were based on equations which describe basal or standard metabolic rate with increments for the energy cost of additional activities. A growing body of data on water turnover of wild animals now enables researchers to base their predictions on equations which actually describe the field metabolic rate of different groups of animals. This has often been shown to be greater than expected and sometimes scales to body mass in a different fashion from basal metabolic rate (Nagy 1987). As a fourth method of determining the prey capture rate of black eagles, I use various metabolic formulae including Nagy's (1987) equation for all birds (eqn. no. 30) to predict daily energy requirements. Mean mass for black eagles was determined from a collection of museum and my own records. The number of hyrax needed to fulfil these requirements were calculated using the assimilation efficiency revealed by the feeding trials, dietary information (Chapters 9 & 10), and morphological attributes of hyrax used for similar purposes in Chapter 7, and given by Gargett (1982a).

RESULTS & DISCUSSION

A test of the effectiveness of monitoring nests by time-lapse photography

During the 196 h of direct observation of nesting pairs while time-lapse cameras were monitoring their behaviour at the nest, observers witnessed the delivery of nine prey items. These comprised five medium-sized items (three rock hyrax, one red rock rabbit and one bird), and four small items (three juvenile rock hyrax and one juvenile viverrid/ small rodent). All time-lapse films were analysed together. An assistant double-checked my findings for 67% of the period in question and both our counts tallied. These analyses were conducted without knowledge or expectation of the prey deliveries by checking against the direct observations, so no extra effort was spent searching for prey deliveries on these sections of films. Deliveries of all five medium-sized prey items during the monitoring period were noticed on analysing the time-lapse films. However, only one of the four small prey items delivered (a juvenile rock hyrax) was noticed. The deliveries of two juvenile rock hyrax and one juvenile viverrid/small rodent were missed.

The deliveries of juvenile rock hyrax were all inferred from observations made at 3km distance from a 'late' nest in November 1987. Juvenile rock hyrax weigh 200g at birth (Millar 1971). Some errors could have occurred if the adult eagles had consumed the prey before arriving at the nest for instance. The delivery of the juvenile viverrid/small rodent was however witnessed at close range, and the observer recorded that the prey was consumed in under five minutes, and then the eagles went on to consume part of a hyrax on the nest. In this case, the prey might only have been on the nest for a single frame on the time-lapse film, and then it might easily have been obscured by the eagles. During analyses of the films, it was often necessary to repeatedly run several frames through the viewer to obtain a clear view of the prey that had been delivered. Eighty five percent of all deliveries could be identified to species (Chapter 9). Most rock hyrax and red rock rabbit prey were still visible on the nest a day after they had been delivered. The time-lapse films appeared to yield accurate estimates of the timing of nest events. The calculated timing of delivery of three prey items showed an average error of 8,3 min (s.d.=4,2 min).

A time interval of just over 3,5 min between frames is evidently frequent enough to monitor the delivery of medium and large size prey, but not frequent enough to monitor the delivery of most small prey items. In the case of juvenile rock hyrax, this should not lead to great errors because nests were monitored during the nestling period which usually spanned August, September, October and seldom extended more than a few days into November. Juvenile rock hyrax were never observed before October 28 in any year, and the majority should have been born around the median birth date estimated to be November 12 (Chapter 4).

Despite some bias against small prey items which may lead to slight under-estimation of overall prey capture rate during nesting, time-lapse photography is considered to give a very reliable indication of the rate at which medium and large-sized prey are captured by the eagles during nesting, and these prey are known to make up the bulk of black eagle food (Chapter 10). It is considered very unlikely that any medium or large-sized prey would be captured and consumed by the adult eagles without some part of it being conveyed to the nest and appearing on the time-lapse films. Time-lapse photography at nests was the only practical method for obtaining a large sample of data on prey capture rate in the field.

Observations on field predation rate and biomass captured

In total, nine black eagle nests in the KRNP were monitored by time-lapse cameras for 701 nest days between 1986 and 1989 whilst the eagles were provisioning chicks with food (prey deliveries to nests only commenced when the eaglets were hatching). An annual breakdown of the number of prey deliveries is given in Table 20. These results indicated that during the nesting season, black eagles delivered 0,55 prey per day (plus some very small items which would have been missed by the cameras), so prey deliveries at nests can be expected slightly more frequently than once every other day.

TABLE 20

ANNUAL PREY CAPTURE RATES BY BLACK EAGLES INDICATED BY TIME-LAPSE PHOTOGRAPHY AT NESTS

For each year, the number of nests monitored, number of days filming, number of prey items delivered and the proportion of these items comprised by rock hyrax is given.

YEAR	NESTS	DAYS	ITEMS	%HYRAX	kills/day	days/kill
1986	1	9.50	4	-	0.42	2.38
1987	6	245.20	121	73	0.49	2.03
1988	5	208.00	130	75	0.63	1.60
1989	5	238.60	134	57	0.56	1.78
TOTAL	9	701.30	389	68	0.55	1.80

The number of kills observed or inferred while eagle pairs were under direct observation are given in Table 21, with a breakdown of each observation period. Overall prey capture rate for 48d of observing breeding and non-breeding eagles in their territories and at their nests was estimated to be 0,51 kills per day. The nest observations may give a slight underestimate of prey capture rate if small prey was captured and consumed away from the nest, but these make up a small portion of the total observations. Direct observations provided the only indication of how prey

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TABLE 21

PREY CAPTURE RATES BY BLACK EAGLES INDICATED BY DIRECT OBSERVATION

Where the number of kills recorded for an observation stint was uncertain, a middle figure is used to calculate kills/day (e.g. 2,5 is used for 2-3 kills). "OBS" indicates whether the eagles or their nest was the target of observations.

PAIR	DATE	OBS	ACTIVITY	DAYS	KILLS	kills/day
KK	Jun-87	eagles	non-breeding	5	1 to 2	0.3
KK	Aug-88	eagles	incubating	5	2 to 3	0.5
PB	May-89	eagles	non-breeding	5	2	0.4
PB	Jul-89	eagles	incubating	5	2 to 3	0.5
subtotal without chicks				20	8.5	0.425
PB	Sep-88	eagles	chick 25d	5	3	0.6
BR	Nov-87	eagles	chick 76d	5	4 to 5	0.9
GD	Oct-88	nest	chick 77d	4	2	0.5
SL	Sep-89	nest	chick 25d	4	2	0.5
LH	Nov-89	eagles	fledgling 107d	5	2 to 3	0.5
PB	Jan-90	eagles	fledgling 145d	5	2	0.4
subtotal with chicks				28	16	0.571
OVERALL				**48**	**24.5**	**0.51**

capture rate varied in and out of the nesting season. Prey capture rate during the nesting season as determined by direct observation (0,57 prey d^{-1}) was only 4% higher than that determined by time-lapse photography. Black eagles provisioning chicks captured an additional 0,15 prey per day when compared with those not provisioning chicks (Table 21). This trend was not statistically significant ($t=-1,46$; $p=0,09$) but sample size was only four for the non-breeding observation periods. It is expected that breeding eagles would actually catch more prey in order to meet the extra food requirements of nestlings and fledglings, and this is important when comparing values of prey capture rate with those of other studies (nearly all of which were derived during the nesting period). The nestling and post-fledging periods of black eagles span 6,6 months (Gargett 1980, 1990), much longer than the comparable period for golden eagles (4 - 5 months, Collopy 1980, 1986). At 0,571 prey d^{-1} during this period, and 0,425 prey d^{-1} for the rest of the year, a breeding pair of black eagles would catch 185 prey per year. Non-breeding pairs probably catch only 155 prey per year. If 46% of pairs raise chicks (Chapter 6), then overall prey capture rate in an eagle territory may be calculated as 169 prey $pr^{-1}y^{-1}$. At a ratio of one non-breeding bird per fifteen territorial pairs (0,07 non-breeding vagrants per territory, see Chapter 6), and assuming that the prey capture rate by non-breeding individuals is half the prey capture rate of non-breeding pairs (0,21 prey d^{-1}), it is calculated that this component of the eagle population may account for an additional five prey per territory per annum. This would bring the total, overall prey capture rate by black eagles during the present study to 174 prey per territory per annum.

The mean mass of all prey items monitored by time-lapse photography was estimated to be 2438g. The mean mass of prey items collected beneath black eagle nests at the end of each breeding season was estimated to be 2565g, and this is a more considered figure based on a much larger sample (n=3586) (see Chapter 9). Using the latter estimate and the inference on prey capture rate from the time-lapse photography it is calculated that the biomass of prey captured by a nesting pair of eagles was $1423gd^{-1}$. Direct observations of the eagles suggested that this varied from $1090gd^{-1}$ when not provisioning chicks, to $1465gd^{-1}$ when provisioning. It can be inferred that breeding pairs of black eagles catch approximately 473kg of prey each year and that non-breeding pairs catch 398kg. Overall prey biomass captured by all pairs should approach 433kg per territory per annum, with an additional 13kg of prey captured by non-breeding vagrants.

From visual estimates of the proportion of each prey item that was delivered to nests, it was calculated that 24,8% of the prey was consumed prior to delivery. Thus the 1423g of prey captured per day was represented by 1070g of prey delivered to nests. Upon delivery to nests, prey items had an estimated mean mass of 1689g and ranged from 179g for small, unidentified prey to 3570g for an entire klipspringer lamb that was estimated to be 30% of adult mass. This record implies that black eagles are able to convey prey which is almost the same mass as themselves to their nests. Normally, the portion consumed prior to delivery was greater for larger prey captured ($r=0,52$; $p<0,01$), and this would have facilitated transport. Only 15% was consumed on average from small mongooses prior to delivery, in comparison with 22% from hyrax, 30% from scrub hares and 65% from domestic lambs. The adult birds were probably responsible for all of the prey consumption which occurred before the prey was delivered to nests. But this cannot be taken as representative of the food consumption by the adults, as has been done in other studies, because adults were also observed to feed on the nest and would regularly remove prey to feed on it and then return it to the nest (in the analyses of the time-lapse films, care was taken not to double-count these particular items).

TABLE 22
PRESENT FINDINGS ON THE PREY CAPTURE RATE BY KAROO BLACK EAGLES COMPARED WITH OTHER SIMILAR STUDIES

Prey biomass is expressed in terms of the amount captured, and the amount actually delivered to nests. Scientific names: crowned eagle *Stephanoaetus coronatus*; harpy eagle *Harpia harpyja*

SPECIES	SOURCE	KILLS/DAY	MEAN PREY MASS (g)	BIOMASS CAUGHT (g/d)	BIOMASS DELIVERED (g/d)
golden eagle	Collopy (1980, 1984)	1.80	1182	1814	1417
black eagle	Gargett (1972, 1980, 1990)	1.40	1546	2164	
golden eagle	Lockhart (1976)	0.94	947	1570	885
golden eagle	McGahan (1967)			1470	
various large	Brown (1955)	0.87			
crowned eagle	Brown (1966)	0.60			
black eagle	present study	0.57	2565	1465	1102
black eagle	Jenkins (1984)	0.40			
harpy eagle	Rettig (1978)	0.29			

Numbers and biomass of prey captured and delivered to nests in the present study are compared with corresponding values for other studies and other eagles in Table 22. With the exception of Jenkins' (1984) study of black eagle foraging behaviour in the Magaliesberg, it is evident that the rate of prey capture observed in the present study was far lower than that in most other investigations of predation by *Aquila* eagles, notably Gargett's (1990) study of black eagles in the Matobo Hills. Gargett considered that an overall prey capture rate of 365 hyrax per year was applicable for breeding pairs and 292 hyrax per year for non-breeding pairs. Besides *Procavia capensis*, the Matobo Hills is home to a second smaller species of rock hyrax, *Heterohyrax brucei*. Gargett estimated a mean hyrax mass of 1546g, which is smaller than mean mass recorded for hyrax in the present study (2040g), but adult hyrax attained even greater mass in the Matobo Hills (max 4,5kg) than in the KRNP (max 3,7kg), so one cannot necessarily conclude that the greater prey capture rate of hyrax by black eagles in the Matobo was the result of smaller prey size. Gargett's observations on prey capture rate in the Matobo were conducted in 1970 when a growing hyrax population was presumed to be especially vulnerable during a dry year (Chapter 12: Figs. 107 & 131). So it seems more likely that the difference resulted from greater prey availability in the Matobo study, and Gargett's study conveniently yields an indication of maximum potential black eagle prey capture rate. Estimates of prey capture rate by the Matobo black eagles might also be slightly exaggerated if observation periods tended to coincide with peak hunting periods of those eagles (afternoon). The low prey capture rate recorded by Jenkins (1984) is surprising since high levels of hunting success (per strike) of these birds was indicative of high prey availability (see Chapter 6). But these observations (300h) were not necessarily confined to the nesting season.

With the exception of the Matobo black eagles, higher prey capture rates observed for *Aquila* eagles in other studies (Table 22) can mostly be explained in terms of smaller prey size. All the golden eagle studies indicated a much higher prey capture rate, but on account of the small prey captured by golden eagles (despite the fact that golden eagles hold most of the records for largest prey taken by eagles - see Chapter 11), the calculations of prey biomass captured and delivered to nests were much more comparable to those in the present study (Table 22). Golden eagles raise up to three chicks in a much shorter nestling period of 70d to attain a larger body mass (Collopy 1980, 1986), so one would actually expect their family food requirements to be much greater than those of black eagles. Although raptors should be able to increase foraging effort and thus success as needs be, many studies have shown that prey capture rate by raptors does not necessarily correspond to family food requirements and is probably more limited by prevailing foraging success (Tinbergen 1940; Snyder & Snyder 1973; Newton 1978; Collopy 1980, 1984).

The values in Table 22 mostly relate to the brood-rearing phase. There has been some indication that prey capture rate drops during the post-fledging phase of black eagles (Gargett 1972), crowned eagles (Brown 1966) and golden eagles (Collopy 1980). But prey capture rate is difficult to assess when the eagles are not nest-site bound because kills are more likely to be unseen or undetected. Daily food requirements of nestlings and fledglings are not very different (Collopy 1980), so for the purposes of calculating annual prey capture rate in this study and for the sake of simplicity I have assumed that prey capture rate during the post-fledging period is the same as that during the nestling period, and that prey capture rate during incubation is the same as that during the non-breeding period.

Food consumption and energetic considerations

As a nestling, Samburu was larger than most. At 10 weeks of age the eaglet weighed 3641g, as compared to 3350g for an eaglet raised by Gargett, and a mean value of 3402g for eleven wild 10-week old eaglets (Gargett 1982a). However, Samburu attained a mean post-fledging mass of 3775g which falls below the mean weight of 3969g for six female eagles from South Africa (A.C. Kemp *in litt.*; pers. rec.). The possibility exists that rapid growth of Samburu may have been encouraged by a rich food supply in captivity, and this should be borne in mind in the following interpretation.

During the nestling phase (6-94d), Samburu was fed predominantly on laboratory rats (89% of food) with the remainder being made up of smaller rodents. Three feeding experiments (Table 23) demonstrated that she achieved a very high and remarkably constant level of assimilation efficiency (87%) on this diet. Dry matter concentration and calorific content (as determined by bomb calorimetry) of food stuffs, pellets and excreta are presented in Table 24. Laboratory rats are rich in energy and yield approximately 8KJ for each gram wet weight (Bird & Ho 1976; the present study; see Tables 24 & 25). Most raptors assimilate only 75% of the energy that they ingest (Kirkwood 1981). However, only small amounts of fur were ingested in one of the trials and no pellets were regurgitated during the experiments. Stalmaster & Gessaman (1982) noted that captive bald eagles achieved high assimilation efficiency (85%) on an energy-rich duck diet, but that their assimilation efficiencies on a salmon or rabbit diet were normal (75%). Golden eagle nestlings hand-raised by Collopy (1980, 1986) had a standard assimilation efficiency of 75% on a diet of predominantly lagomorphs. There is no evidence yet which suggests that black eagles would be more or less efficient than this on a hyrax diet.

TABLE 23
RESULTS OF THREE FEEDING TRIALS ON A HAND-FED NESTLING BLACK EAGLE

(see text for details)

	FEEDING TRIALS		
Expmt. No.	1	2	3
Age at start (d)	17	21	48
Duration of trial (d)	3	3	2
Weight at start (g)	1333	1617	3420
Mass gain during trial (g)	218	175	50
Dry matter consumption (g/d)	71,3	68,7	95,0
Dry matter regurgitated (g/d)	0	0	0
Dry matter excreted (g/d)	20,1	20,7	26,4
Energy consumed (KJ/d)	1654	1594	2204
Energy excreted (KJ/d)	207	213	272
Energy metabolised (KJ/d)	1447	1381	1932
Assimilation efficiency (%)	87,5	86,6	87,7

TABLE 24
DRY MATTER CONCENTRATION AND ENERGY CONTENT OF FOODSTUFFS USED AND EXCRETA PRODUCED IN THE FEEDING TRIALS OF A HAND-FED NESTLING BLACK EAGLE

(energy content expressed as KJ/g dry weight)

	SAMPLE SIZE	WATER CONTENT (%)	DRY MATTER CONCENTRATION (%)	MEAN ENERGY CONTENT (KJ/g)
Skinned rat	10	68,7	31,3	23,2
Entire rat	10	62,2	37,8	23,4
Rat skin	5	49,2	50,8	26,8
Gerbil	10	67,2	32,8	25,1
Pellets	5	73,2	26,8	22,0
Excreta	10	-	-	10,3

From six days old until fledging (at 94 d old), Samburu consumed 6714g (dry matter) of food with an energy content of 165106KJ. The dry weight of pellets regurgitated during this entire period was 116g with an energy content of 2561KJ. The dry weight of excreta for the same period was estimated to be 2084g with an energy content of 21464KJ. The assimilation efficiency over the nestling period was considered to be 85% after energy regurgitated as pellets had been taken into account.

Changes in the mass and the daily food consumption of Samburu are shown for the entire 'dependent' period in Figure 64. This encompasses ages 0-94d as a nestling and ages 95-200d as a post-fledging 'dependent' (after Gargett 1980 & 1990 for wild eaglets). Maximum daily food consumption as a nestling occurred in week five near the end of a very rapid growth phase and shortly before maximum mass of 3500 - 4000g was attained. This agrees with the findings of Collopy (1980, 1986) and others that eaglet food needs are greatest when they are 60-80% of adult mass. After this period, food consumption dropped until the post-fledging period when it became very erratic owing to the eaglet's ability to gorge and then fast. This ability is very adaptive for wild eaglets which sometimes must survive up to 9d without food (see later). Very low food consumption rates in weeks 20 and 27-29 were due to Samburu's resistance to a change in diet. Peaks in prey consumption were also partly due to low energy food.

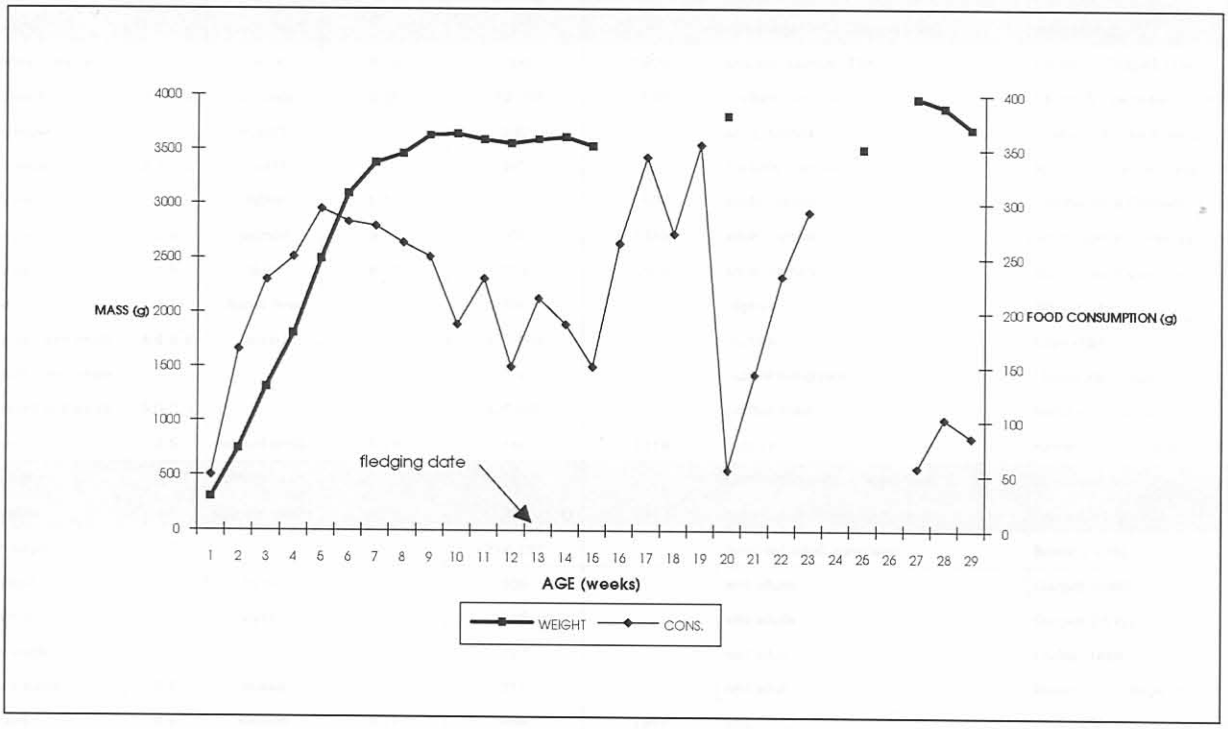


Figure 64. Mass gain and food consumption (wet weight) of a hand-fed juvenile black eagle during the 'dependent' period.

Other authors consider that the overall daily food requirements of nestling and fully-grown eagles are not dissimilar (McGahan 1967; Lockhart 1976; & Collopy 1980). Overall daily food consumption (wet weight) by Samburu was 218gd^{-1} during the nestling period on a diet of rodents, and it declined slightly to 197gd^{-1} during the post-fledging dependent period when she was fed predominantly on sheep heart. Values of daily food and energy consumption by black eagles in the present study are compared with those of other studies on large eagles in Table 25. The rates of food and energy consumption shown by Samburu during the post-fledging period were exactly matched by a wild-caught adult male black eagle (mass 3,7kg) which was kept in captivity for 38d. Despite increasing amounts of exercise and declining temperatures, the food consumption of Samburu dropped slightly in the 107d following the post-fledging dependent period when she was fed 80% sheep heart (Table 25).

TABLE 25
DAILY FOOD AND ENERGY CONSUMPTION OF EAGLES ON VARIOUS DIETS IN THIS AND OTHER STUDIES

(see text for details)

EAGLE SPECIES	EAGLE MASS (kg)	DIET	FOOD ENERGY CONTENT (KJ/g wet)	DAILY FOOD CONSUMPTION (g/d wet)	DAILY ENERGY CONSUMPTION (KJ/d)	NOTES	SOURCE
Black eagle	0,1-3,7	laboratory rats	7,69	218	1676	hand-fed nestling (94d)	present study
Black eagle	0,1-3,8	hyrax		320		hand-fed nestling (93d)	Gargett (1982a)
Golden eagle	0,1-4	lagomorphs	5,13	395	2026	nestlings, captive (70d)	Collopy (1980)
Golden eagle	0,1-4	lagomorphs	5,13	329	1688	nestlings, wild (70d)	Collopy (1980)
Black eagle	3,8	sheep heart		197		hand-fed post-fledging, exercised (106d)	present study
Black eagle	4,2	hyrax		328		hand-fed post-fledging, captive (105d)	Gargett (1982a)
Black eagle	3,8	hyrax		260		hand-fed subadult, captive (34d)	present study
Black eagle	3,7	sheep heart		197		wild-caught adult, captive (38d)	present study
Wedge-tailed eagle	3,7	rabbit	5,13	356	1826	juvenile, captive (48d)	Brooker & Ridpath (1980)
Golden eagle	3,3-5,4	ungulate	6,20	188-308	1538	4 adults, captive	Fevold & Craighead (1958)
Golden eagle		meat?		340		adult, captive	Fowler in Brown & Watson (1964)
Golden eagle	3,7-5,2	meat?		207		2 adults, captive	Wood in Brown & Watson (1964)
Bald eagle	4,0	rabbit	5,13	299	1534	adult, captive	Stalmaster & Gessaman (1982)
Bald eagle	3,9	salmon	3,77	359	1353	adult, captive	Stalmaster & Gessaman (1982)
Bald eagle	3,9	duck	8,21	254	2085	adult, captive	Stalmaster & Gessaman (1982)
Bald eagle	4,5	fish & liver		336		captive	Stewart (1970)
White-tailed sea eagle	4,8-6,9	mixed		409-618		captive	Love (1979)
White-tailed sea eagle				500		captive full-grown	Uttendorfer (1939)
White-tailed sea eagle	5,0-5,3			400-550		captive male	Barth in Willgohs (1961)
Bateleur	2,5	day-old chicks	6,23	180	1116	captive	Kirkwood & Thompson (1983)
Black eagle	3,8	sheep heart		183		hand-fed immature, exercised	present study
Black eagle	3,8	day-old chicks	6,23	230	1433	hand-fed immature, exercised	present study
Golden eagle	3,7			214-253		hand-fed adult, exercised	Brown (1976)
Black eagle		hyrax		300		wild adults	Gargett (1980)
Black eagle		hyrax		385		wild adults	Gargett (1972)
Golden eagle				227		wild adult	Lockie (1964)
Crowned eagle	3,5	mixed		210		wild adult	Brown (1970, page 217)
Bald eagle	4,5	salmon	3,77	489	1844	wild	Stalmaster & Gessaman (1984)
White-tailed sea eagle		mixed		625		wild adults and nestlings (8d)	Willgohs (1961)

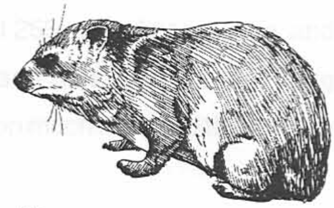
In fact the food consumption rate of Samburu showed greater variation with changes in diet than with changes in temperatures or amount of exercise. It increased by about 15% on a diet of day-old chicks, and by 20 - 30% on a diet of hyrax (Table 25). Food was always supplied liberally in accordance with the appetite of the bird. Unfortunately, weight changes were not determined for all these periods. Stalmaster & Gessaman (1982) also found that the food consumption of captive bald eagles differed greatly on three diets (Table 25). Raptors are expected to ingest greater quantities of energy-deficient food (Kirkwood 1981), and the highest values of daily food consumption were for the large *Haliaeetus* eagles feeding on fish, which have a high water content (Table 25). If the food consumption values in Table 25 are averaged for the large *Aquila* eagles (excluding estimates for wild birds) then it appears that these birds need about 270g of food per day (s.d.=69) for maintenance. As discussed, this amount will depend on the energy content of the food.

Food consumption rates by black eagles in the present study fall below this level, whereas those of black eagles studied by Gargett (1982a) fall above it. This suggests that the diets used in this study were significantly more rich in energy than the hyrax diet fed to the eagles in Gargett's (1982a) study. The total food consumption by Samburu during the dependent period (41,4kg) was 34% lower than the total food consumption by the eaglet raised by Gargett (1982a) over the same period (63,1kg), despite the fact that Samburu appeared to grow faster.

When values of food consumption in Table 25 are converted to energy consumption according to diet, the variation between studies and eagles is much reduced. The average energy consumption of all studies involving large eagles which were hand-fed indicates that such birds need just under 1700KJ per day for maintenance. The standard deviation on this mean (254) is equivalent to 15% of the mean value, whereas the standard deviation on the findings of daily food consumption was equivalent to 26% of the mean daily food consumption. For the two feeding trials in the present study where the energy content of the feed was known, values of daily energy consumed by Samburu were slightly lower than the mean value ($1684KJd^{-1}$). If it is assumed that the black eagles in Gargett's (1982a) study needed 1684KJ per day, then the rate of food consumption on a hyrax diet (@ $320gd^{-1}$) suggests that hyrax would have to contain about $5{,}3KJg^{-1}$ wet weight, in order to meet this requirement. Hyrax are probably only slightly richer in energy than lagomorphs. Daily consumption of hyrax by Samburu was lower than this (Table 25) but this feeding trial was relatively short (34d) and Samburu may have lost weight over this period. However, greater rates of consumption of hyrax by Samburu than of day-old chicks suggest that the energy content of hyrax is less than $6{,}2KJg^{-1}$ wet weight. Feeding trials of black eagles on a hyrax diet still need to be done, in conjunction with calorimetry.

During the 34d period when Samburu's diet consisted mostly (93%) of hyrax, a total of ten small (mean mass=1086g; range 715 - 1274g) hyrax were presented to Samburu in an aviary at not less than two day intervals. Hyrax remains were collected at the end of each feeding day and weighed to assess wastage and leftovers. Samburu consumed an average of 699g from each carcass in the day (range 415 - 817g), and left approximately 42% of the carcasses by mass. The maximum amount consumed from a carcass by Samburu was not much lower than that by martial eagles which are known to consume up to 925g (Brown 1976). Crowned eagles *Stephanoaetus coronatus* are reportedly able to consume up to 1100g and golden eagles up to 1500g (Brown 1976). These records are testament to the ability of eagles to gorge themselves on large prey. Brown & Watson (1964) considered that carcass wastage by golden eagles varied between 20% and 50% depending on the size of the prey. Gargett (1982a) simulated that black eagles waste 31-37% of small hyrax, 38-49% of medium-sized hyrax, and 35-46% of large hyrax. Grobler (1981) showed that caracals waste 45% of hyrax carcasses. A wastage factor of 40% of hyrax carcasses by black eagles would appear appropriate from all these studies. This would mean that in order to achieve a consumption rate of 300g of hyrax per day, a black eagle would need to achieve an overall catch rate of about 500g of hyrax per day, or one average-sized hyrax roughly every four days.

The food consumption rates by hand-fed eagles in Table 25 cannot give a direct indication of prey capture rate in the field. Wild eagles are subject to greater energy demands than captives. Also, it is not always possible for wild eagles to catch prey at convenient regular intervals, although the effects of irregular prey capture may be buffered somewhat by the ability of eagles to gorge and lay down fat deposits. But as measures of the food and energy needed by large eagles for maintenance the values in Table 25 can, however, be used to indicate a minimum prey capture rate which would at least maintain wild eagles in their territory if they were relatively inactive.



The amount of hyrax needed daily by black eagles in the feeding studies varied between about 260 - 320gd^{-1}. The figure of 300gd^{-1} used by Gargett (1980) for food consumption by adult black eagles seems a fair approximation of food requirements on a hyrax diet, at least for maintenance (if hyrax have a food energy content of 5,5KJg^{-1}, this rate of food consumption would provide 1650KJ per day). To achieve this daily rate of food consumption a pair of non-breeding eagles would need to consume a minimum of 219kg of hyrax per annum. To do this the pair would need to catch a minimum of 365kg per annum. At a mean prey mass of 2565g, this would be fulfilled by a minimum prey capture rate of 142 prey per annum or 0,389 prey per day. To fulfill the additional needs of a dependent juvenile present in a breeding territory for nearly seven months in the year, the pair would need to catch and supply at least an extra 100kg of hyrax in those 200 odd days (this is based on a food consumption rate of 300gd^{-1} for the juvenile). This would be fulfilled by another 39 prey of mean mass 2565g, which would necessitate an increase of the prey capture rate by 0,195 prey per day to 0,584 prey per day during the breeding season. Breeding pairs would need to catch 465kg prey per annum in order to consume 279kg. The estimate of prey biomass consumed by breeding pairs, based on direct observations of prey capture rate, was 284kg. The closeness of this value to the prediction of minimum consumption rate indicates that black eagles during the study period were operating very close to, and even below their minimum required rates of predation, and that the total energy demands of wild adult eagles cannot be much greater than the estimates of food needed for maintenance based on hand-fed individuals.

The observed prey capture rate by non-breeding eagles (0,425 prey d^{-1}) was actually 9% greater than the predicted minimum (0,389 prey d^{-1}). Whereas the observed increase in prey capture rate when provisioning juveniles (0,146 prey d^{-1}) was 25% lower than the predicted minimum (0,195 prey d^{-1}). This suggests that the food consumption rates of wild adults may be greater than 300gd^{-1}, while the food consumption rates of juveniles may be lower than this. The food requirements of wild adults are expected to be greater than those of hand-fed birds on a maintenance diet, because wild adults need to actively hunt and defend their territory. Wild dependent juveniles however, do not need to hunt and are usually relatively inactive (Steyn 1982; Chapter 6: Fig. 51). So it is unlikely that the food consumption rates of wild juveniles would be much greater than those of captives. In fact captive golden eagle nestlings ate considerably more than wild golden eagle nestlings (Collopy 1980: see Table 25). This is probably due to an *ad libitum* food supply in captivity, and wild black eagle nestlings may actually be able to grow healthily on less than 300g of hyrax per day. The observed increase in prey capture rate during the nesting season (0,146 prey d^{-1}) can be expected to yield an additional 225g food per day, but the adults may also have reduced their wastage during this period.

The estimates of total food consumption by breeding pairs of black eagles reached in the present study (279 - 284kg per annum) are lower than those determined elsewhere. Based on nest observations of prey deliveries conducted in 1970, Gargett (1972) calculated that a pair of eagles and their offspring consumed 360kg of hyrax per annum. But data on the food requirements of the young hand-fed eagle suggested an annual consumption rate of 302kg for a breeding pair and their offspring (Gargett 1982a). From Brooker & Ridpath's (1980) estimate of 120kg food needed per adult bird, a total family requirement of about 330kg per annum can be inferred for a breeding pair of wedge-tailed eagles with offspring. Other estimates of annual food consumption by eagle families are lower than this: Brown & Watson (1964) calculated that a pair of golden eagles and their offspring need about 253kg food per annum; and Brown (1970) considered the family food requirements of a pair of black eagles and their chick to be 220kg consumed. It is considered unlikely though that black eagles could breed successfully on much less food than 280kg per annum (unless their diet is unusually rich in energy).

Additional food and energy requirements of wild black eagles above maintenance requirements can also be investigated by metabolic predictions based on body size. Sapsford & Mendelsohn (1984) calculated that the daily energy expenditure of free-living raptors is normally about 30% greater than their energy requirements for maintenance or existence. Drent, Ebbinge & Weijand (1978) showed that the field metabolic rate of some birds is 2,6 - 2,8 times greater than their standard or basal metabolic rate.

The mean mass of 15 South African black eagles from personal and museum records (A.C. Kemp *in litt.*) was 3819g (s.d.=419g). Mean mass for males was 3744g (n=4; s.d.=377g), and for females was 3969g (n=6; s.d.=502g). Overall representation of the sexes should be equal for black eagle families, so I use the mean mass of 3819g throughout (which is also very close to Samburu's post-fledging mass of 3775g). Some Drakensberg black eagles may, however, be much larger than this (see Brown in Gargett 1990). The standard metabolic rate of a 3819g black eagle may be calculated using the equation provided by Lasiewski & Dawson (1967) for non-passerine birds where SMR (KCal d^{-1}) = 78,3 x MASS (kg)^{0,723}. This equation yields a value equivalent to 863KJ d^{-1} for an average black eagle. At an assimilation efficiency of 75% (Collopy 1980, 1986; Kirkwood 1981), this would require a food energy content of 1151KJ d^{-1}.

The energy requirement of an average black eagle for maintenance may be calculated from mean body mass using Kirkwood's (1981) equation for captive birds of prey where MEm (KCal d^{-1}) = 110 x MASS (kg)^{0,68}. This equation yields a value equivalent to 1145KJ d^{-1} for a 3819g black eagle, requiring a food energy content of 1526KJ consumed per day (assimilation efficiency = 75%). This is only 9% lower than the mean value for large hand-fed eagles in Table 25, half of which were larger than the average black eagle. Samburu consumed 1676KJ d^{-1} as a nestling, and 1433KJ d^{-1} for maintenance (with some exercise) on a diet of day-old chicks.

The field metabolic rate of an average black eagle may be calculated from mean body mass using Nagy's (1987) equation No. 30 for birds where FMR (KJ d^{-1}) = 10,9 x MASS (g)^{0,640}. This relationship described 91% of the variation in bird FMR, but high representation of seabirds and breeding birds in the sample may lead to exaggerated FMR at large body mass. The equation yields a value of 2137KJ d^{-1} for a 3819g black eagle in the wild. This value is 2,5 x greater than the figure for standard metabolic rate and 40% greater than the maintenance requirement, and would require a daily food energy content of 2849KJ (assimilation efficiency = 75%).

Using this last value for field metabolic rate and assuming that hyrax have a food energy content of 5,5KJ g^{-1} wet weight, it follows that an adult pair of wild eagles would need to consume 1036g of hyrax per day, which in turn means they would need to catch 1727g of hyrax per day (40% wasted). At a mean prey mass of 2565g, this corresponds to a prey capture rate by the pair of 0,673 prey d^{-1} which is far larger than the observed prey capture rate of a non-breeding pair (0,425 prey d^{-1}), and even larger than the observed rate when breeding (0,571 prey d^{-1}).

If, as Sapsford & Mendelsohn (1984) suggest, field metabolic rate of an average black eagle is taken as only 30% greater than the maintenance or existence requirement predicted from Kirkwood's (1981) equation, this would indicate a daily food consumption rate of 360g $bird^{-1}$, and a daily catch rate of 1203g $pair^{-1}$ (same reasoning as above). This corresponds to a prey capture rate of 0,469 prey d^{-1}, which is more compatible but still greater than the observed rate and indicates that the predictions from Nagy's (1987) equation are over-exaggerated at least for large eagles. But again, both predictions show how close the prey capture rate by wild black eagles in the present study was to their expected minimum food and energy requirements whether breeding or not. This, no doubt, was due to low hyrax abundance and availability (Chapter 4 & Synthesis). Black eagles might be able to survive on a lower overall prey capture rate than that observed in the present study, but reduced breeding attempts and success would have been expected as a preliminary consequence to any further decline in the prey. At the other extreme, very high rates of prey capture observed by Gargett (1972) probably represent near maximum.

Factors influencing prey capture rate by black eagles

Direct and indirect observations on prey capture rate by different black eagle pairs at different times in the study permit investigation of the factors that affect prey capture rate. Certain pairs were consistently good (e.g. GD, KK) or consistently poor (e.g. DH, LH, BR) at catching prey or delivering prey to nests. Using the time-lapse films as sampling units (each representing several days of observations at an eagle's nest), differences in the rate of kills per day could not be demonstrated significantly for the different pairs (K^2=8,2; d.o.f.=8; p=0,08). However, when all observations on prey capture rate were pooled for each pair (n=9) and compared with various characteristics of the different pairs by correlation analyses, certain patterns emerged. Most notably, high prey capture rate was associated with pairs which took a large portion of lagomorph prey in their diet as revealed by collections of prey remains (r=0,72; p=0,03). Correlations were stronger with the proportions of scrub hare (r=0,58) and red rock rabbits (r=0,47) in the diet, than with the proportion of Cape hares (r=-0,13). There was also a slight tendency for high prey capture rate to be associated with greater amounts of small grey mongooses in the diet (r=0,57; p=0,11). Greater rates of prey capture might be expected for eagles preying mainly on small red rock rabbits and mongooses, but this reasoning does not explain the observed and stronger association of high prey capture rate with the large scrub hares.

Although the small sample size did not lend itself to statistical testing of associations, these findings were corroborated to some degree when prey capture rate was compared with habitat characteristics of the eagles' territories. There were trends for prey capture rate to be greater in territories which encompassed more middle plateau habitat (r=0,58; p=0,10), more lower escarpment (r=0,54; p=0,14), and less bottom plains habitat (r=-0,63; p=0,07). There was no suggestion of higher prey capture rates by farm birds. Bearing in mind that this analysis is confined to lower escarpment pairs (where time-lapse photography of nests was feasible), peripheral eagle pairs which hunted out over the bottom plains (favoured by Cape hares) apparently could not supply as many prey to their nestlings as eagle pairs which hunted over the more rocky, mountainous habitats where scrub hares, red rock rabbits and small grey mongooses were more abundant (Chapters 5 & 9). No associations could be detected between prey capture rate of eagle pairs and the amounts of hyrax in their diets or in their territories. These findings suggest again that the hyrax prey base was well protected within the confines of their rocky habitats, and also probably evenly-distributed between lower escarpment eagle pairs. High levels of food-provisioning by these eagles were evidently more dependent upon a plentiful supply of alternate prey, notably lagomorphs. The increase in red rock rabbit numbers in the park between 1987 and 1989 (Chapter 5) conveniently supplied certain eagle pairs with important additional prey resources.

For the nine pairs with substantial observations on prey capture rate, no associations could be found between prey capture rate and the effort or success of these pairs at breeding. Also there were no detectable associations between prey capture rate and evidence of food stress, such as late breeding or opening of hyrax crania (Chapter 10). This is to be expected because the sample is mostly made up of eagle pairs which, by necessity, were successful breeders (time-lapse photography could not be carried out for non-breeders). A positive correlation between high prey capture rate and successful breeding may have been obtained if there were sufficient data available on prey capture rate for all pairs.

There must be a minimal prey capture rate, below which breeding is not possible. The Lion's Head pair showed a consistently low rate of food provisioning. Their 1989 nestling had to survive intervals of 7-9d between prey deliveries, and their 1987 nestling died from impaction of the crop when it finally received prey after a period of food shortage. The rate of prey deliveries by the Lion's Head pair in 1987 (0,433 prey d^{-1}) was the lowest recorded for all monitored nestling periods, and was only slightly higher than the overall prey capture rate observed for non-breeding pairs (0,425 prey d^{-1}). The Lion's Head territory contained the most hyrax groups of the four territories mapped (Chapter 6), but they may have been well protected and much of the territory was plains - affording poor flying conditions. The Sloop pair successfully raised a chick in 1989 with an overall prey delivery rate of 0,488 prey d^{-1}, but this must be close to the minimum possible provisioning rate for breeding, and these eagles were observed to minimise wastage in 1989 by consuming even the dry hyrax pelts. Consumption of pelts was also observed by Cottrell (1970). Gargett (1990) reported that pelts are sometimes not eaten, so this behaviour (like the opening of hyrax crania - see Chapter 10) may be indicative of the degree of food shortage experienced by the birds.

The absence of a correlation between prey capture rate and breeding success may also be partly due to variation in the hunting and breeding proficiencies of individual eagles or pairs of eagles. The Kortkloof pair achieved a very high level of prey capture in 1989 (0,689 prey d^{-1}) but were very poor breeders overall. In this case the female was assumed to be old and laid an infertile egg in 1988. Old eagles may still be able to catch prey, but raptors are known to become less fertile with age (Newton 1979). The success of the Kortkloof pair in 1989 however, may have more to do with the dramatic increase in red rock rabbits in their territory at this time, than with other factors.

The highest rate of food provisioning (0,711 prey d^{-1}) was at the Gamka Dam nest in 1988 (this territory had good habitat for red rock rabbits and scrub hares, and the mountainous topography afforded good flying conditions).

Overall prey capture rate for all monitored pairs was highest (0,625 prey d^{-1}) in 1988 and was 27% greater than that in 1987 (0,494 prey d^{-1}). In 1989 overall prey capture rate for monitored breeders was 0,562 prey d^{-1}. The 1988 nestlings did not have to go longer than 4d without food, whereas certain chicks had to fast for up to 9d in 1989, and for up to 6d in 1987 (Figure 65). These differences in daily prey capture rate between the three years of intensive observation proved to be statistically significant (X^2=7,48; $p<0,05$) when the time-lapse films were used as sampling units for comparison, and can best be explained in terms of long-term changes in prey availability and abundance.

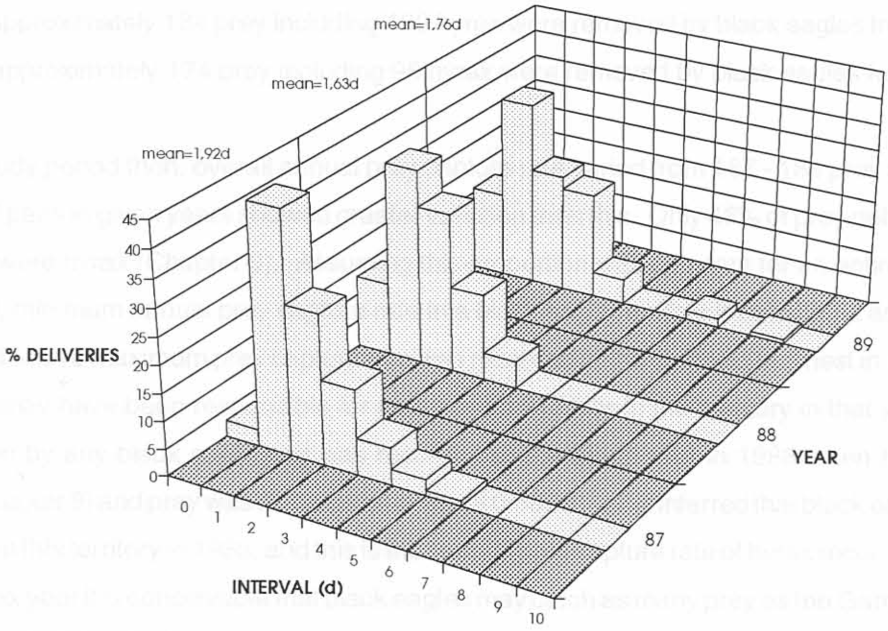


Figure 65. Frequency distributions of the intervals between prey deliveries at all nests in the three years monitored.

Both the December counts at colonies and incidental sightings of hyrax in the veld indicated that the hyrax population declined significantly during 1988 (Figure 40a, page 81). Predation by black eagles was partly responsible for this decline (Chapter 12). Summer rainfall at the end of 1987 and at the end of 1988 was below average for both seasons, leading to impoverished vegetation and possibly increased vulnerability of hyrax to eagle attack. An apparent increase in hyrax availability during 1988 despite their declining abundance is supported by the observation that hyrax comprised the largest portion of prey delivered to eagle nests (as monitored by the time-lapse cameras) in this year (Chapter 9; Fig. 83, p. 198). In 1988 the eagles also took the greatest portion of juveniles amongst their hyrax prey - this is symptomatic of low hyrax:eagle ratio (see Chapter 10), and it probably accounts for increased incidence of opened hyrax crania in 1988 (see Chapter 10, Fig. 98, p. 220). Subsequently prey capture rate declined again in 1989 and hyrax comprised the smallest portion of prey deliveries in this year. This was probably due to significantly reduced hyrax numbers which became less susceptible to attack after rains improved vegetation conditions in 1989. A much lower prey capture rate might have been expected for 1989 had it not been for a seven-fold increase in red rock rabbit numbers between 1987 and 1989 (Fig. 40b, page 81), which was also reflected in the proportion (Chapter 9; Fig. 83, p. 198) and frequency (Fig. 71, p. 171) of prey deliveries comprised by this species.

By combining appropriate data on breeding success, diet and prey deliveries, it is possible to estimate the overall prey capture rate by black eagles in the study area for these three years of intensive study. In 1987 only 33% of pairs raised chicks, average prey capture rate during the breeding season (200d) was 0,494 prey d^{-1} (this can be increased by 4% to compensate for any small prey items that may have been missed by the cameras - see earlier); average prey capture rate by non-breeders can be assumed to be 0,425 prey d^{-1}, and by vagrant black eagles 5 prey yr^{-1} (see earlier); and hyrax comprised 73,2% of prey deliveries (Chap. 9). It follows that in 1987 approximately 167 prey including 122 hyrax were removed by black eagles from the average territory. In a similar way it is calculated that in 1988 approximately 184 prey including 136 hyrax were removed by black eagles from the average territory; and in 1989 approximately 174 prey including 98 hyrax were removed by black eagles from the average territory.

During the study period then, overall annual prey capture rate varied from 167 - 184 prey and from 98 - 136 hyrax. But individual pairs in given years showed greater variation than this. Only 46% of prey delivered to the Lion's Head nest in 1989 were hyrax (Chapter 9). Assuming this proportion was constant for an entire year and that the birds did not breed, minimum annual prey capture rate in a black eagle territory is calculated as 160 prey and 73 hyrax. As mentioned above maximum prey capture rate was recorded at the Gamka Dam nest in 1988. It is estimated that black eagles may have been responsible for as many as 217 kills in this territory in that year. But the highest toll of hyrax taken by any black eagle pair was recorded at the Sloop nest in 1988 when hyrax comprised 83% of deliveries (Chapter 9) and prey was delivered at a rate of 0,586 d^{-1}. It is inferred that black eagles may have removed 159 hyrax from this territory in 1988, and this is the highest prey capture rate of hyrax recorded for the present study. In a good hyrax year it is conceivable that black eagles may catch as many prey as the Gamka Dam pair did in 1988, and that 83% of all these might be hyrax. In this scenario black eagles might be expected to remove as many as 181 hyrax from a territory in one year. This is the upper limit to prey capture rate that is indicated by this study. However it is still only half an early estimate of hyrax predation by single black eagle pairs in the Matobo Hills (Gargett 1972). Gargett later (1990) estimated the annual toll to be 321 hyrax / territory / year. As mentioned earlier, Gargett's observations were conducted when hyrax may have been highly available, and mean prey mass may possibly have been lower in her study. Gargett's estimate is based on one pair in one season, so it should not be extrapolated to indicate an overall prey capture rate for the Matobo. Even if the eagle pairs in the present study maintained maximum (breeding) prey capture rate throughout the year and ate solely hyrax, total annual toll would be about 270 hyrax per territory. It is considered highly unlikely that karoo black eagle pairs would ever kill more than 350 hyrax per annum. This is more than double the overall prey capture rate recorded in the present study, so wastage at this level of predation would be excessive.

Variation in prey capture rate within the year, in and out of the nesting season, has already been treated. Within the nestling period some variation in prey capture rate might be expected, for instance with the food requirements of the chick (see earlier), or with nest-attendancy by the adults. The proportion of time that any adults were attending their chicks was assessed for four nestling periods using the time-lapse films. This is shown in Figure 66 in relation to chick age. Nest-attendancy was apparently climate-related. A south-facing nest (KK) which was not exposed to the sun experienced lowest nest attendance by adult birds; whereas a north-facing nest (SL) experienced prolonged nest-attendancy by the adult birds into the second month of the nestling period, presumably while they afforded shade to their nestling from the hot sun. The overall pattern showed that adults were very attentive (about

80% time) for the first three weeks, but thereafter nest attendance declined to about 20% of the time by the sixth week and to only 10% of the time for the last few weeks of the nestling period. This suggests that endothermy of black eagle chicks develops from about 20d old which is a week later than in golden eagle chicks (Collopy 1980). Gargett (1990) recorded nest attendances of 83% in the first month of the nestling period, about 35% in the second month and 19% in the last month. Slightly higher nest attendancy by Matobo eagles may be due to a hotter environment and/or reduced food stress. The need for high nest attendancy by at least one adult in the first few weeks of the nestling period means that tandem-hunting by nesting adults can only re-commence when the chick is 4-5w old. Hunting success by tandem-hunting adults appeared to be greater than by adults hunting solo (Chapter 6). One would expect prey deliveries to increase when the chick reaches 4-5w old, which is also the period of maximum food consumption by the chick. Weekly prey delivery rate was assessed from the time-lapse films for 10 more or less complete nestling periods. Prey delivery rate to these nestlings was highly erratic even for the same pairs in different years or for different pairs in the same years (Figure 67 - overleaf). Prey delivery was erratic for both hyrax and other prey items but a heavy reliance on other prey was evident in 1989 for KK and LH (Figure 67). Overall weekly prey delivery rate was fairly constant throughout the nestling period when data for all 10 nestlings were combined, and showed no significant relationship to either nest attendancy or food requirements of the chick (Figure 68 - below). This implies that the male must make a greater effort to compensate for the poorer success of solo-hunting during

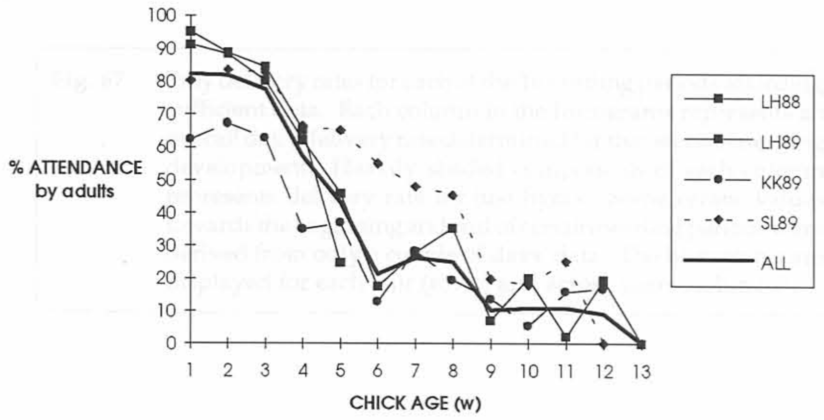


Figure 66. Percentage nest attendancy by any adults in relation to nestling age.

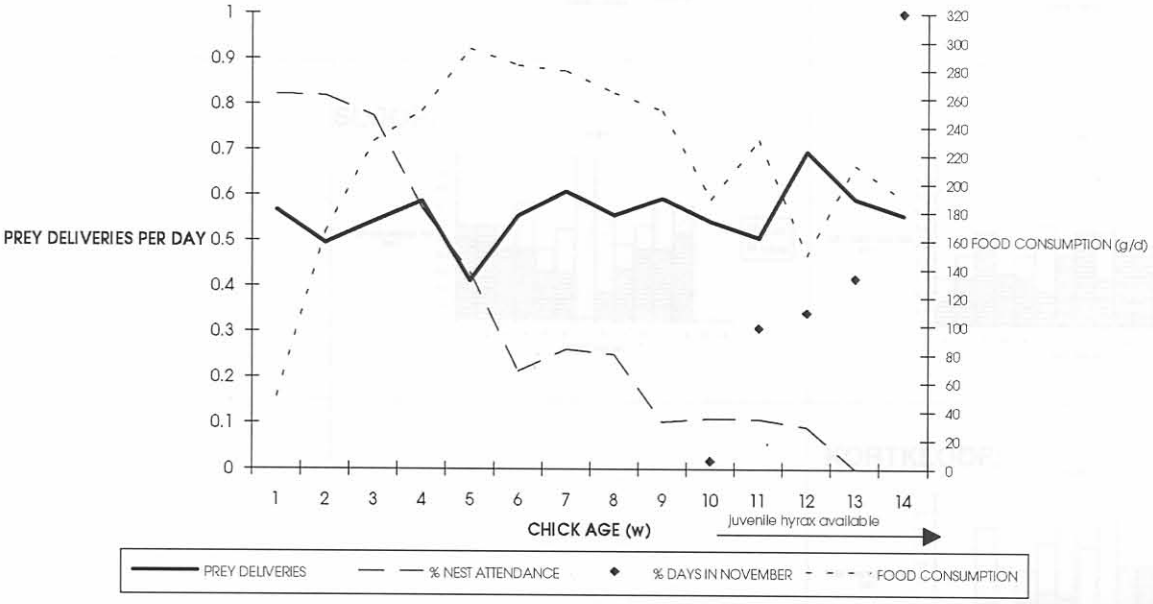
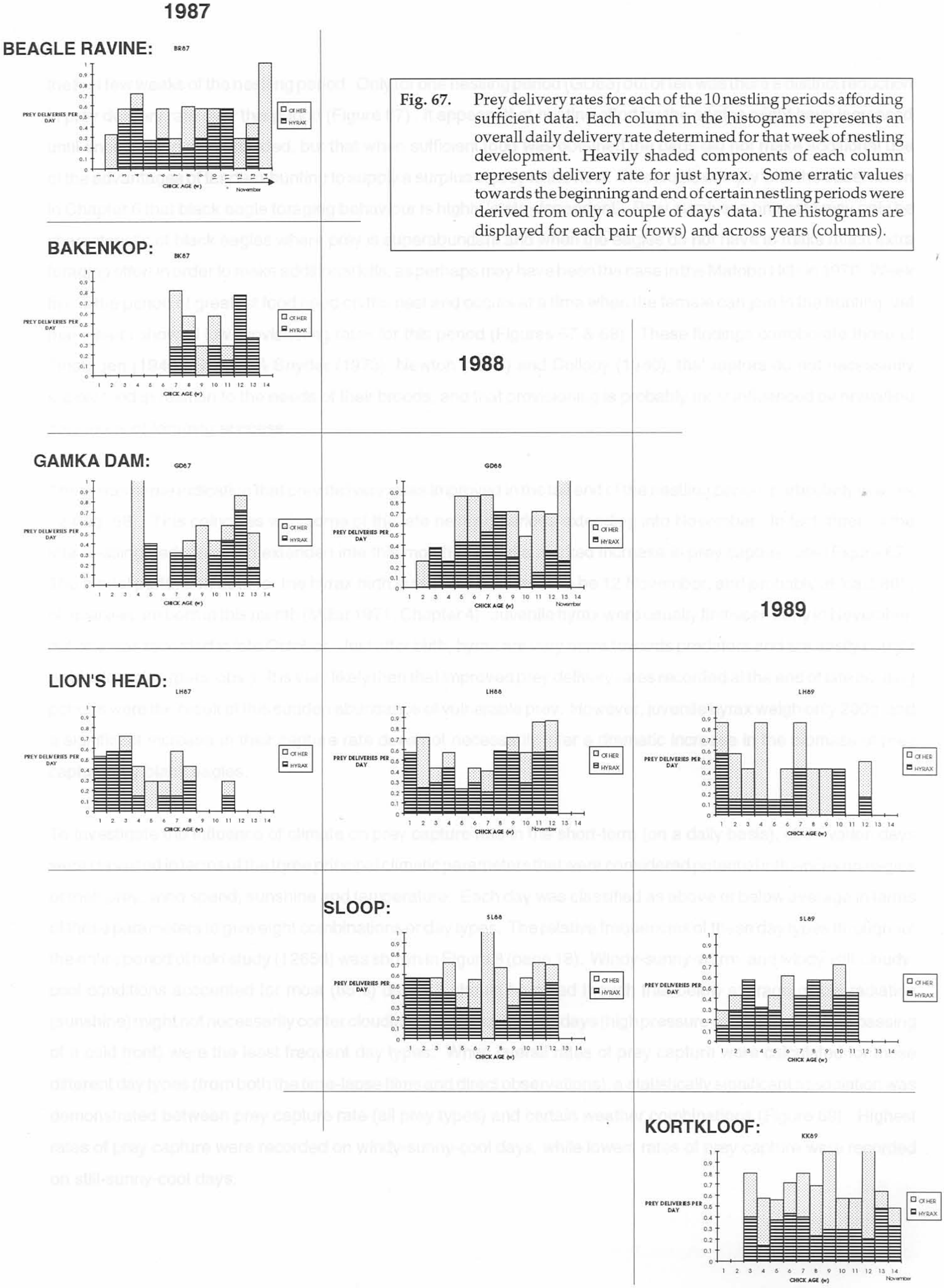


Figure 68. Change in overall prey delivery rate (to all nests) with nestling age, in relation to nest attendancy by adults and food need of the nestlings. The proportion of days in November is also shown for the end of the nestling periods when juvenile hyrax become available.

Fig. 67. Prey delivery rates for each of the 10 nestling periods affording sufficient data. Each column in the histograms represents an overall daily delivery rate determined for that week of nestling development. Heavily shaded components of each column represents delivery rate for just hyrax. Some erratic values towards the beginning and end of certain nestling periods were derived from only a couple of days' data. The histograms are displayed for each pair (rows) and across years (columns).



the first few weeks of the nestling period. Only for one nestling period (GD88) out of ten was there a distinct reduction in prey delivery rate over this period (Figure 67). It appears that hunting effort by the eagles might have increased until enough food was provided, but that when sufficient food was obtained the birds did not make additional use of the advantages of tandem-hunting to supply a surplus of prey to the nest. This would comply with the observation in Chapter 6 that black eagle foraging behaviour is highly 'state-dependent'. Prey surpluses on nests may only be characteristic of black eagles where prey is superabundant and when the eagles do not have to make much extra foraging effort in order to make additional kills, as perhaps may have been the case in the Matobo Hills in 1970. Week five is the period of greatest food need on the nest and occurs at a time when the female can join in the hunting, yet many pairs showed low provisioning rates for this period (Figures 67 & 68). These findings corroborate those of Tinbergen (1940), Snyder & Snyder (1973), Newton (1978) and Collopy (1980), that raptors do not necessarily supply food in relation to the needs of their broods, and that provisioning is probably most influenced by prevailing conditions of foraging success.

There was some indication that prey delivery rates improved in the tail end of the nestling period, particularly in week 12 (Fig. 68). This coincides with some of the late nestling periods extending into November. In fact, three of the four nestling periods which extended into this month showed a marked increase in prey capture rate (Figure 67). The modal parturition date for the hyrax birth pulse was calculated to be 12 November, and probably at least 80% of juveniles are born in this month (Millar 1971; Chapter 4). Juvenile hyrax were usually first seen early in November, but one was recorded in late October. Just after birth, hyrax are very naive towards predators and are easily caught by black eagles (pers. obs.). It is very likely then that improved prey delivery rates recorded at the end of late nestling periods were the result of this sudden abundance of vulnerable prey. However, juvenile hyrax weigh only 200g, and a significant increase in their capture rate does not necessarily infer a dramatic increase in the biomass of prey captured by black eagles.

To investigate the influence of climate on prey capture rate in the short-term (on a daily basis), observation days were classified in terms of the three principal climatic parameters that were considered potential influences on eagles or their prey: wind speed, sunshine and temperature. Each day was classified as above or below average in terms of these parameters to give eight combinations or day types. The relative frequencies of these day types throughout the entire period of field study (1265d) was shown in Figure 8 (page 18). Windy-sunny-warm, and windy/still-cloudy-cool conditions accounted for most (65%) days. It should be noted though that below average global radiation (sunshine) might not necessarily confer cloudiness. Still-sunny-cool days (high pressure conditions after the passing of a cold front) were the least frequent day types. When overall rates of prey capture were calculated for these different day types (from both the time-lapse films and direct observations), a statistically significant association was demonstrated between prey capture rate (all prey types) and certain weather combinations (Figure 69). Highest rates of prey capture were recorded on windy-sunny-cool days, while lowest rates of prey capture were recorded on still-sunny-cool days.

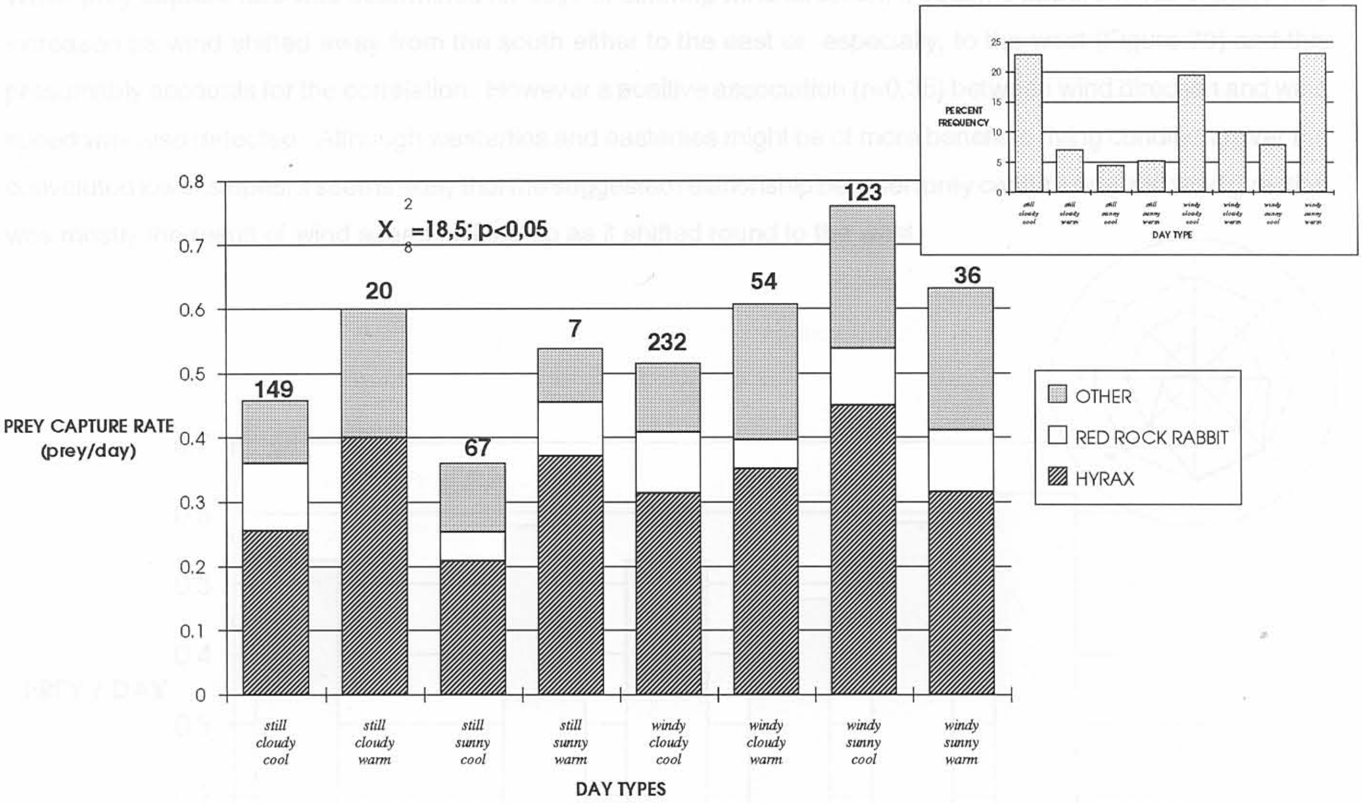


Figure 69. Overall delivery rates of hyrax, red rock rabbits and other prey to black eagle nests on different types of day (days were classified as above or below average for three important climatic variables). The frequency of these day types during monitoring by time-lapse photography is given at the top of each column. The frequency distribution of day types throughout the study period (1265d) is shown as an insert of Fig. 8 from page 18.

Capture of hyrax specifically appeared to be largely responsible for this trend (Fig. 69), and the particular weather combinations suggested that wind was the key factor. Indeed, prey delivery rate to nests on windy days (0,61 prey d^{-1}) was found to be nearly 40% greater than prey delivery rate on still days (0,44 prey d^{-1}), and this difference proved to be statistically highly significant (X^2=10,2; p<0,01). Wind is known to enhance black eagle flying and foraging behaviour (Chapter 6). By contrast, the efficiency of the early warning system employed by hyrax on group foraging bouts would be severely impaired by windy conditions because individuals travelling down to riparian thickets may be unable to hear the alarm calls of the sentinels. It is relevant to note that hyrax did not embark on group foraging bouts down to riparian thickets on very windy days (Chapter 4). This behaviour was most prevalent on still-sunny-cool days after cold fronts - when prey capture rate by eagles was lowest (Fig. 69).

When correlation analyses were employed on a daily database to investigate possible associations between prey delivery rate to nests and a variety of climatic factors, the same influence of wind speed was detected (r=0,14; p=0,02), as well as a significant positive association with wind direction measured as degrees from true north (r=0,14; p=0,02), although the latter relationship was lost for some reason when direct observations on prey capture rate were included in the sample. Wind in Beaufort West emanates mainly from the south and south-east (Fig. 7, page 18). When prey capture rate was determined for days of differing wind direction, it became apparent that capture rate increased as wind shifted away from the south either to the east or, especially, to the west (Figure 70) and this presumably accounts for the correlation. However a positive association (r=0,35) between wind direction and wind speed was also detected. Although westerlies and easterlies might be of more benefit to flying conditions over the convoluted lower slopes, it seems likely that the suggested relationship between prey capture rate and wind direction was mostly the result of wind speed picking up as it shifted round to the west.

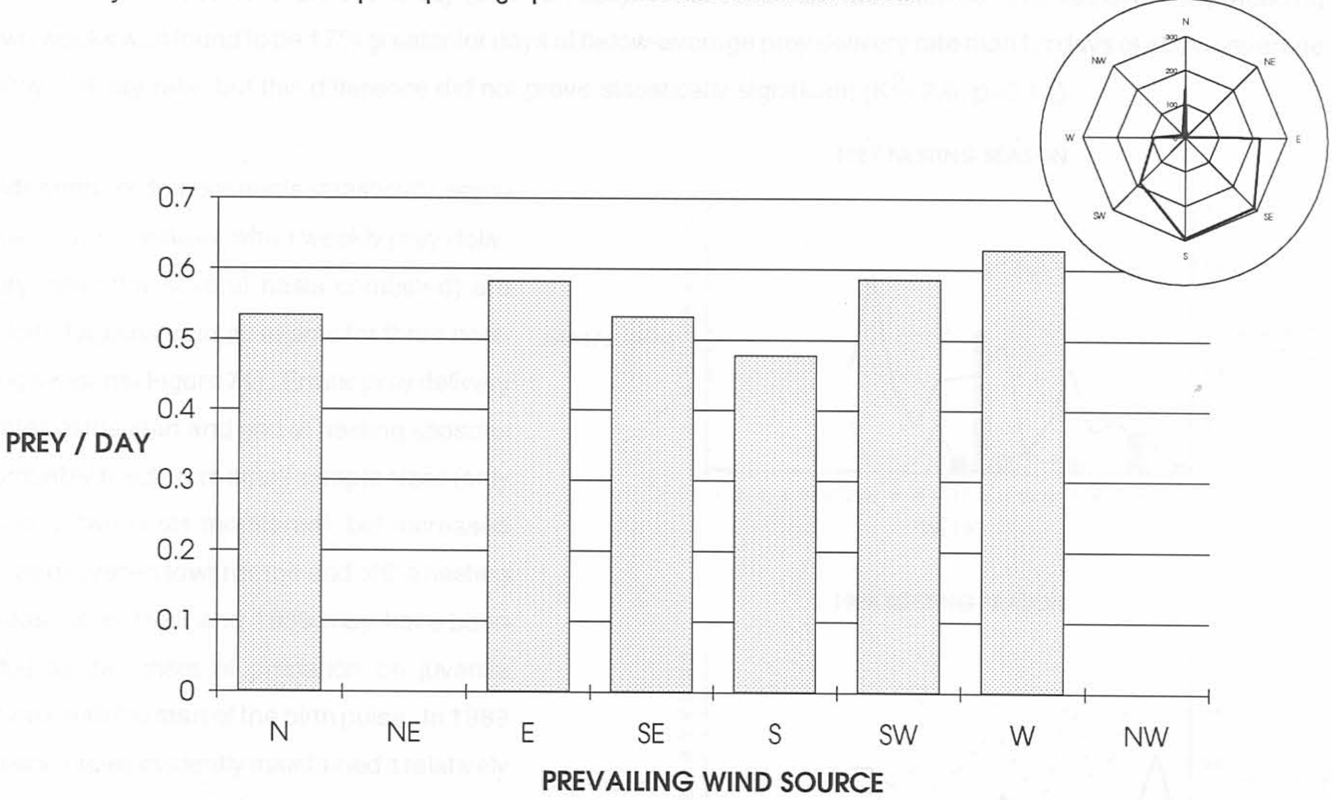


Figure 70. Prey delivery rates to black eagle nests for days of different wind directions. Frequencies of different wind directions over the study period (1265d) are shown as an insert of Fig. 7 from page 18.

No other associations between total prey or hyrax capture rates and climatic factors were detected by this correlation analysis, but there were statistically significant indications that fewer red rock rabbits were captured on longer (summer) days (r=-0,12; p<0,05) and on very humid days (r=-0,12; p<0,05). It seems unlikely that red rock rabbits were less abundant on these days. Perhaps the rabbits occupy more vulnerable 'forms' or are more active on short winter days. Reduced capture rates of red rock rabbits on long summer days was countered by increased capture rates of other 'non-hyrax' prey types (r=0,11; p<0,05). Capture rate for the latter (which includes unidentified prey) was also significantly greater on sunny days (r=0,20; p<0,01). It is not clear why this category should be more vulnerable to eagle attack on days of high global radiation but these relationships are not necessarily consequential.

Daily atmospheric pressure and rainfall were not related to daily prey capture rate in any obvious detectable way. But rainfall can be expected to have some negative influence on the capture of hyrax by eagles either directly, or indirectly mediated through the vegetation. Heavy rains are known to keep hyrax in their shelters for up to three days

(Coe 1962; pers. obs.). Within days or weeks, good rains can replenish over-grazed vegetation resources in the immediate vicinities of hyrax colonies. Certain plants are known to respond within a day to very small rainfall events (5mm) in semi-arid regions (Sala & Lauenroth 1982). After significant rains, hyrax should be able to fulfill their forage requirements within a safer distance of their rocky shelters, and perhaps within a shorter time period. To test the hypothesis that hyrax vulnerability declined after rains, daily prey capture rates were correlated with a measure which summed rainfall for the preceding 40d for each observation day. This measure was found to be a useful indication of karoo veld condition in another study (Davies 1985). No association was detected. Rainfall over the preceding two weeks was found to be 17% greater for days of below-average prey delivery rate than for days of above-average prey delivery rate, but this difference did not prove statistically significant (K^2=2,6; p=0,11).

Although not demonstrable statistically, some trends are apparent when weekly prey delivery rates (for several nests combined) are plotted against rainfall events for three nesting seasons (Figure 71). Erratic prey delivery rates at the start and end of nesting seasons probably result from small sample sizes (only one or two nests monitored), but increased prey deliveries towards the end of the nesting seasons in 1988 and 1989 may have been due to the onset of predation on juvenile hyrax with the start of the birth pulse. In 1989 black eagles evidently maintained a relatively constant prey delivery rate while shifting emphasis from red rock rabbits at the start of the season to hyrax at the end of the season. The matter of 'switching' from one prey to another is treated in Chapter 9. There was some indication of a gradual increase in hyrax delivery rate during extended dry spells in 1988 and 1989. A decline in hyrax delivery rate one to two weeks after rainfall events was not very clear in 1989, but was very apparent in 1987 and 1988. Delivery rates for all prey are influenced by these patterns in hyrax deliveries. Delivery rate of red rock rabbits however, appeared to be largely independent of rainfall events. These patterns are suggestive that hyrax vulnerability does decline somewhat after rainfall (in agreement

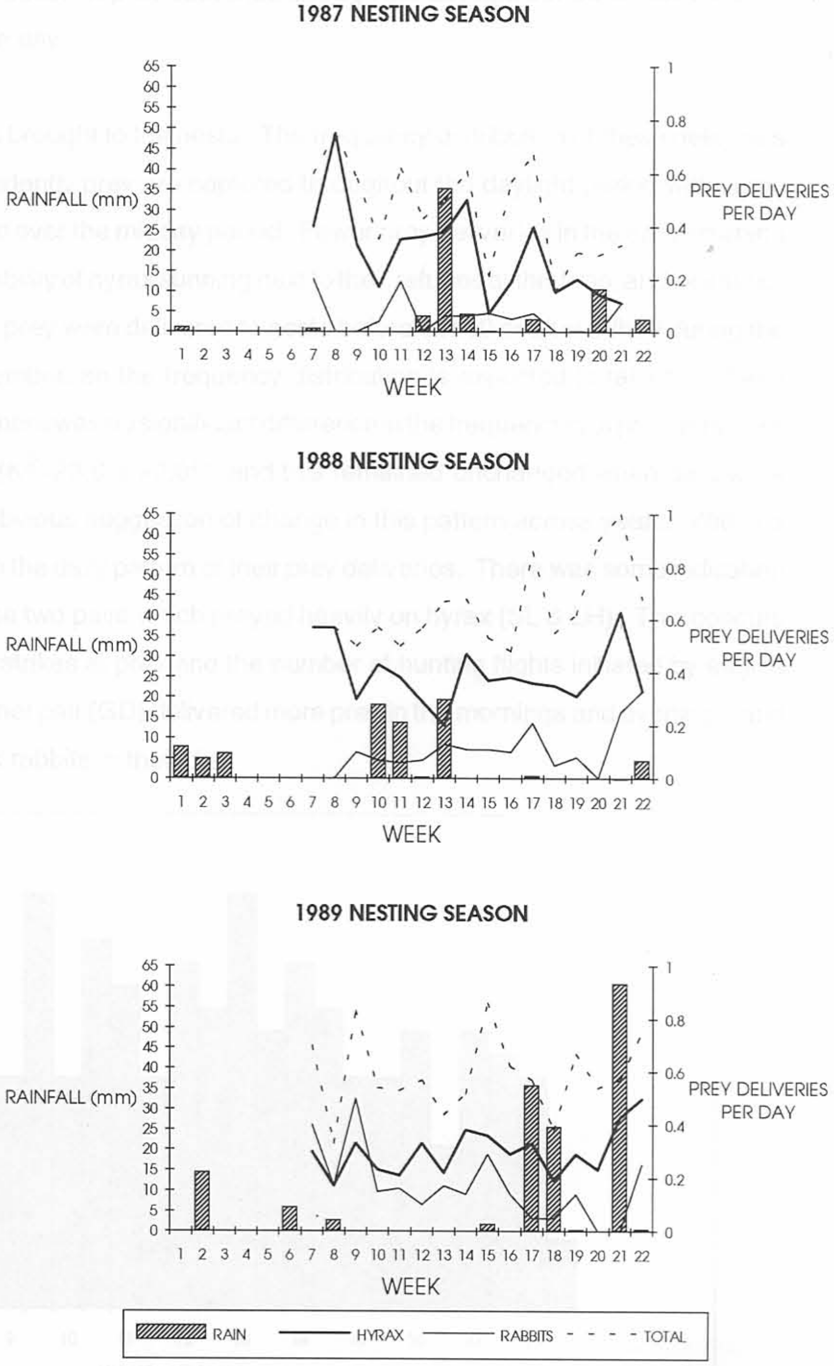


Figure 71. Delivery rates of hyrax, red rock rabbits and all prey to black eagle nests for the three nesting seasons monitored, in relation to the timing and magnitude of any rainfall events. (values were calculated by week).

with indications from direct observations of hyrax movements - see Chapter 4, and relationships between eagle breeding success and rainfall - see Chapter 6), but the magnitude of the decline and its timing after the rainfall event probably vary with many factors, especially the size of the event, the degree of drought-stress and the hyrax population pressure.

The time-lapse films could also be analysed for diurnal variation in prey capture rate. Timing of prey deliveries or other events on nests could be determined within an accuracy of 10min (see earlier) from the time-lapse films. Although the timing of prey deliveries to nests does not exactly represent the timing of prey capture, direct observations indicated that prey was usually delivered immediately to nests after capture and not later than 40min after capture if the captor fed first. So the distribution of prey deliveries through the daylight period should be a fair indication of the distribution of kills through the day.

Timing of delivery was determined for 293 kills brought to the nests. The frequency distribution of these deliveries for 30min intervals is shown in Figure 72. Evidently prey are captured throughout the daylight period with some indication that more are captured and delivered over the midday period. Fewer prey deliveries in the early morning (06h00 - 08h00) may be due to reduced vulnerability of hyrax sunning next to their refuges at this time, and/or inferior flying conditions for the eagles at this time. No prey were delivered to nests before 06h00 or after 18h29 during the shorter, late winter days in August and September, so the frequency distribution is expected to tail off at these extremes. With these time intervals excluded, there was no significant difference in the frequencies of prey deliveries for different time periods throughout the day (K^2=23,6; p>0,05), and this remained unchanged when data were analysed on an hourly basis. There was no obvious suggestion of change in this pattern across years. Within a year, different pairs did show a wide variation in the daily pattern of their prey deliveries. There was some indication of a 3 - 4 hourly rhythm in prey deliveries for the two pairs which preyed heavily on hyrax (SL & LH). This concurs with a similar activity rhythm in the number of strikes at prey and the number of hunting flights initiated by eagles indicated in Chapter 6 (Fig. 47, page 95). Another pair (GD) delivered more prey in the mornings and evenings, and this may relate to a greater portion of red rock rabbits in their diet.

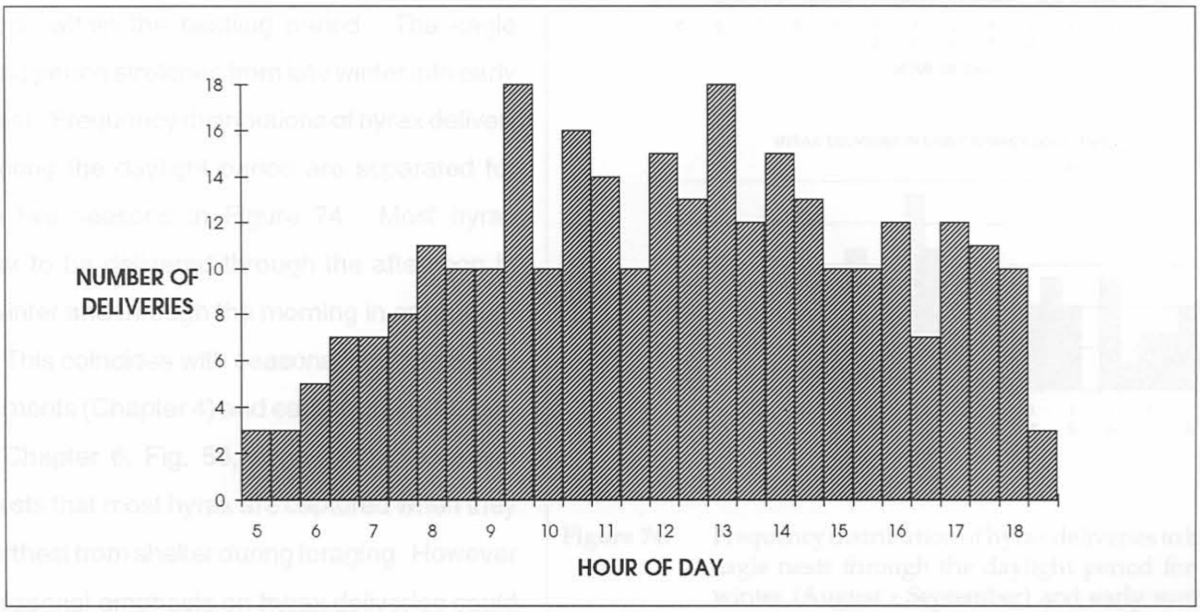


Figure 72. Frequency distribution of all prey deliveries (n=293) to black eagle nests throughout the daylight period.

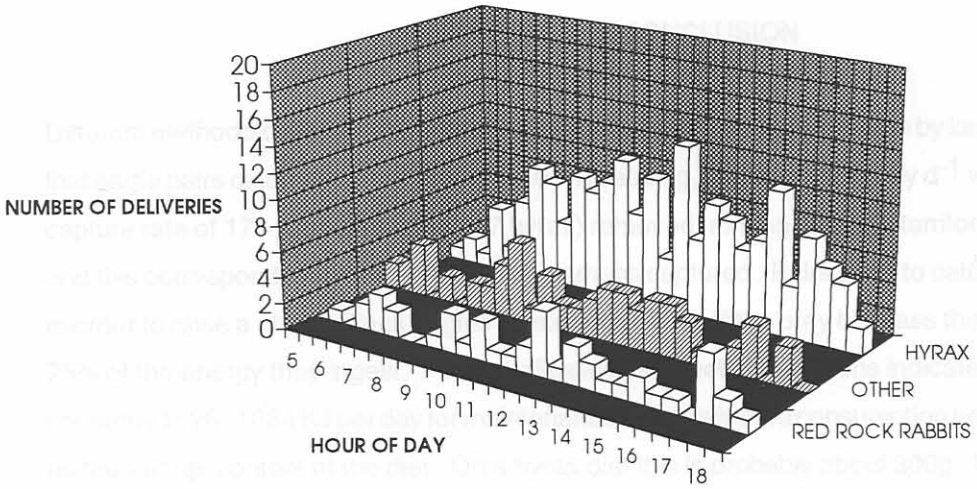
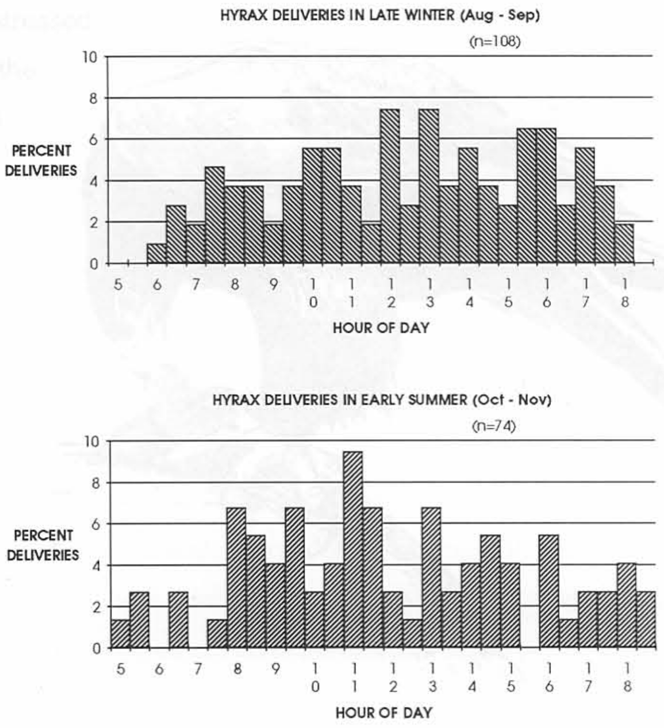


Fig. 73. Frequency distribution of hyrax, red rock rabbit and other prey deliveries to black eagle nests throughout the daylight period.

Frequency distributions of the timing of deliveries are shown for different prey types in Figure 73. Red rock rabbits were delivered to nests throughout the day indicating that this nocturnal and cryptic species might be vulnerable to eagle attack at almost any time of the day. Perhaps many of these rabbits are detected and captured when they move resting sites in response to microclimate change. But there was no obvious indication of a clumping of rabbit deliveries around the midday period. Early morning and late evening deliveries of red rock rabbits may represent animals captured while they are actively foraging, indicating auroral and crepuscular habits. Other prey (including a large unidentified element) were also delivered in the mornings and evenings with no obvious suggestion of a midday peak, unlike the hyrax deliveries. The pattern of hyrax deliveries (which tails off in the mornings and evenings) is evidently largely responsible for the overall pattern. The absence of any obvious 3-4h rhythm amongst these deliveries may be due to the confounding influences of variation between pairs and between different seasons within the nestling period. The eagle nestling period stretches from late winter into early summer. Frequency distributions of hyrax deliveries during the daylight period are separated for these two seasons in Figure 74. Most hyrax appear to be delivered through the afternoon in late winter and through the morning in early summer. This coincides with seasonal hyrax foraging movements (Chapter 4) and eagle hunting behaviour (Chapter 6: Fig. 58, page 122), and again suggests that most hyrax are captured when they are furthest from shelter during foraging. However the seasonal emphasis on hyrax deliveries could not be demonstrated statistically (K^2=3,2;p>0,10).


HYRAX DELIVERIES IN LATE WINTER (Aug - Sep) (n=108)

HYRAX DELIVERIES IN EARLY SUMMER (Oct - Nov) (n=74)

Figure 74. Frequency distribution of hyrax deliveries to black eagle nests through the daylight period for late winter (August - September) and early summer (October - November).

CONCLUSION

Different methodologies employed in the determination of prey capture rate by karoo black eagles largely concurred that eagle pairs catch about 0,6 prey d^{-1} when breeding, and about 0,4 prey d^{-1} when not breeding. An overall prey capture rate of 174 prey (including 117 hyrax) removed from an average territory is indicated for an average year, and this corresponds to about 446kg prey biomass captured. Pairs need to catch an additional prey item every 6d in order to raise a chick. Black eagles waste about 40% of the prey biomass they capture and probably assimilate 75% of the energy they ingest. Food studies and energetic predictions indicate that a 3,8kg black eagle needs to consume 1526 - 1684 KJ per day for maintenance. The daily food consumption necessary to achieve this will depend on the energy content of the diet. On a hyrax diet this is probably about 300g. Nestling black eagles may be able to get by on less than this overall, whereas active wild adults may need up to 25% more. The indications from this study are that prey capture rate may vary from about 160 prey and 70 hyrax per territory per year up to 220 prey and 180 hyrax per territory per year. Other studies indicate an absolute upper limit of 350 hyrax captured per pair in years of optimal prey availability. Estimates of prey capture rate in this study were generally lower than those recorded for large eagles elsewhere but because of large prey size, the indications on biomass captured were not so different. Predictions of minimum predation requirements suggest that the eagles in the present study were operating very close to this. Better provisioning by eagle pairs with a good supply of alternate prey (lagomorphs) indicates that hyrax were not very available since their recent decline. Prey capture rate was found to vary more with changes in prey availability than with changes in eagle food requirements or with changes in their potential hunting abilities. Prey availability can mostly be related to climate. Good rains probably improve prey abundance in the long-term but appear to lead to temporary reductions in prey vulnerability through vegetation effects. Hyrax were most heavily preyed upon when most drought-stressed.

Prey capture rate is also influenced by behaviour of the prey and predator. More prey were caught on days when wind assisted eagle hunting behaviour, and possibly at times of the day when foraging behaviour by the prey may have rendered them more vulnerable to attack.