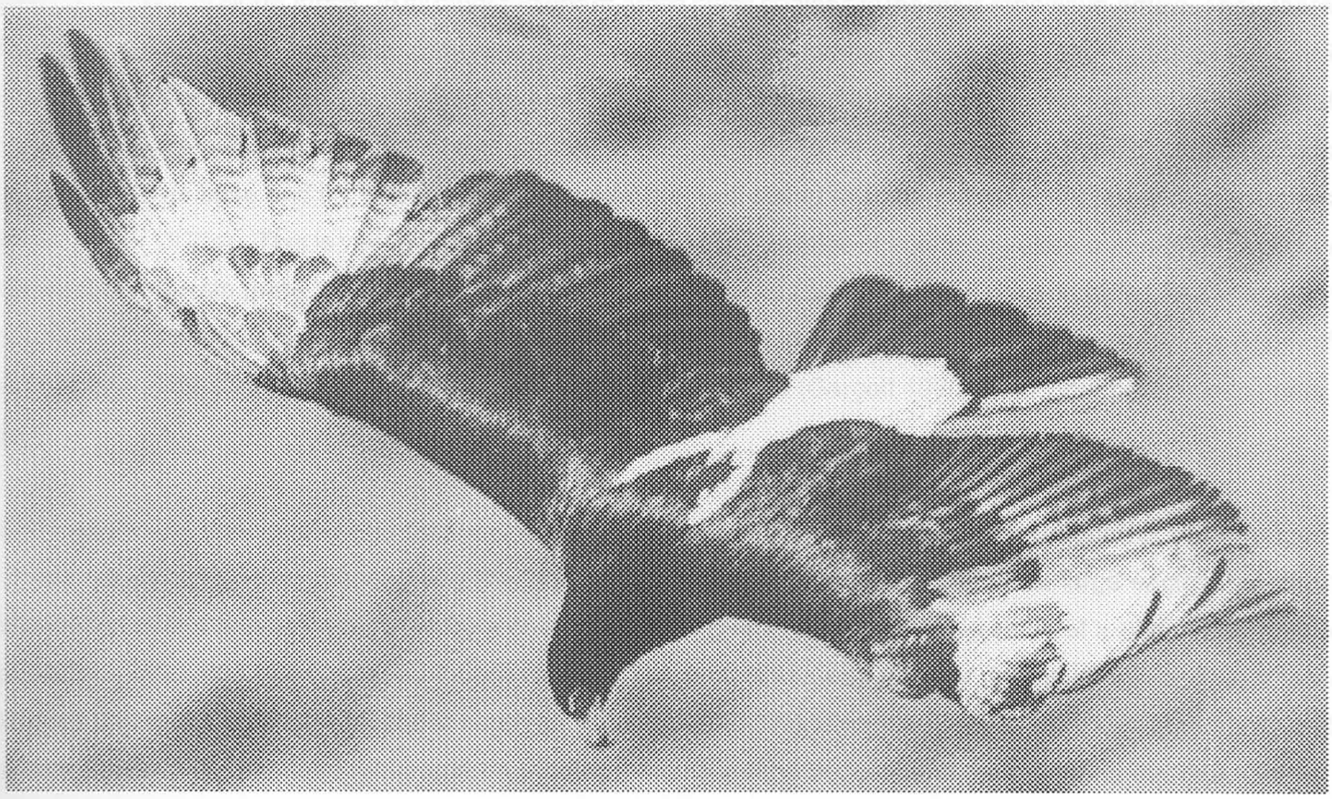
THE PREDATOR GUILD



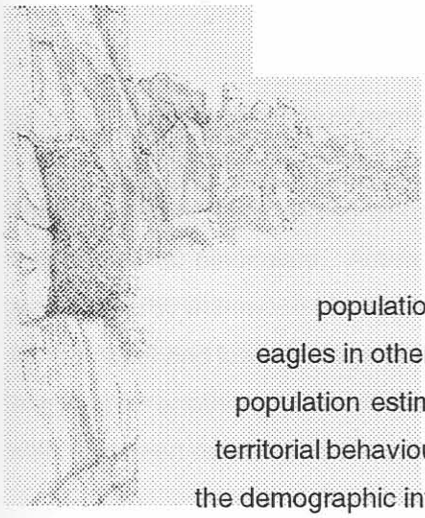
CHAPTER 6

BLACK EAGLE DEMOGRAPHY AND BEHAVIOUR

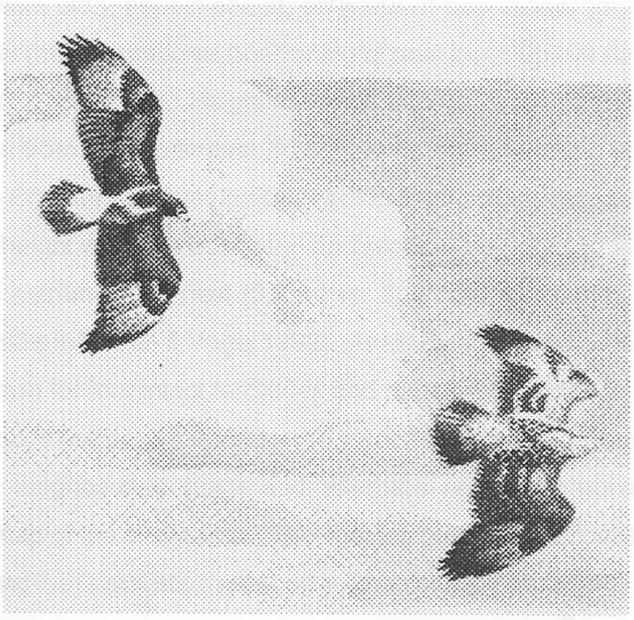
INTRODUCTION

With a wingspan of over 2 m and weighing approximately 4 kg (Gargett 1990; pers. rec.), black eagles are very large *Aquila* eagles, second only to the golden eagle which is 14% larger by mass (A.C. Kemp *in litt.*) and occurs in the Atlas Mountains of North Africa. In all other regions of Africa black eagles are the most rapacious *Aquila*. They share the continent with two other particularly rapacious large eagles, the martial and crowned eagles, but all three are clearly separated by habitat: black eagles frequenting the mountains and rocky areas; martial eagles the plains and savannas; and crowned eagles the forests and dense bush (Brown 1976). The long wingshape of black eagles is tapered towards base and tip, and this high aspect ratio is well-suited to soaring in slope lift rather than thermals (Pennycuick 1972a). This is very evident when contrasting flight abilities of interacting black and martial eagles in mountainous terrain (pers. obs.). Black eagles are reliant on rocky habitats for nest sites on cliffs. There are very few records of black eagles nesting on other substrates such as microwave towers and electricity pylons (Boshoff & Fabricius 1986; Ledger, Hobbs & Van Rensburg 1987) and trees (Gargett 1990; C. Skinner pers. comm.; pers. rec.).

Black eagles are spectacular and conspicuous birds, and they occupy relatively small territories or home ranges. These are probably main reasons why the black eagle is one of the best-studied of all large eagles, but most knowledge of this species emanates from one in-depth, long-term and large-scale study of a particularly dense population in the Matobo Hills, led by Valerie Gargett. This project was instigated by Vernon (1965), and since then Gargett and co-workers have looked at nearly all aspects of breeding biology (especially siblicide), territoriality and spacing behaviour, diet, food requirements, feeding behaviour, time budgets and the pair-bond etc. (e.g. Gargett 1971, 1972, 1975, 1977, 1978, 1982a, 1982b, 1984). All previous aspects of the study are reviewed in Gargett (1990). Elsewhere black eagles have been the subjects for studies on breeding biology (Rowe 1947; Siegfried 1968), nest-spacing and territory/range size (Allan 1984, 1988; Boshoff & Palmer 1988; Brown 1988b), and hunting behaviour (Jenkins 1984). For more general information on black eagles see Steyn (1982) and Tarboton & Allan (1984). This extensive research has highlighted a number of unusual characteristics for this large eagle: a highly specialised diet; relatively small, well-defended territories or ranges; a very strong pair-bond; a conservative reproductive rate with obligate siblicide and a lengthy nestling period; and a breeding season which consistently occurs at much the same time of the year throughout Africa. So the preference for rock hyrax as prey by black eagles was well known, but the importance of this predation in terms of prey population dynamics had not been researched (the hyrax prey-base in the Matobo Hills is now receiving attention - Gargett 1993 unpubl.; Barry pers. comm.). The extent of livestock predation by black eagles in sheep-farming areas also warranted research. The need to cover these aspects of black eagles and their prey, together with the eminent suitability of this system for study, were prime motives for the present research (see Chapter 1).



To assess black eagle predation on rock hyrax in the KRNP it was essential to know how many pairs there were in the study area; whether they were territorial and excluded other eagles; over which rock outcrops, and hyrax colonies they foraged; whether they were nest-site limited; how often they raised chicks; and what factors affected this breeding rate, etc.. The present chapter provides this necessary background information on the black eagle population. The findings are contrasted with the abundant information available on black eagles in other areas, and density estimates in karoo mountain ranges are used to provide a population estimate in this region. With regard to behaviour, full details of the foraging and territorial behaviour of black eagles are provided in this chapter where they are directly relevant to the demographic influence of black eagle predation on rock hyrax. For the purposes of this thesis it was more important to know how many hyrax (and what population classes) are removed by the eagles from their ranges each year (Chapters 8 - 10) than details of when and how these hyrax are captured. However, such observations are of interest when considering the possibility of co-evolution between predator and prey, so a preliminary analysis is included here. It was also felt that these detailed observations might provide an insight as to why certain population classes of rock hyrax are more susceptible to foraging black eagles, and in such ways contribute to a better understanding of the system. Some of the more important factors affecting foraging behaviour and success are addressed, and some morphometric data are provided where these are relevant to behaviour. Further details pertaining to factors affecting prey capture rate are derived from a much larger database provided by time-lapse photography at black eagle nests in Chapter 8.



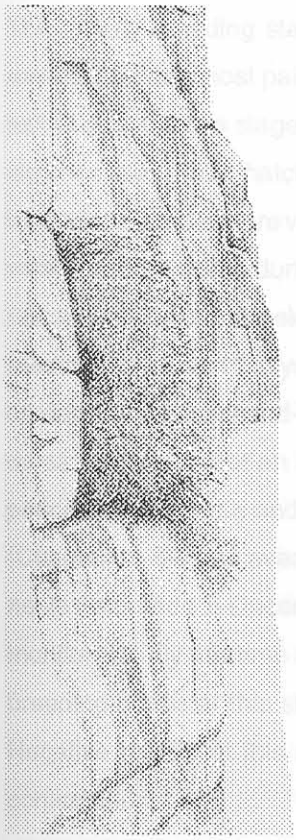
METHODS

Location and identification of nesting pairs of black eagles

Nesting pairs of black eagles were located within the study area by scrutinizing suitable cliffs with a pair of Swift Satellite 20*80 binoculars. Active nests were most obvious after the breeding season when they had become surrounded by whitewash (mutes). Location of pairs became predictable when approximate nest spacing was known for the upper and lower escarpments. Some additional unused nest sites were located during the course of habitat mapping for another part of this study (Chapter 3). By the end of the study all eagle pairs were well known and all cliffs had been carefully scrutinized for nest sites - it is unlikely that a significant number of nests were missed.

No adult resident birds were marked for this study, so productivity is given by nest-sites and their respective territories rather than by individual birds. Attempts to trap adult resident eagles with balchatris (using guinea pigs as bait) were abandoned after two weeks of intensive, unsuccessful effort. Five nestling black eagles were ringed and window-marked prior to fledging in 1987, but there were no resightings of these birds after the fledgling period, so this practice was also discontinued. For the purposes of assessing black eagle predation on rock hyrax it was not essential to be able to recognise individual eagles. It was quickly discovered that resident pairs could be identified by their behaviour, and that sexes could be distinguished on the basis of flight pattern (see later). However certain individuals were recognisable from unusual plumage characters (white feathers) and sometimes from moult patterns.

Nest-site selection and spacing between pairs



To permit investigation of nest-site selection, the following parameters were recorded for each nest site: resident pair; nest number; exact locality; nest base (bush/ledge etc.); substrate of nest cliff (dolerite/sandstone/mixed etc.); substrate form (sheer cliff/pillars etc.); aspect of cliff; estimate of nest height (m); estimate of nest cliff height (m); proportional positioning of nest locus up cliff (to give height above ground); and altitude. Heights of some cliffs were measured initially, as were distances from cliff top to nest (to enable accurate focusing of time-lapse cameras - see Chapter 8). Later estimates of cliff height were based on this experience. Nest height was also estimated and sticks were collected at 0,5 m intervals from one extremely tall nest (3,6 m) for age-determination by radio-carbon analysis (details in Davies & Vogel 1992). Availability of the various types of nest cliff was known for four intact territories and parts of four adjacent territories where rock outcrops had been mapped and described in detail (Chapter 3). Distances between neighbouring nests and alternate nest sites were measured off a 1:25000 map of the study area. The spacing pattern of resident pairs was investigated using the G-statistic described in Chapter 4 (pages 39-40).

Calculating population density

A density estimate was calculated for eighteen pairs of eagles: a perimeter was drawn around the known ranges of the outermost pairs, and encompassed 435 km^2. The derived estimate compared favourably with that of Boshoff & Palmer (1988) for elsewhere in the Nuweveld mountains. This enabled prediction of breeding population size in these and similar mountain ranges in the Karoo. Areas encompassed by these mountain ranges were determined by superimposing a grid upon 1:500000 and 1:1000000 topographical maps of the Cape.

Inferences on the non-breeding black eagle population were drawn from knowledge of the production and fledgling periods of chicks, and from observations on the incidence of territorial intrusions. The latter were recorded during behavioural observations (see later). Intruding juveniles and subadults could all be considered as part of the non-breeding or 'floating' population. Unidentified adults however, could be either 'floaters' or neighbours. These were separated on the basis that all birds flying in pairs could be considered neighbours and that resident birds consistently spent about four minutes flying in pairs for each minute flying alone (see later). In this way, probably about 20% of unidentified intruding adults flying alone were neighbouring residents. The remainder were added to the juveniles and subadults to give some indication of the structure of the floating population. Relative density of residents to floaters was derived as the ratio of the number of times that residents were observed flying against the number of times that floaters were observed flying.

Assessing breeding performance

The annual breeding status of each pair was monitored by three visits during the nesting period. It was soon established that most pairs were laying eggs during June (see Fig. 44), so the first visits were timed during the first half of July - by this stage nearly all pairs making a breeding attempt should have begun incubation, although early clutches may have hatched already. Breeding status was usually assessed by viewing the nests with 20*80 binoculars, but the more viewable nests (most lower escarpment pairs) were visited to assess clutch size. Nests were visited a second time during September to monitor development of any chicks and to detect any very late breeders. Black eagle chicks develop in easily recognizable stages (Steyn 1982; Gargett 1990) and hatching dates could be predicted to within 10 days by allocating chicks to these stages. These age determinations were facilitated by drawing on experience from hand-raising a young black eagle. Laying dates (first egg) could be predicted from these hatching dates on the basis of an incubation period of 44-45 days (Steyn 1982; Gargett 1990). Some nests (9 full nestling periods) were directly and continuously monitored by time-lapse photography to provide information on feeding habits (Chapters 8 & 9), so events and the fate of hatchlings in these nests could be determined precisely. A final visit to nests was made in December each year in order to assess productivity (mean number of chicks produced per pair monitored). By this time all chicks of that year had fledged but remained in the vicinity of the nest area. Assessing breeding status at this stage was timed to coincide with collection of prey remains from beneath the nest cliffs. Negative results at this stage (disappearance of large chicks) required intensive effort and repeated visits for confirmation.

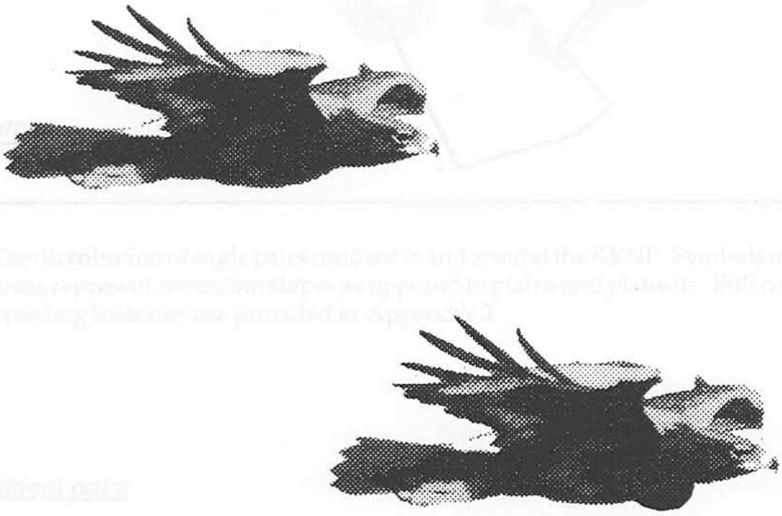
Correlation analyses (Ingraham *et al.* 1988) were employed to elucidate which factors may affect breeding success or failure. Annual productivity was considered in relation to rainfall and dynamics of prey populations (Chapter 4). Breeding success was considered in relation to timing of breeding, to dietary composition of the respective pairs (Chapter 9), to certain nest site parameters, and to the following characteristics of the eagle territories: total area; extent of the major topographical habitats; extent of farmland; extent of escarpment; and estimates of rock hyrax and red rock rabbit populations (derived from density estimates in the major habitats: Chapters 4 & 5). All areas were calculated by superimposing a grid over a detailed habitat map encompassing all territories. Escarpment was measured by planimeter off a 1:25000 map of the areas, and by GIS for the mapped area (Chapter 3). All statistical methods employed were carried out using the SAS computer system (Ingraham *et al.* 1988).

Behavioural observations

Chosen resident pairs (n=4) of black eagles were observed in stints of five continuous days (pentades). These observations were planned to evaluate the ranges of those pairs and to cover all the major periods of the year (pre-breeding, incubation, nestling, fledgling). Dawn to dusk watches were conducted from the most prominent and commanding viewpoints within each range. I did lose sight of distant flying birds on some occasions, but with practice and using the 20*80 binoculars I could track flying birds at up to seven km distance. Most pairs were not observed to travel this far from their core area, and detailed observations of the one pair that did (from different locations) suggested that this was the extreme limit of their range. Great effort was made to maintain visual contact of flying and perching eagles because they were difficult to relocate if contact was lost. For certain pairs nesting in kloofs (e.g. Kortkloof) it was impossible to view the entire range from a single location. In these cases I moved locations on different days and I also enlisted the help of observers in radio-contact (usually at the nest sites). From a sharp ridge near the Penberi nest site I had a commanding view of the entire range of this pair, and soon discovered that this was the only pair that I could keep in view almost continuously. I directed half of the total observation effort at this one pair because they yielded so much data. This pair were also clearly dimorphic (see later) permitting closer examination of the roles of the sexes. Nest sites were not always visible during these observations of foraging and territorial behaviour. Separate detailed observations were conducted at nest sites to check events on the nest against revelations of the time-lapse cameras. These observations are considered in Chapter 8.

Black eagles prefer to fly where the lift is greatest at the top of a slope. They habitually skirt around escarpment and other rock outcrops, maintaining close contact with the topography at most times. During a flight I used a dictaphone to describe the route and activity of the flying birds as I watched. The only time when this technique became somewhat ambiguous was when the eagles rarely engaged in high altitude soaring flight over their ranges. In these instances I often had to wait for the birds to descend level with landmarks on the mountains before I could reconstruct their route with some confidence. Immediately after each flight, I replayed the recording and plotted the flight path either onto detailed habitat maps which I had compiled for the territory or onto transparent overlays superimposed on aerial photographs showing the topography and rock outcrops. These flight paths were then digitised onto the geographical information system compiled for the area. In the case of plots over distorted aerial photographs, reference points along escarpments and river courses were compared with the real locations of these landmarks (on the GIS) and all flight path coverages were corrected by 'rubber-sheeting' on the GIS.

Each flight path was given a unique ID. on the GIS to enable linking with attribute data. I recorded the following parameters for each flight: date; pair; id. (male/female/unidentified adult/pair/juvenile); time at onset; duration (measured by stopwatch in seconds where possible); origin (from perch/flight/unknown); end point (to perch/another flight/lost); primary motive (e.g. hunting, territorial display, directional flight); secondary and tertiary motives if any; ambient temperature in the shade; wind speed; wind direction; % cloud cover; % humidity; any rainfall; mean height above ground; altitude (a.s.l.); inter-mate distance; which sex led; whether the birds had full crops; which slopes they viewed; which slopes they visited; number of strikes at prey; whether they killed; and the approximate division of flying time between slow gliding flight, fast gliding flight, circling, flapping, rising in lift (unidirectional), hanging, undulating, and stooping. Distances of each flight path were later measured on the GIS and compared with respective durations to compute an overall travel speed for each flight. A database was compiled of any strikes made at prey. Unseen kills could often be inferred when the eagles were seen flying with full crops. Similar but appropriate parameters were recorded for each perching session observed, and a database was also compiled for details of each perch location (not analysed here). At regular intervals throughout each observation day important weather variables were recorded at the viewpoint. Databases were later linked on date to climatic data obtained from the automatic recording station at Beaufort West (Weather Bureau). Attributing motives to each behaviour session was complicated because perching birds could be either resting or hunting or both. Also, birds could change mid-flight from territorial display to making a strike at prey. All behavioural indications were weighed up in such circumstances (for instance perching birds were considered to be resting when seeking shelter or shade on the nest cliff, and hunting when actively choosing perches with commanding views of prey habitats).



bulging crops indicating a feed are very noticeable on flying birds

RESULTS

Twenty three pairs of black eagles were located in and around the Karoo National Park at Beaufort West (Fig. 41). Three of these pairs are excluded from most of the following analyses either because of poor data (TG); or because the pair were seldom in occupation of their territory and never bred (MP); or because the pair occupied a different habitat outside the main study area (LX).

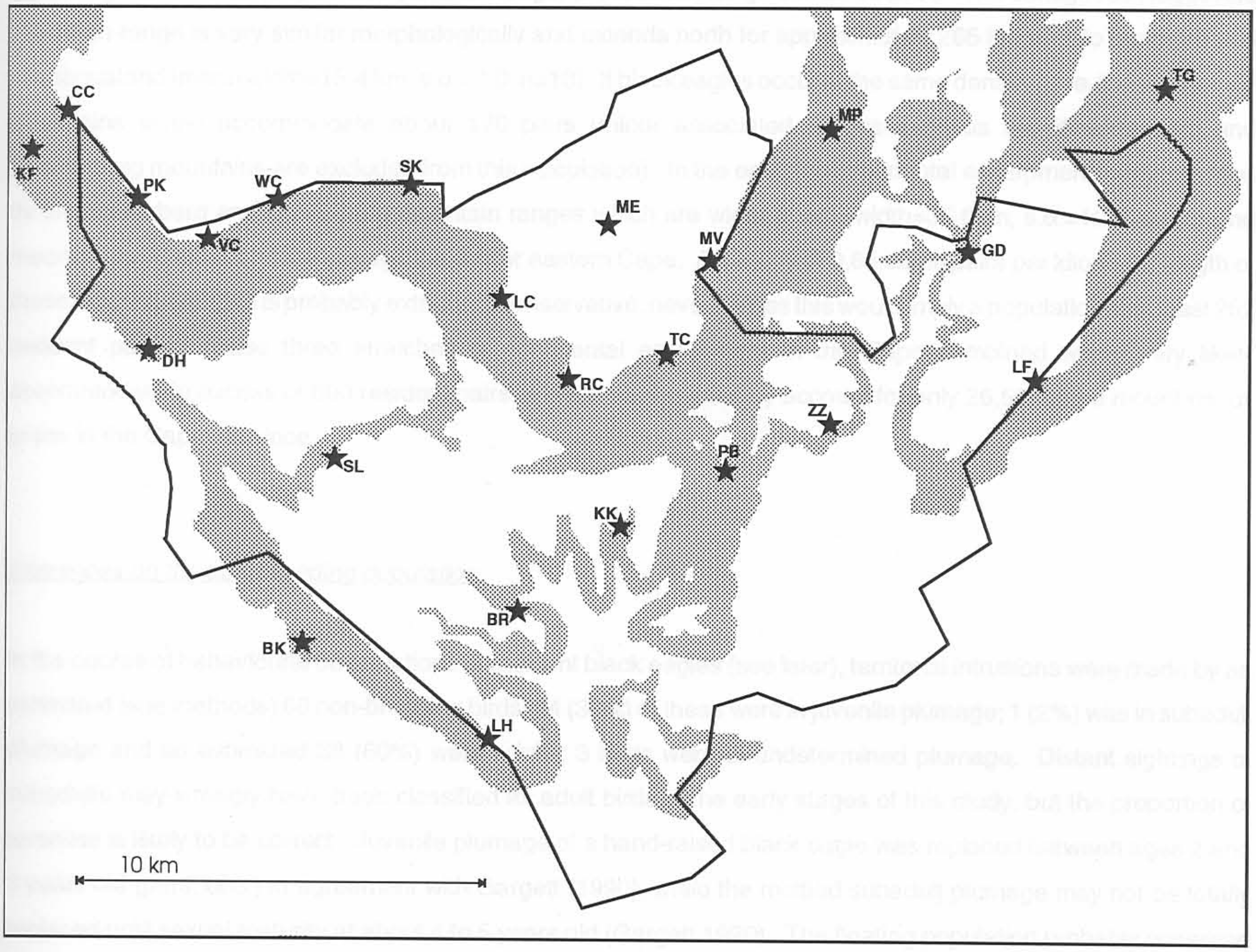


Figure 41. The distribution of eagle pairs resident in and around the KRNP. Symbols mark their principal nest sites. Shaded areas represent mountain slopes as opposed to plains and plateaus. Full names of each pair and their respective breeding histories are provided in Appendix 3.

Density of resident pairs

Eighteen pairs, whose ranges became well known, occupied 435 km^2. of terrain, yielding an accurate density estimate of 4,14 pairs/100 km^2 for the Nuweveld mountain habitat. Black eagles are very territorial in this area - they range over all habitats with slight overlap between pairs (see behavioural observations), so an average territory size of about 24 km^2 can be deduced.

Size of breeding population

The Nuweveld mountain range extends for approximately 237 km through the Great Karoo at a mean width of 15,5 km (measured at 10 random localities; s.d.=3,2 km). It thus encompasses approximately 3674 km^2 of mountainous terrain similar to that of the study area. This mountain range probably accommodates about 152 resident pairs of black eagles, and a density of 0,64 pairs/km length of mountain range can be inferred. The contiguous Roggeveld mountain range is very similar morphologically and extends north for approximately 265 km up into the more arid Namaqualand (mean width=15,4 km; s.d.=3,0; n=10). If black eagles occur at the same density here, the Roggeveld mountains would accommodate about 170 pairs (minor associated ranges such as the Koedoesberg and Bastersberg mountains are excluded from this calculation). In the east, the continental escarpment is represented by the Sneeuberg and Winterberg mountain ranges which are wider (mean width=35,0km; s.d.=12,7; n=10) and meander for at least 410 km through the wetter eastern Cape. A density of 0,64 eagle pairs per kilometre length of these mountain ranges is probably extremely conservative, nevertheless this would imply a population of at least 262 resident pairs. These three stretches of continental escarpment in the Cape combined would very likely accommodate in excess of 600 resident pairs of black eagles yet they account for only 26,5% of the mountainous areas in the Cape Province.

Inferences on the non-breeding population

In the course of behavioural observations of resident black eagles (see later), territorial intrusions were made by an estimated (see methods) 66 non-breeding birds: 24 (38%) of these were in juvenile plumage; 1 (2%) was in subadult plumage and an estimated 38 (60%) were adults; 3 birds were of undetermined plumage. Distant sightings of subadults may wrongly have been classified as adult birds in the early stages of this study, but the proportion of juveniles is likely to be correct. Juvenile plumage of a hand-raised black eagle was replaced between ages 2 and 3 years old (pers. obs.) in agreement with Gargett (1990), while the mottled subadult plumage may not be totally replaced until sexual maturity at about 4 to 5 years old (Gargett 1990). The floating population probably consisted of at least 40% immature (<4,5y old) birds.

Resident black eagles made 30 times more flights over their territories than non-residents. Although subject to observer biases this flight frequency ratio gives a crude indication of relative density and suggests that there is one non-breeding bird for every fifteen resident pairs (this does not represent the black eagle population outside of breeding habitat, where non-breeders may predominate). In addition to the floating population described above, fledglings are present in 46% of territories (see later) for 3 - 4 months in each year. One can conclude that the breeding estimate of 4,14 pairs/100km^2 given earlier probably corresponds to an overall long-term population density of at least nine birds per 100km^2 within breeding habitat in the Nuweveld mountains. A total population estimate of over 1300 black eagles can be inferred for the continental escarpment areas of the Karoo, and just over 30 individuals for the KRNP.

Nest spacing

Most resident pairs of black eagles in the study area had a few alternative nest sites (range 1 - 5; mean=2,2; s.d.=1,2; n=20 pairs). Alternative nest sites varied between 0,04km and 2,39km from the most active nest of a particular pair (mean=0,49km; s.d.=0,49; n=24 distances). There was a statistically significant tendency for pairs suffering a greater amount of breeding failure to possess more alternate nest sites (r=0,46; p<0,05). This relationship prevailed despite one pair suffering very heavy nest predation being limited to only one site. There was also some indication that the number of alternate sites was related to the amount of escarpment available (r=0,39; p<0,10).

The average distance between the active nest of a particular pair and that of their closest neighbour was 2,72 km (range 1,34 - 4,51; s.d.=0,95; n=20 pairs). Analyses of these distances yielded a G-value of 0,79 which indicates that this dispersion pattern approaches regularity. However, active nests of resident pairs were spaced more widely along the lower escarpment (mean distance between sequential pairs 4,64 km; range 2,97 - 7,05; s.d.=1,47; n=11 distances) than along the upper escarpment (mean=2,71 km; range 1,49 - 4,31; s.d.=0,98; n=8 distances), see Figure 41. This difference was statistically highly significant (t-test for equal variances: t=3,23; p<0,01). The average length of escarpment encompassed by territories of upper escarpment pairs (@3,6 km) was one quarter that (@14,3 km) encompassed by territories of lower escarpment pairs.

Nest site selection

Most nest cliffs chosen were either dolerite cliffs (20 nests, 39%) or dolerite pillars (19 nests, 37%); eight other nests (16%) were built on sandstone cliffs; and a further four nests (8%) on cliffs of mixed substrate. With regard to nest base: four nests (8%) were sited on bushes, 43 nests (84%) were sited on cliff ledges, and another 4 nests (8%) were sited on top of dolerite pillars. One bush nest and one ledge nest disintegrated or were destroyed by baboons during the study period, both had been built on sandstone cliffs.

In the area where all rock outcrops had been mapped, there was a statistically highly significant association between nest sites and certain nest cliff substrates (X^2=9,21; d.o.f.=2; p=0,01). A comparison of proportional use of nest cliff substrates against proportional availability of these substrates (Figure 42) revealed that sheer dolerite cliffs were highly preferred by the nesting eagles, over dolerite pillars or sandstone cliffs.

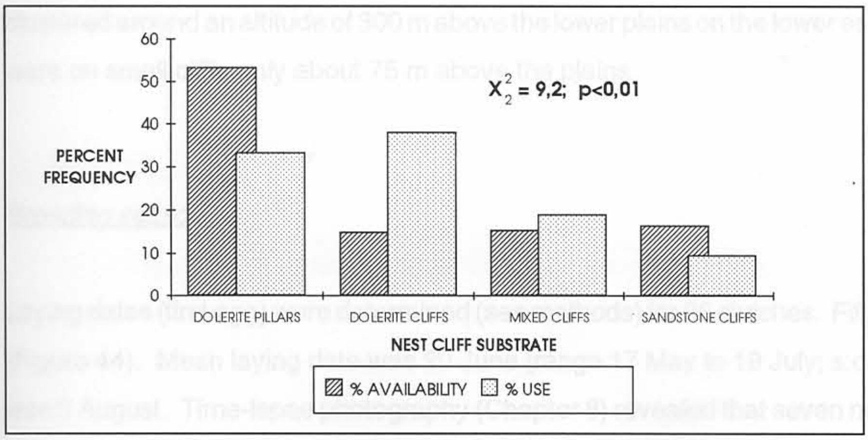


Figure 42. The use of different cliff substrates for nest sites, in relation to the availability of those substrates.

The estimated height of nests varied between 0,4 and 3,6 m (mean=1,2; s.d.=0,7; n=51). Radio carbon dating of sticks from different levels in a 3,6 m nest indicated that the material was about 14y old when brought to the nest, that the nest structure was only about 20y old, and that about 20cm of nest material is added each year (Davies & Vogel 1992). One pair (SK) attached a satellite nest to the base of a very tall nest when headroom beneath an overhang ran out. There was a slight tendency for larger nests to be found more frequently on tall cliffs (r=0,25; p=0,076).

Nesting eagles chose cliffs that ranged between 15 and 110 m high (mean=45,9; s.d.=23,4). Nests were sited on average 56,6% up these cliffs (range 15-95%; s.d.=19,7). Deduced height above ground ranged between 6 and 64m (mean=24,5; s.d.=13,0). Nests occurred proportionately higher up on small cliffs and lower down on large cliffs (r=-0,33; p<0,05), such that most nests occurred between 15 m and 40 m above the ground.

Forty nine percent of nests were sited on cliffs facing south; 27,5% faced west; 15,7% faced east; and only 7,8% faced north. Much of this pattern was no doubt due to availability of the various aspects. North-facing cliffs were the least available (12,7% of total escarpment length). But comparison of observed and expected (calculated from the extent of escarpment facing each direction) occurrences of nests revealed a statistically highly significant association between nest sitings and certain aspects (X^2=11,6; d.o.f.=3; p<0,01). In particular, south-facing cliffs were favoured and east-facing cliffs avoided (Figure 43).

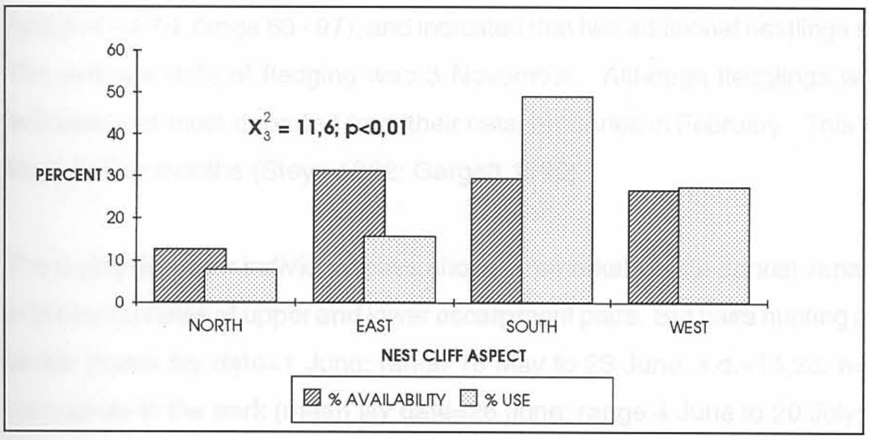


Figure 43. The use of different cliff aspects for nest sites, in relation to the availability of those aspects.

Thirty five percent of nests occurred on the upper escarpment cliffs, 920 m above the lower plains; 61% of nests were clustered around an altitude of 300 m above the lower plains on the lower escarpment cliffs; and a further 4% of nests were on small cliffs only about 75 m above the plains.

Breeding season

Laying dates (first egg) were determined (see methods) for 36 clutches. Fifty three percent of these were laid in June (Figure 44). Mean laying date was 20 June (range 17 May to 19 July; s.d.=16,8d). The average date of hatching was 3 August. Time-lapse photography (Chapter 8) revealed that seven nestlings spent an average of 88,3d in the

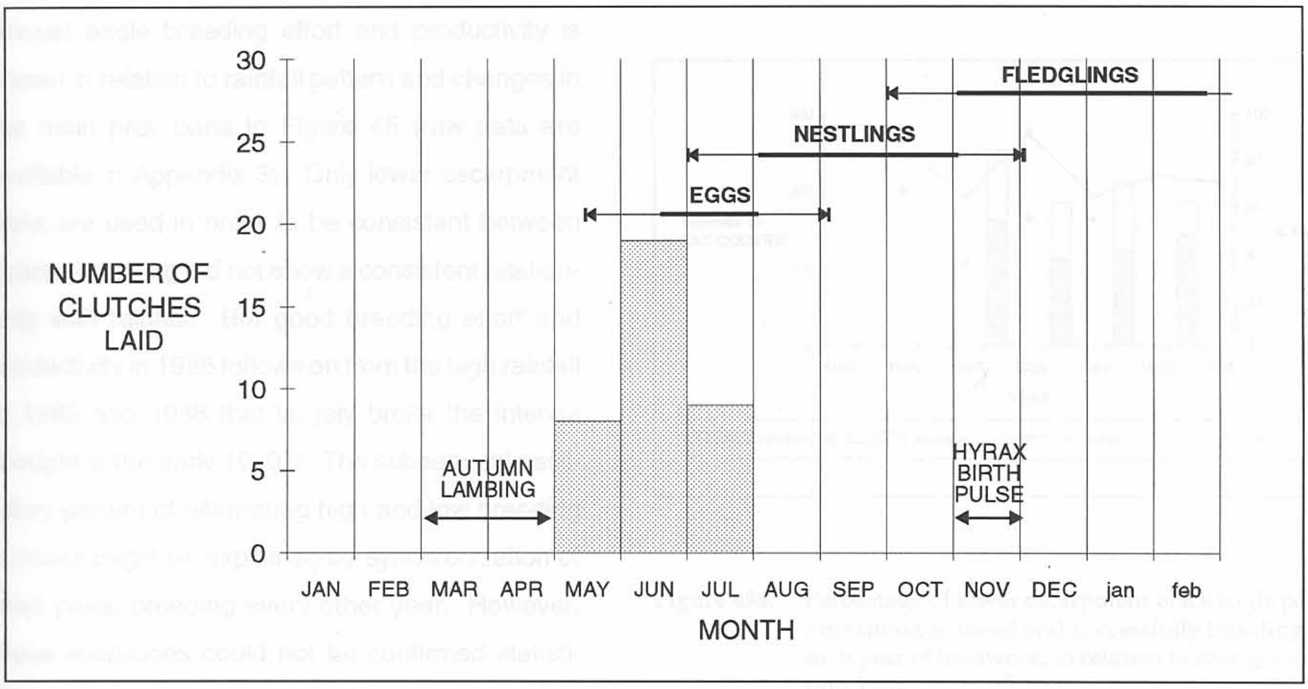


Figure 44. Breeding seasonality of black eagles in the Nuweveld Mountains during the present study. Columns represent the number of clutches laid; thick black horizontal lines represent development phases of the average chick; thin black lines represent the range of each major phase. The principal lambing season for Beaufort West farmers is shown.

nest (s.d.=4,7d; range 83 - 97), and indicated that two additional nestlings spent in excess of 81 and 88d on the nest. The average date of fledging was 3 November. Although fledglings were not closely monitored, observations indicated that most departed from their natal territories in February. This would concur with a dependent period of three to four months (Steyn 1982; Gargett 1990).

The laying dates for individual pairs showed remarkably little annual variation. There was no significant difference in the laying dates of upper and lower escarpment pairs. But pairs hunting almost exclusively on farmland (n=5) bred earlier (mean lay date=1 June; range 18 May to 23 June; s.d.=14,2d; n=10) than pairs (n=15) hunting mainly or exclusively in the park (mean lay date=26 June; range 4 June to 20 July; s.d.=10,7d; n=25). This difference was statistically highly significant (t-test for equal variances: t=6,0; p<0,01). Furthermore, pairs with more domestic bovid (sheep and goat) in their diet bred earlier (r=-0,81; p<0,01): this factor explained 65% of the variation in laying date. Farmers in the region inform me that about 65% of their lambs are born in March-April and about 35% in September.

Breeding success

The breeding status of established pairs became known over 84 pair years. Overall breeding effort (percentage of pairs that reached the incubation stage) was 61%. Overall productivity was 0,46 chicks/pair/year. In lower escarpment eyries I observed eight single egg clutches and 14 double egg clutches (mean=1,64; s.d.=0,49; n=22).

Annual eagle breeding effort and productivity is shown in relation to rainfall pattern and changes in the main prey base in Figure 45 (raw data are available in Appendix 3). Only lower escarpment pairs are used in order to be consistent between years. Breeding did not show a consistent relationship with rainfall. But good breeding effort and productivity in 1986 follows on from the high rainfall in 1985 and 1986 that largely broke the intense drought of the early 1980's. The subsequent oscillatory pattern of alternating high and low breeding success might be explained by synchronization of most pairs, breeding every other year. However, these suspicions could not be confirmed statistically. In any given pair year (including results for ten pairs monitored in 1991) there was a 65% likelihood of breeding and a 35% likelihood of not breeding. Certain pairs were consistently poor breeders. Thus the likelihood of a breeding attempt following on from a non-breeding season was low (39% likelihood; n=23). The likelihood of a breeding attempt following on from a successful breeding season was more or less as expected (68% likelihood; n=40). But more pairs tended to make a breeding attempt if the last breeding season failed (85% likelihood; n=13). In the few known instances (n=6) of pairs successfully raising chicks relatively late in the year, there was no suggestion that this led to reduced breeding effort in the following year. But early-nesting pairs did make more breeding effort ($r=-0,57$; $p<0,05$) and they were more successful ($r=0,50$; $p<0,05$).

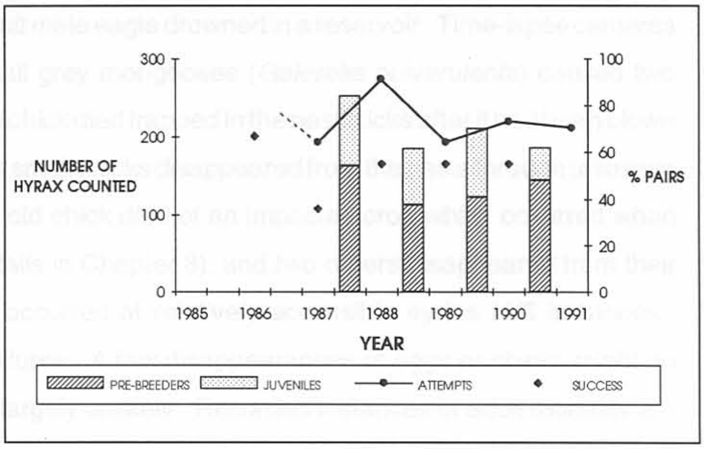


Figure 45a. Percentage of lower escarpment black eagle pairs attempting to breed and successfully breeding for each year of fieldwork, in relation to changes in the prey base

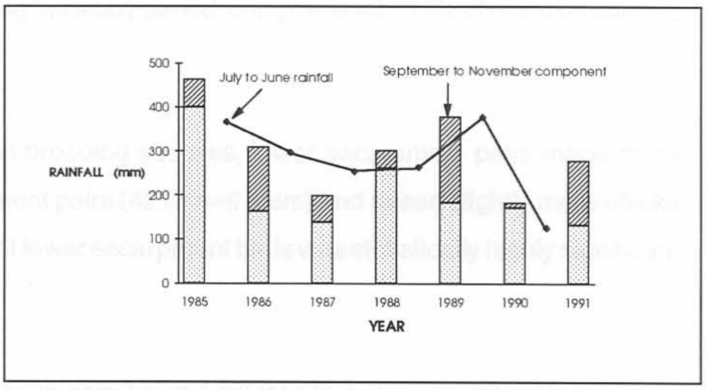


Figure 45b. Patterns in the rainfall recorded in the KRNP prior to, and during fieldwork.

Nineteen chicks hatched from 24 eggs that were closely monitored (79,2% viability). These eggs occurred in eight single egg clutches and eight double egg clutches. Inviability was twice as likely (4 eggs/16=25%) in double egg clutches as in single egg clutches (1 egg/8=12,5%), but only caused a breeding failure in the single egg clutch. An egg disappeared from a double egg clutch (perhaps stolen by egg-collectors), but this was not the ultimate cause of this nest failure. Siblicide occurred on all occasions (n=4) when two eggs were seen to hatch in the same nest.

Breeding failure occurred most often when small chicks were in the nest (6-7 out of 11 failures, see Appendix 3). In one instance a 10d old chick was abandoned when the adult male eagle drowned in a reservoir. Time-lapse cameras revealed that predation of newly-hatched chicks by small grey mongooses (*Galerella pulverulenta*) caused two consecutive failures at one eyrie, and that one two-day old chick died trapped in the nest sticks after it had been blown out of the nest bowl by gale-force winds. In other instances small chicks disappeared from the nests through unknown causes. Large chicks suffered lower mortality: one 78d old chick died of an impacted crop which occurred when feeding after an extended period without food (more details in Chapter 8), and two others disappeared from their eyries. Disappearance or predation of chicks usually occurred at relatively accessible eyries (4/6 instances). Circumstances were unknown for only two other nest failures. A few disappearances of eggs or chicks might be attributed to human depredations, but this is considered largely unlikely. Recorded instances of adult mortality are given in Appendix 3.

A link between nest failure and nest site accessibility could be demonstrated by comparing nest sites where failures occurred (n=11) with nest sites that consistently succeeded (n=15). Unsuccessful nests tended to be smaller and closer to the ground than successful nests. Nest cliffs where nest failures occurred were significantly smaller (mean height=35,8m; s.d.=15,8) than nest cliffs (mean height=55,9m; s.d.=26,3) where successful nests were sited (equal variances t-test: t=-2,3; p<0,05). Nest failure was not apparently linked with other nest site characteristics such as position on cliff or aspect, but did appear to be influenced in part by the substrate of the nest cliff. As much as 75% of nests on sandstone cliffs experienced some failure during the study period, compared with 37% of nests on dolerite and 33% of nests on mixed substrate cliffs.

With regard to the influence of habitat characteristics on breeding success, lower escarpment pairs made more breeding attempts (73%; n=11 pairs) than upper escarpment pairs (42%; n=9 pairs) and raised slightly more chicks (0,53 vs 0,35 chicks/pr/y). The enhanced breeding effort of lower escarpment birds was statistically highly significant (Kruskal-Wallis test: X^2=7,2; d.o.f.=1; p<0,01).

Various characteristics of the eagles' territories were used in correlation analyses to explain variation in breeding effort and success by the eagle pairs. Correlation models incorporating seven of the territory variables explained up to 83% of the variation in breeding effort but not more than 51% of the variation in breeding success, the latter being influenced by the somewhat stochastic effect of nest failure. Greater breeding effort was made in territories which were larger (r=0,69; p<0,01), had a greater extent of bottom plains (r=0,69; p<0,01), a greater extent of lower slopes (r=0,60; p<0,05), a greater extent of farmland (r=0,50; p<0,05), and a smaller extent of upper plateau (r=-0,58; p<0,01). The extent of the other major habitats did not appear to be involved with breeding effort.

Eagle pairs were divided into those (n=5) whose territories encompassed predominantly farmland, and those (n=16) whose territories encompassed predominantly parkland. Farm birds (20 pair years) showed an overall breeding effort of 85%, an overall productivity of 0,70 chicks/pr/yr, and a failure rate of 18%. Park birds (69 pair years) by contrast, showed an overall breeding effort of 59%, an overall productivity of 0,43 chicks/pr/yr, and a failure rate of 27%. These differences could not be demonstrated to be statistically significant, but the data were not well suited for statistical comparison.

Breeding effort was not greater in territories containing more red rock rabbits, but it was greater in territories containing more rock hyrax (r=0,49; p<0,05; prey population sizes estimated from data in Chapters 4 & 5). Comparison of breeding record and dietary parameters for the different pairs revealed no significant relationship between breeding effort and the number of species taken, or the proportion of red rock rabbits or domestic lambs in the diet. But pairs with a greater proportion of rock hyrax in their diet did make a significantly greater breeding effort (r=0,59; p<0,05). This was also the only variable which indicated some correlation with breeding success (r=0,45; p=0,07).

Behaviour

Time budgets and activity rhythms

During 30d observation outside the incubation period at least one member of each observation pair was in sight for 40% of the time. Coverage for the Penberi pair was much greater than this. Outside incubation, eagles spent 24,3% of their time flying and 75,7% of their time perched. When flying, individuals spent 85,4% of their time in tandem and 14,6% of their time solo. When perched, individuals spent 75% of their time together and 25% of their time apart. During incubation (10d obs.), the pair obviously spent more time perched/incubating and more time apart. Slow gliding flight and circling flight comprised most time in the air. Energetically costly flapping flight was minimised to just under 2% of flight time (Figure 46). Hunting activity occurred in three major peaks during the day separated by 3,5-4h intervals: at 08h30, 12h00 and 16h00 (Figure 47). Most flying occurred after mid morning and this was dependent on flying conditions. On very still days, smaller eagles such as booted eagles could get airborne on thermals at about 09h00, but black eagles usually began soaring two hours later than this. More supportive flying conditions may explain why most non-hunting flights by black eagles were initiated around midday and early afternoon (Fig. 47). Eagles would often indulge in territorial displays around midday.

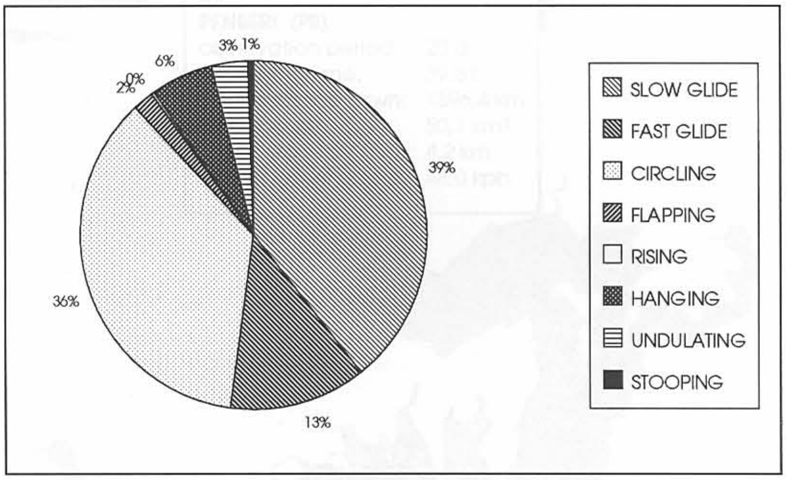


Figure 46. Relative duration of different flight styles used by black eagles.

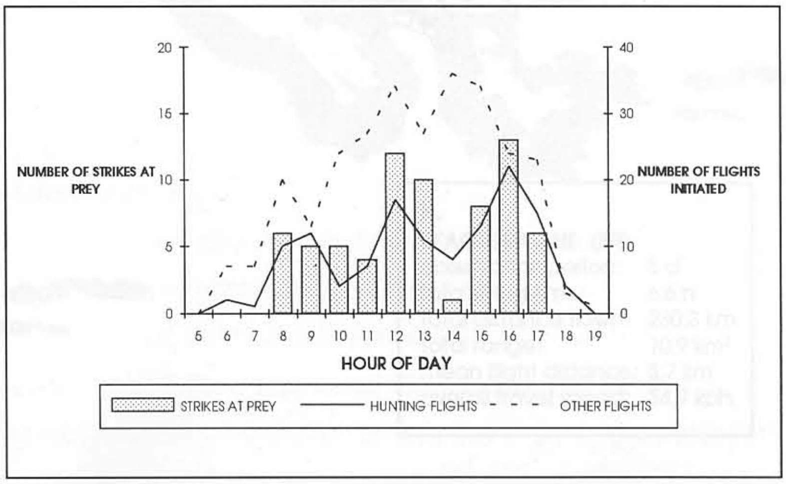


Figure 47. Overall daily activity rhythm of black eagles.

Use of habitats

During the full 40d of observation of four neighbouring black eagle pairs 693 flights were observed and recorded. These flight paths are shown for the separate pairs in Figure 48 along with various flight statistics. It is evident that most flying occurred over the mountain slopes and especially along the escarpment, but it should be noted that pairs with access to bottom plains (e.g. PB and LH) made extensive use of this habitat, while other pairs (BR & KK), which do not have access to the plains, appeared to be sandwiched into their smaller mountainous ranges by neighbours.

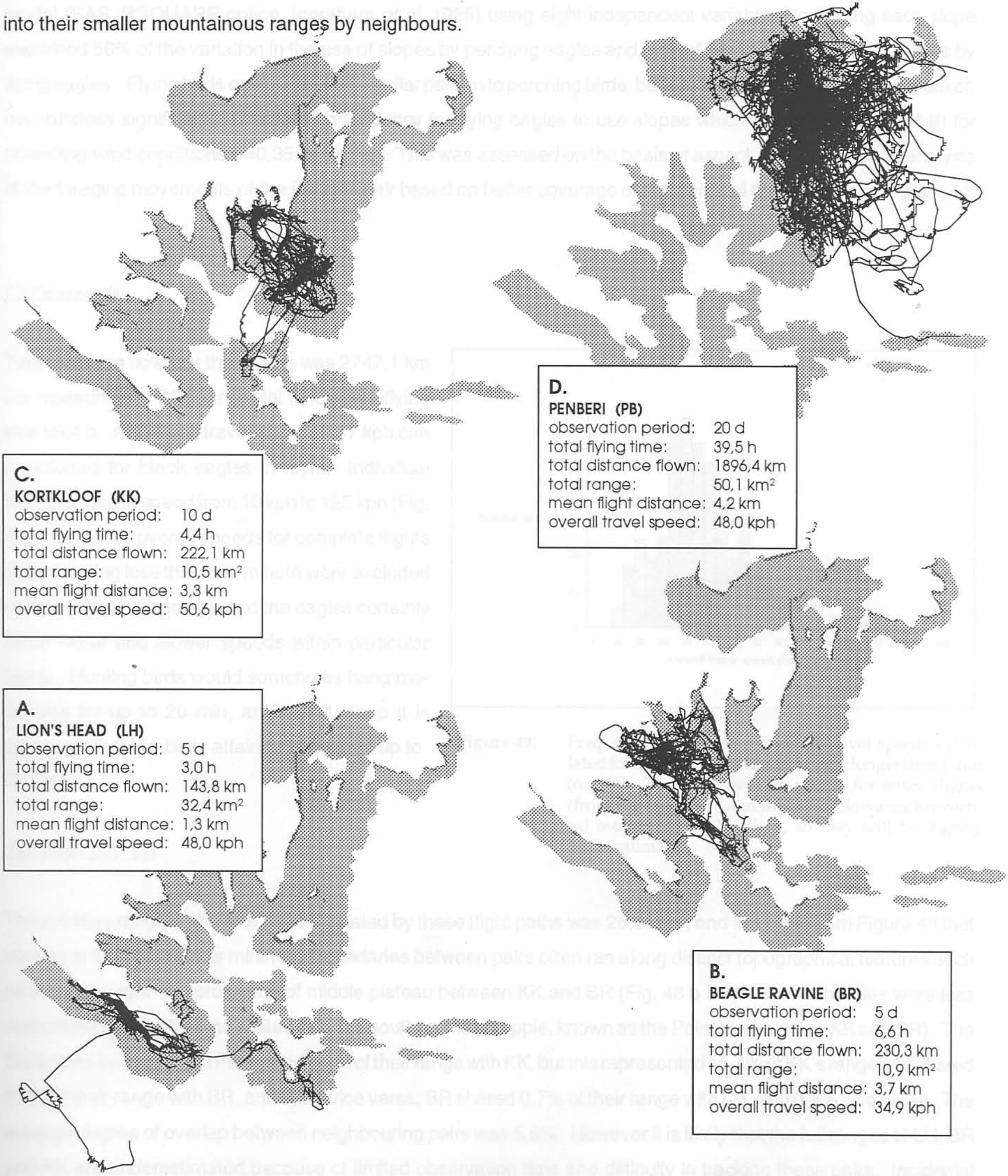


Figure 48. Flight paths of four adjacent pairs of black eagles in the KRNP shown against mountain slopes (grey) and escarpment (dark grey).

A preliminary correlation analysis on the use of slopes (no. times visited/viewed) by the Kortkloof pair revealed that perched birds made more use of slopes within their range that were more boulder-strewn (r=0,63; p<0,01), had more white-wash streaks on the rocks indicating hyrax presence (r=0,48; p<0,01), had more escarpment (r=0,47; p<0,01), were closer to the nest (r=-0,41; p<0,05), and had more ideal sandstone outcrops for hyrax (r=0,38; p<0,05). Use of slopes did not correlate significantly with area of slope, number or density of rock crevices, number or density of hyrax as predicted by an early method (see Chapter 4), nor any other quantity of refuge micro-habitats. A correlation model (SAS, RSQUARE option, Ingraham *et al.* 1988) using eight independent variables describing each slope explained 56% of the variation in the use of slopes by perching eagles and 47% of the variation in use of slopes by flying eagles. Flying birds exhibited a very similar pattern to perching birds, but correlations were somewhat weaker, nevertheless significant. There was a tendency for flying eagles to use slopes which had a high index of lift for prevailing wind conditions (r=0,35; p=0,052). This was assessed on the basis of aspect. A more detailed analysis of the foraging movements of the Penberi pair based on better coverage of this pair and their prey base is planned.

Flight speeds

Total distance flown by the eagles was 2747,1 km (as measured by GIS), and total time spent flying was 58,4 h. An overall travel speed of 47 kph can be inferred for black eagles in flight. Individual flights ranged in speed from 10 kph to 125 kph (Fig. 49). These are overall speeds for complete flights (flights lasting less than one minute were excluded for the sake of accuracy), and the eagles certainly attain faster and slower speeds within particular flights. Hunting birds would sometimes hang motionless for up to 20 min, and in full stoop it is estimated that the birds attained speeds of up to 200 kph.

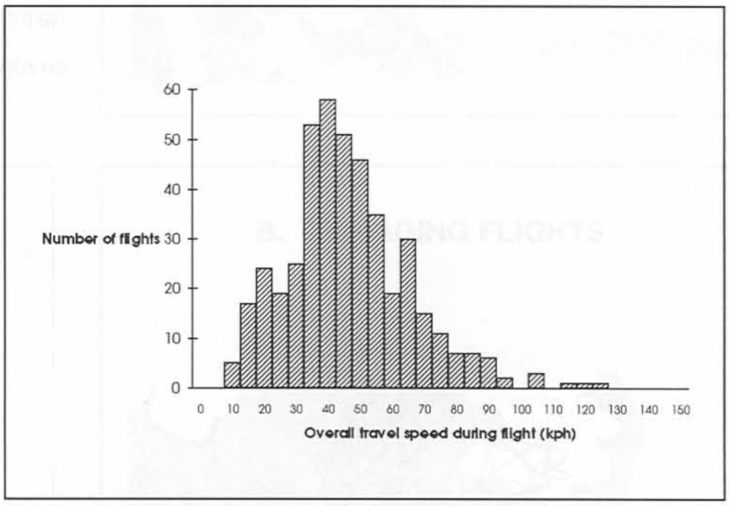


Figure 49. Frequency histogram of overall travel speeds calculated for all black eagle flights lasting longer than 1 min (n=826). These are average speeds for entire flights (from start to finish) and make no allowance for vertical movement of the birds, so they will be slightly underestimated.

Territorial overlap

The average range of the four pairs indicated by these flight paths was 26,0 km^2, and it is clear from Figure 48 that overlap in the ranges was minimal. Boundaries between pairs often ran along distinct topographical features such as the long finger-like projection of middle plateau between KK and BR (Fig. 48 b & c). But boundaries were less well defined farther from nest sites (e.g. the southernmost koppie, known as the Pointer, shared by KK and BR). The flight paths indicated that PB shared 3,2% of their range with KK, but this represented 15,4% of KK's range; KK shared 6,9% of their range with BR, and 6,6% vice versa; BR shared 0,7% of their range with LH, and 0,3% vice versa. The average degree of overlap between neighbouring pairs was 5,5%. However it is likely that the full ranges of LH, BR and KK are underestimated because of limited observation time and difficulty in tracking these pairs. Incidental observations indicated that the kloof between LH and BR (Gymnogene Gorge) was shared by both pairs, and that KK ranged farther east along the Pointer. So average range size for lower escarpment pairs may be larger than indicated by these flight paths and the degree of overlap between neighbours might approach 10%. Overlap between full ranges of neighbouring pairs does not necessarily confer overlap in foraging ranges. Intensive observations of the Penberi pair indicated that flights where hunting was the prime motive (mean flight distance 5,7km) were more confined to a core area than the far-ranging flights (mean flight distance 8,2km) where territorial display was the prime motive (Figure 50). Simple directional flight (perch to perch) was the third apparent major motive for flights, and these flights were short (mean flight distance 2,3km). Statistical comparison of complete flights (perch to perch) revealed that there was a highly significant difference in flight distance for these three major motives (K^2=69,7; d.o.f.=2; p<0,001).

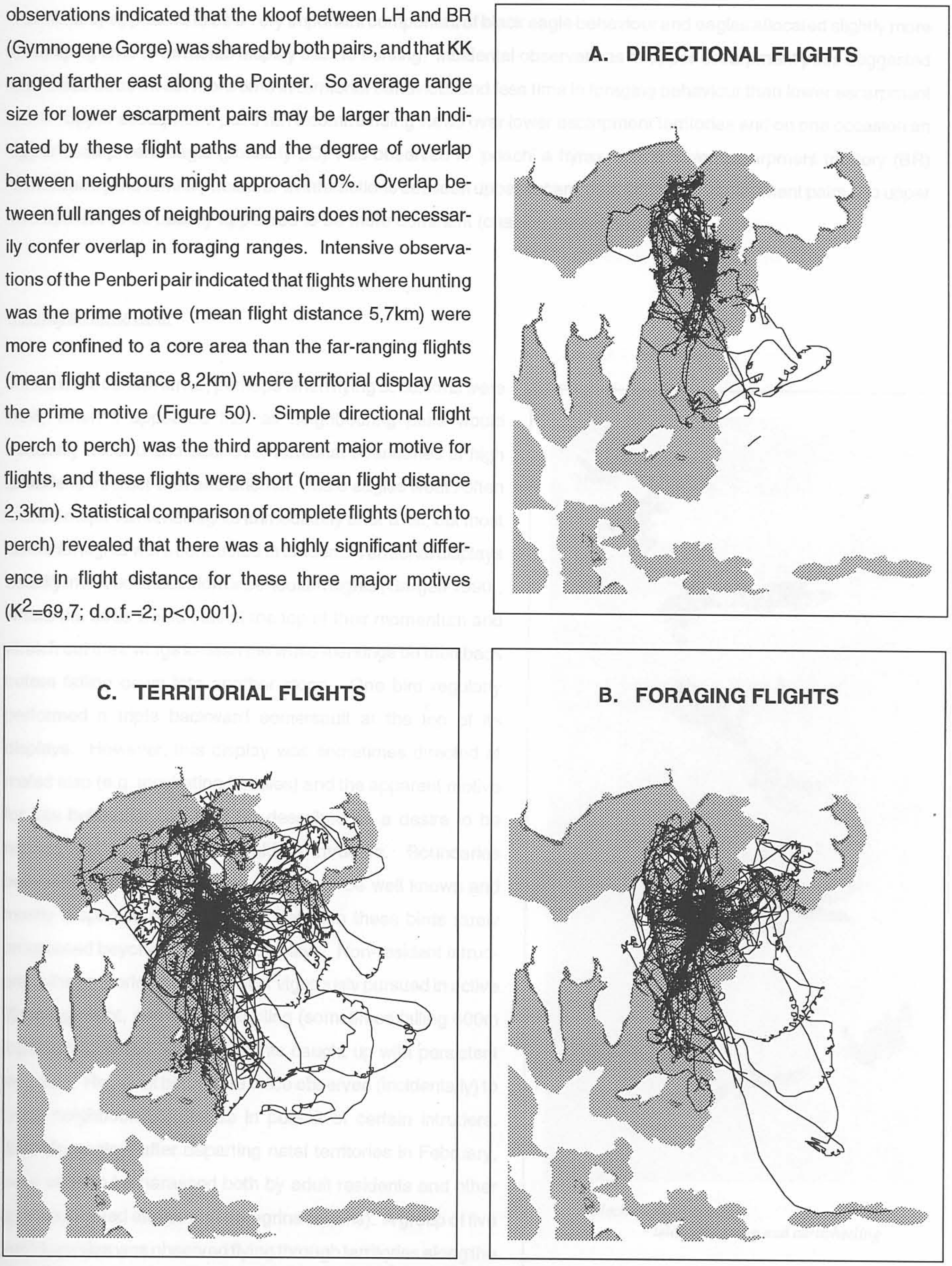
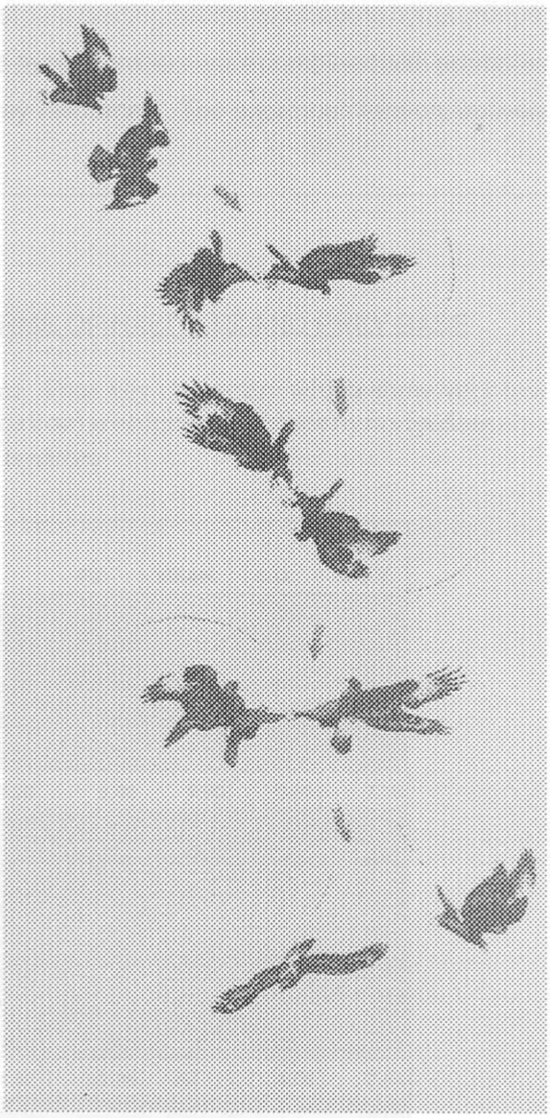


Figure 50. All flight paths of the Penberi eagles when their primary motive could be identified as (A) directional flight, (B) foraging behaviour, and (C) territorial behaviour. Some resolution was lost converting the ARCINFO coverages into WINDOWS METAFILE format, so the circling routes appear very angular. Elongated zig-zag routes are evident and these mark the location of pendulum displays (see text). Mountain slopes shaded.

Territoriality appeared to be a very important component of black eagle behaviour and eagles allocated slightly more (7%) flying time to territorial display than to hunting. Incidental observations of upper escarpment pairs suggested that these birds invest more time in territorial behaviour and less time in foraging behaviour than lower escarpment pairs. Upper escarpment pairs have commanding views over lower escarpment territories and on one occasion an upper escarpment eagle (possibly LC) was observed to 'poach' a hyrax from a lower escarpment territory (BR) unnoticed by the territory holders. In interactions between upper escarpment and lower escarpment pairs, the upper escarpment birds usually appeared to be more dominant (chasing rather than fleeing).

Territorial behaviour

There were certain times, perhaps when flying conditions were best, when it appeared that all neighbouring pairs would suddenly ascend and soar over territorial boundaries at high altitude to interact with one another. Male eagles would often launch major territorial flights immediately after a kill, but most territorial flights were conducted in tandem. Territorial displays usually involved undulation or pendulum flights (Gargett 1990), where the birds would stall at the top of their momentum and stretch out their wings to flash the white markings on their back before falling down into another stoop. One bird regularly performed a triple backward somersault at the top of its displays. However, this display was sometimes directed at mates also (e.g. incubating females) and the apparent motive for this behaviour can best be described as a desire to be noticed and a warning to would-be intruders. Boundaries between neighbouring pairs appeared to be well known and mostly respected so aggression between these birds rarely progressed beyond undulation displays. Non-resident intruders to the territories were however vigorously pursued in active (flapping) flight, and talon-grappling (sometimes falling 600m together) occurred when residents caught up with persistent intruders. Resident birds were twice observed (incidentally) to cross neighbours' territories in pursuit of certain intruders. Juvenile eagles, after departing natal territories in February, were seen to be harassed both by adult residents and other species (booted eagles and peregrine falcons). A group of five such juveniles was observed flying through territories along the upper escarpment. Both escarpments appeared to be used as major 'flyways' by the non-breeding population. Harassment of a free-living, hand-raised eagle by wild resident adults in the KRNP became more intense when the hand-raised bird moulted into adult plumage.



Black eagle aggression
- talon grappling and cartwheeling

A comparison of territories

Some territories (e.g. PB) were much larger than others (e.g. KK). To elucidate whether this variation was due to behaviour of the owners or the distribution of resources, various characteristics were statistically compared (Table 14) for the four neighbouring territories where the prey base and its refuge environment had been intensively mapped by GIS (Chapters 3 & 4). Each slope in the mapped area (Chapter 3, page 29) was allocated to a particular territory on the basis of flight paths (earlier) and incidental observations of the pairs. Slope data were then summed according to territory. Slopes had been defined as they would be observed by foraging eagles, and as most territorial boundaries followed obvious topographical features such as ridges separating slopes, this approach seemed appropriate.

There was great variation in the extent of some of the major habitats and in the extent of areal rocky habitats defended by the pairs. Despite wide variation in territory size, all pairs defended remarkably similar amounts of mountain slopes, lineal rock outcrops, hyrax groups and especially the amount of safe feeding habitat available to hyrax groups. Variation between territories was not reduced when estimates of rock hyrax numbers were combined with estimates of red rock rabbit numbers to give a more complete overview of prey resources. The enormous territory actively

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TABLE 14

A COMPARISON OF FOUR EAGLE TERRITORIES IN TERMS OF HABITATS AND PREY BASE

Surface area calculations included compensation for slope gradient. Four key characters which show very low variability (as expressed by standard deviation and coefficient of variation) are highlighted. Safe hyrax feeding area was calculated on the GIS as all areas within 15m of rocks in each territory.

parameter	units	LH	BR	KK	PB	MEAN	S.D.	% C.V.
SURFACE AREA	km2	32.00	19.30	21.10	30.30	25.68	6.40	24.94
BOTTOM PLAINS	km2	19.89	2.61	6.76	19.04	12.08	8.71	72.11
LOWER SLOPES	km2	8.59	8.00	9.18	7.65	8.36	0.67	8.06
MIDDLE PLATEAU	km2	3.59	8.72	5.17	1.79	4.82	2.95	61.14
UPPER SLOPES	km2	0.00	0.00	0.00	1.79	0.45	0.90	200.00
MOUNTAIN SLOPES	km2	8.60	8.00	9.20	9.40	8.80	0.63	7.19
NUMBER OF OUTCROPS	#	755	707	498	658	655	112	17.05
ESCARPMENT	km	10.38	16.07	11.01	12.32	12.45	2.55	20.48
SANDSTONE + DYKES	km	49.84	36.21	40.61	40.04	41.68	5.78	13.88
KOPPIES + KNOLLS	km2	0.79	2.4	2.31	0.39	1.47	1.03	70.13
SCREES	km2	1.77	2.33	2.75	2.97	2.46	0.53	21.52
LARGE ROCKS	#	14801	18854	23966	25626	20812	4936	23.72
BOULDERS	#	441	559	780	908	672	211	31.39
TOTAL LINEAL OUTCROPS	km	60.22	52.28	51.62	52.36	54.12	4.08	7.54
TOTAL AREAL OUTCROPS	km2	2.56	4.73	5.06	3.36	3.93	1.17	29.83
ROCK SURFACE AREA	km2	3.40	5.72	5.92	4.20	4.81	1.21	25.24
SAFE HYRAX FEEDING AREA	km2	5.06	5.53	5.59	5.34	5.38	0.24	4.44
CREVICES	#	35464	48272	48688	44975	44350	6152	13.87
HYRAX GROUPS	#	67	66	59	59	63	4	6.93
HYRAX	#	1099	1082	968	968	1029	71	6.93
RED ROCK RABBITS	#	459	463	327	276	381	94	24.77
PREY	#	1558	1545	1295	1244	1410	165	11.66

patrolled by the Penberi pair actually contained fewer estimated prey resources than the smaller neighbouring territories. It is not obvious from this analysis whether the eagles are able to defend their territories on the basis of hyrax numbers or on the basis of some closely-correlating variable such as mountain slopes or rocky habitat, which might be more easily assessed by the occupants. But it was particularly striking that three territories (BR, KK & PB) should each defend 52km of lineal rock outcrop (coefficient of variation <1% for this variable if LH is excluded), and that the safe feeding area available to hyrax showed the least variability of all parameters, between territories. Defence of greater amounts of lineal rock outcrops (60km) by LH may be compensatory for a lack of other hyrax refuge habitat in this territory, particularly screes.

Strikes at prey

Success of various black eagle foraging tactics could be appraised by considering the outcomes of strikes at prey. Strikes were defined as a definite and purposeful approach towards sighted prey. One strike was witnessed for every 2,6h continuous observations of eagles. One kill was witnessed for every 23,6h continuous observations of eagles. A total of 112 strikes at prey (mostly hyrax) were witnessed in the course of observations and other fieldwork, but only 106 provided complete data for interpreting success. Strikes were launched at distances ranging from 20 - 1900m (mean=679; s.d.=454). These distance measurements include no compensation for gradient of approach. On one occasion the Penberi pair spotted a karoo korhaan in the veld on the bottom plains at exactly 1965m distance and killed it after a flight lasting 1 min 32 sec (their flight speed in a fast glide was 77kph). There was no significant difference in the length of strikes made from perches and those made from searching flight. Most strikes were not far from nests (mean distance from nest=1143m; s.d.=707; range=220 - 3200). Of all strikes yielding complete data (n=106), nine resulted in kills. This represents a success rate of 8,5%. However many of the strikes were abandoned well before the eagles reached their prey. If these are excluded, the eagles achieved a success rate of 12,5%.

Surprise attacks

Only 9% of strikes were made at non-targeted hyrax which were encountered 'by surprise' as the eagles flew around rock outcrops, and none of these were successful. Eagles preferred to sight their prey first from a perch or from a high altitude flight (up to 600m above ground) and then make an attack, i.e. hunting by observation rather than expectation. Often the birds would fly off out of sight before making a concealed approach at high speed, low altitude and close together. Approach paths to prey were often (53% of strikes) estimated to be less than six metres above the ground. Cover was used on 42% of strikes, and the eagles attacked with the sun directly behind them on 12% of occasions. On a few occasions an attacking eagle was observed to take a very indirect route in order to position itself below the skyline against a low sun on its approach to prey.

'Still hunting' versus 'active hunting'

Eagles spent more time hunting from perches ('still hunting') than from searching flight ('active hunting'), but searching flight provided a higher prey encounter rate (0,79 strikes per hour) than perch hunting (0,26 strikes per hour), with the overall result that approximately equal numbers of strikes were made from both methods. The success rates of strikes launched from perches versus searching flight are summarised in Table 15. Strikes made while still hunting were approximately twice as successful as strikes made while active hunting, but these differences could not be demonstrated statistically.

TABLE 15

SUCCESS OF BLACK EAGLE STRIKES AT PREY:
STILL HUNTING VS. ACTIVE HUNTING, AND SOLO HUNTS VS. TANDEM HUNTS
(abandoned strikes included)

	SOLO	TANDEM	SOLO + TANDEM
STILL HUNTING	2/26 = 7,6%	4/26 = 15,4%	6/52 = 11,7%
ACTIVE HUNTING	1/26 = 3,8%	2/28 = 7,1%	3/54 = 5,6%
STILL + ACTIVE	3/52 = 5,8%	6/54 = 11,1%	9/106 = 8,5%

Co-operative hunting behaviour

The success of strikes made while hunting in tandem or solo is also contrasted in Table 15. Tandem strikes were approximately twice as successful as solo strikes, but again this difference was not statistically significant. No successful solo strikes were observed until the Penberi pair were observed for five days during the incubation period in July 1989. Black eagle pairs monitored one another closely when perched together or while flying in tandem. The average estimated distance between mates during a high speed attack was 44m. Four out of five prey items were shared. Some smaller prey (a suricate and a karoo korhaan) and carrion (springbok) were eaten away from the nest. The suricate was killed outside the nesting period. Other prey, including hyrax juveniles and all adults, were conveyed to the nest cliff. Division of labour was apparent on 45% of tandem strikes and on four out of five closely witnessed kills by pairs. During an attack the female would usually flush the prey from cover (sometimes by landing on rocks or bushes), while the male would hang overhead and catch the prey as it flushed. This method was also employed by a resident pair of eagles attacking an intruding sub-adult in their territory. Females were observed to flap more to keep up with males in light airs. Males initiated most of the hunting flights and led 82% of the observed strikes at prey. Females were more inclined to terminate tandem hunting flights.

Movements of male, female and juvenile black eagles within their territory

Intensive observation of the Penberi pair provided sufficient data to compare movements of the pair together, the male alone, the female alone and the 1989 fledgling (Figure 51). Most flights, particularly the far-ranging territorial flights were conducted as a pair. Extensive solo flying by the male was mainly recorded during the incubation period and it is apparent that the male preferred to remain in the core foraging area near to the nest. Female solo movements were very limited and mainly restricted to the nest area. Flights by the pair were longer (mean distance 6,1km; s.d. 6,5) than flights by the male (mean distance 4,1km; s.d. 4,3) or flights by the female (mean distance 2,2km; s.d. 2,1). These differences were statistically highly significant (K^2=12,5; d.o.f.=2; p<0,01). Flights of the juvenile (for 5d about 2,5mth after fledging) were also very limited and restricted to a kloof behind the nest area. The juvenile did not accompany the adults on long flights and was not involved in any of their hunting behaviour.

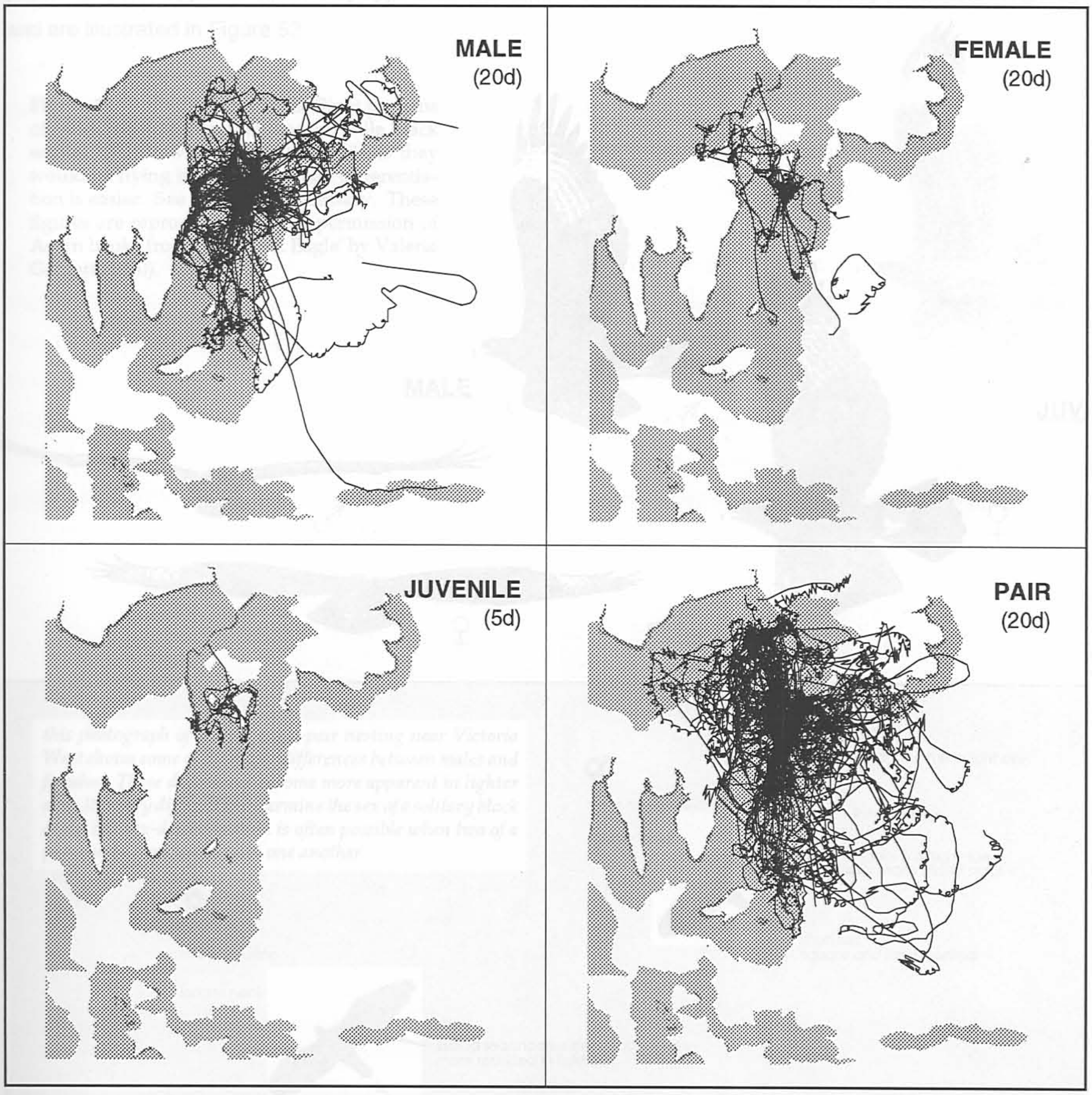
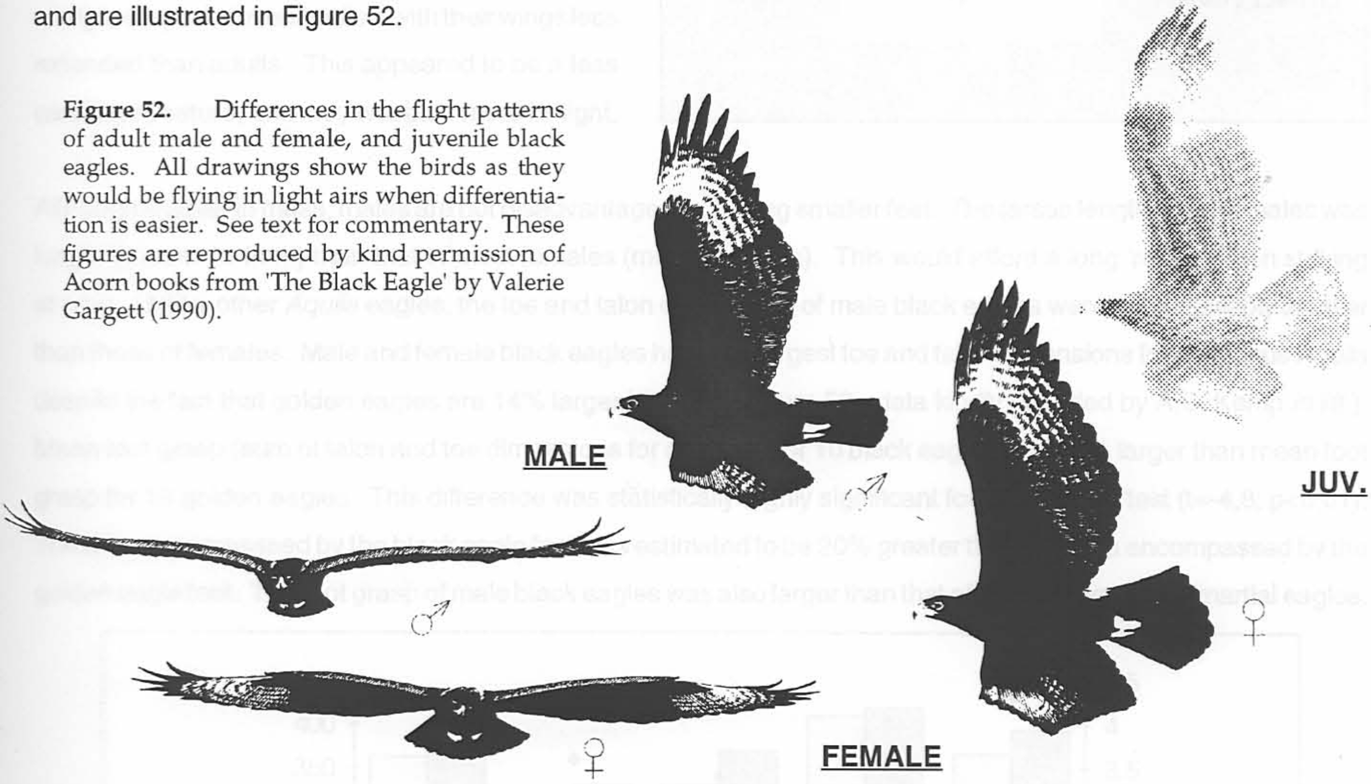


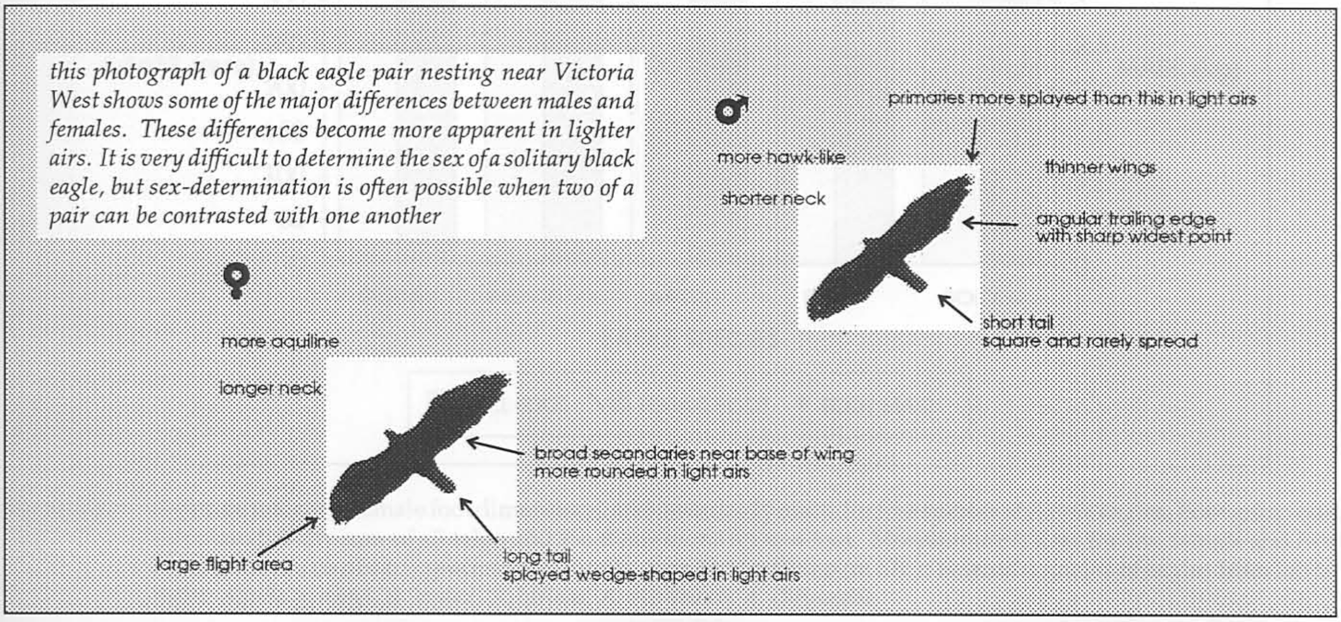
Figure 51. All flight paths of the Penberi eagles separated for tandem flights, solo flights by the male, solo flights by the female, and solo flights by the juvenile. Observation periods are given in brackets. Mountain slopes in grey, escarpment in dark grey.

Morphometrics of male, female and juvenile black eagles

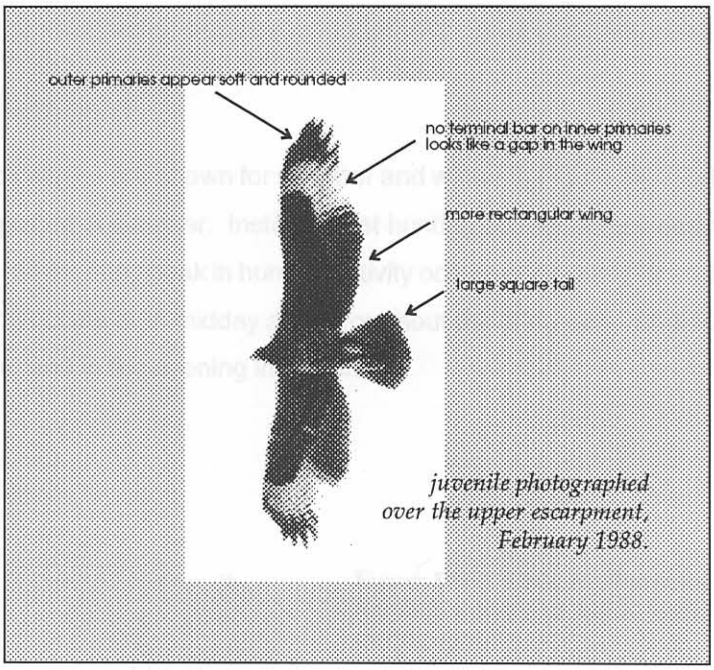
Body dimension data were available for 16 individual black eagles (pers. rec.; A.C. Kemp *in litt.*). Females weighed 13% more than males. Females differed in shape from males: wing areas were 9% larger and tail area was 53% larger (total flight surfaces of females were 15% larger than those of males). Unlike males, females often flew with their large, wedge-shaped tails expanded (Gargett 1990; pers. obs.). Female wings are broader and more rounded at the secondaries, and females fly with their wings more flexed at the carpal joint - consequently the 'finger-tips' of their outer primary feathers are usually less emarginated. Male wings are thinner and more angular with a sharp widest point visible in the trailing edge of the secondaries - this widest point often looks farther out from the torso than on females, but this could be because males usually hold their wings fully outstretched in a slightly negative dihedral posture which is apparent when they approach head-on. These differences were especially noticeable in light airs and are illustrated in Figure 52.

Figure 52. Differences in the flight patterns of adult male and female, and juvenile black eagles. All drawings show the birds as they would be flying in light airs when differentiation is easier. See text for commentary. These figures are reproduced by kind permission of Acorn books from 'The Black Eagle' by Valerie Gargett (1990).




this photograph of a black eagle pair nesting near Victoria West shows some of the major differences between males and females. These differences become more apparent in lighter airs. It is very difficult to determine the sex of a solitary black eagle, but sex-determination is often possible when two of a pair can be contrasted with one another

Differences were also apparent between dimensions of the flight surfaces of juvenile and adult black eagles (see Fig. 52 and accompanying photograph). Juveniles have a large square tail and lack the characteristic bulging secondary feathers of adults. Second plumage secondaries of a hand-raised female eagle were 20 mm longer than the juvenile feathers. The centre (deck) tail feather of this bird became 5 mm shorter in second plumage, and the outer tail feathers became 12 mm shorter, i.e. the tail of this female became smaller and more wedge-shaped. Juveniles flew with their wings less extended than adults. This appeared to be a less confident posture, and they wobbled more in flight.



juvenile photographed over the upper escarpment, February 1988.

Although smaller in mass, males are not disadvantaged by having smaller feet. The tarsus length of most males was longer (mean=114mm) than that of most females (mean=111mm). This would afford a long 'reach' when striking at prey. Unlike other *Aquila* eagles, the toe and talon dimensions of male black eagles were not noticeably smaller than those of females. Male and female black eagles have the largest toe and talon dimensions for the genus *Aquila* despite the fact that golden eagles are 14% larger by mass (Figure 53 - data kindly provided by A.C. Kemp *in litt.*). Mean foot grasp (sum of talon and toe dimensions for one foot) for 10 black eagles was 10% larger than mean foot grasp for 10 golden eagles. This difference was statistically highly significant for a two-tailed test (t=-4,8; p<0,01). The area encompassed by the black eagle foot was estimated to be 20% greater than the area encompassed by the golden eagle foot. The foot grasp of male black eagles was also larger than that of male crowned and martial eagles.

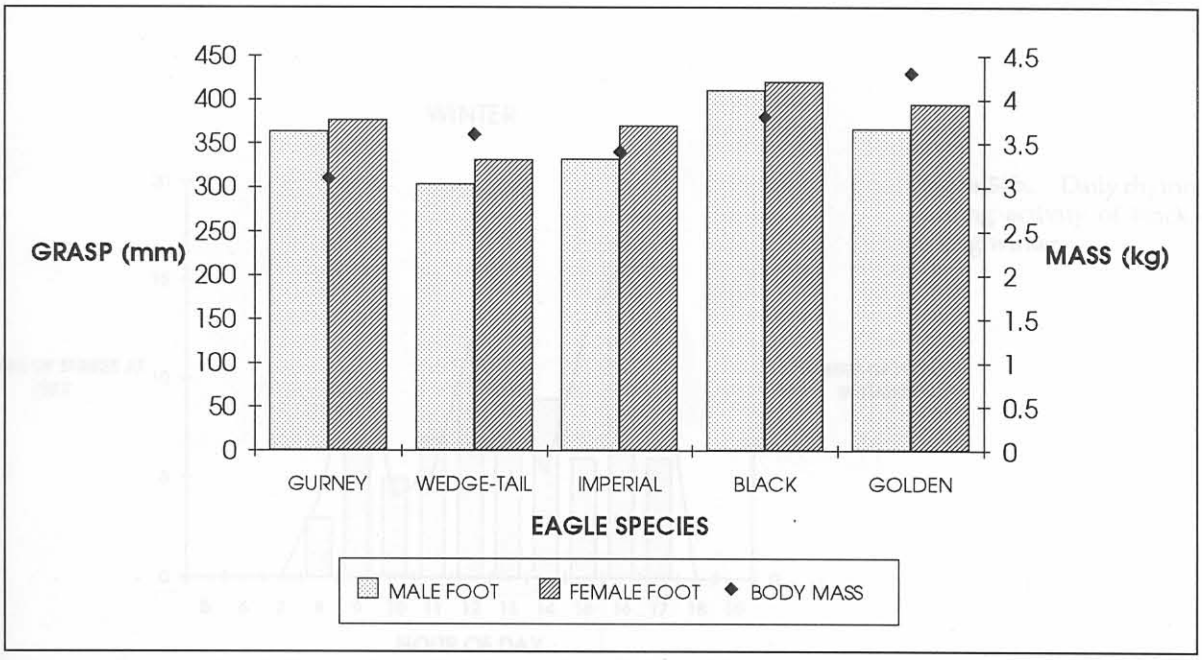


Figure 53. Average male and female foot dimensions, and mean body mass, for five species of *Aquila* eagles. Foot grasp was calculated as the sum of all talon and toe dimensions for one foot. Morphometric data for five female and five male individuals of each species were kindly supplied by Kemp (*in litt.*). Scientific names of eagles from left to right: *Aquila gurneyi, A. audax, A. heliaca, A. verreauxii, A. chrysaetos.*

The influence of season on black eagle behaviour

Daily activity rhythms in the hunting behaviour of black eagles are shown for summer and winter in Figure 54. The midday peak in activity is an hour earlier and less apparent in summer. Instead most hunting activity occurs early morning (08h00) and late evening (18h00). In winter, the morning peak in hunting activity occurs one hour later and the evening peak two hours earlier. Extensive hunting occurs over midday and throughout the afternoon. Strikes at prey were more frequent in the morning in summer, and in the evening in winter.

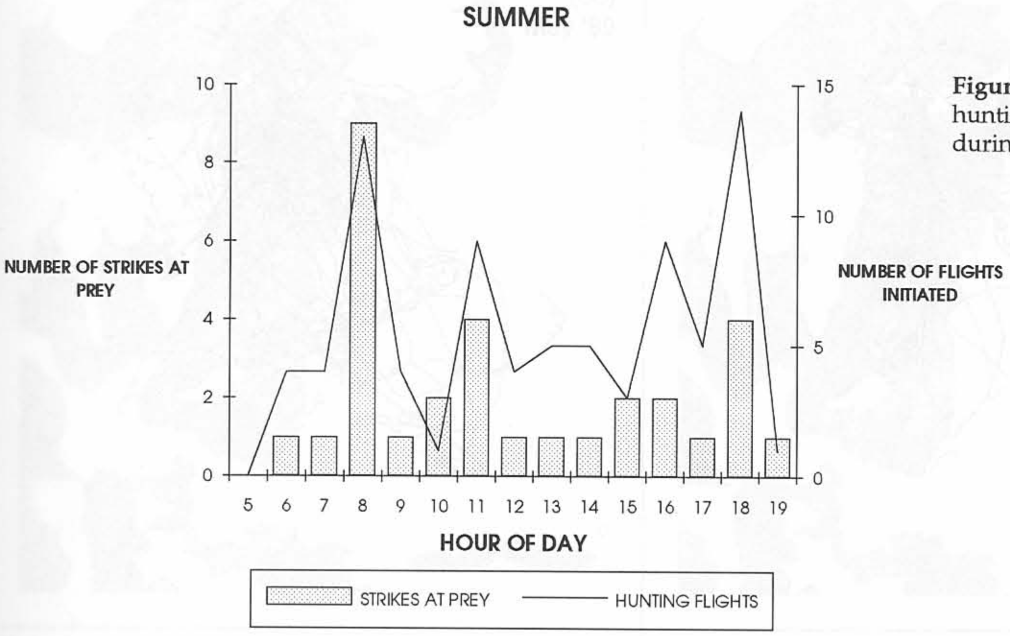


Figure 54a. Daily rhythm in the hunting activity of black eagles during summer.

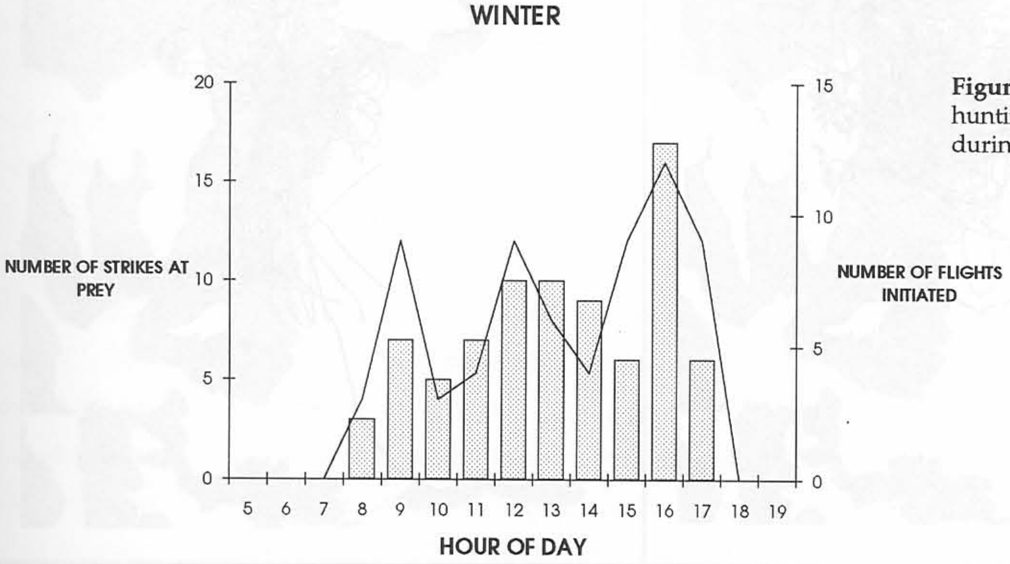


Figure 54b. Daily rhythm in the hunting activity of black eagles during winter.

Movements of the Penberi pair during the four major periods in the year (pre-breeding, incubation, nestling, fledgling) are shown in Figure 55. Movements were far-ranging and less nest-site bound during the pre-breeding and fledgling periods. Territorial displays were most frequent during the fledgling period and least frequent prior to breeding. The pair spent more time together, and more time perching prior to breeding. Movements were very concentrated around the nest site while there were eggs or small chicks in the nest. During the fledgling period, the pair were far-ranging but centred their activity around the area slightly above the nest site where the fledgling was resident, and did not venture far away over the plains. There was no significant difference in the length of flights for different seasons.

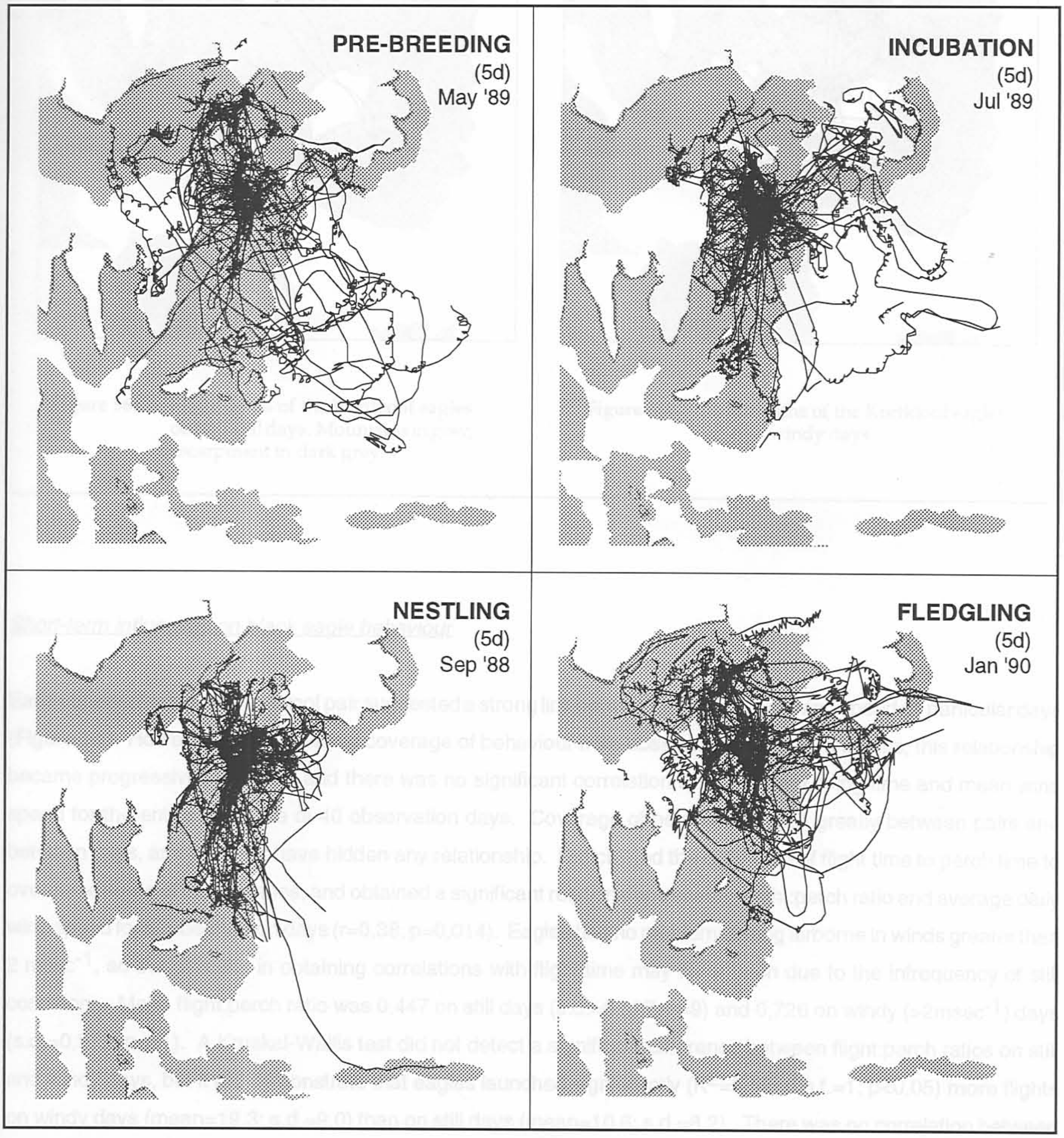


Figure 55. All flight paths of the Penberi eagles separated for the four major periods in a black eagle's year: pre-breeding (112-142d), incubation (45d), nestling (88d) and post-fledging (90-120d). Duration and timing of observation periods are supplied. Mountain slopes in grey, escarpment in dark grey.

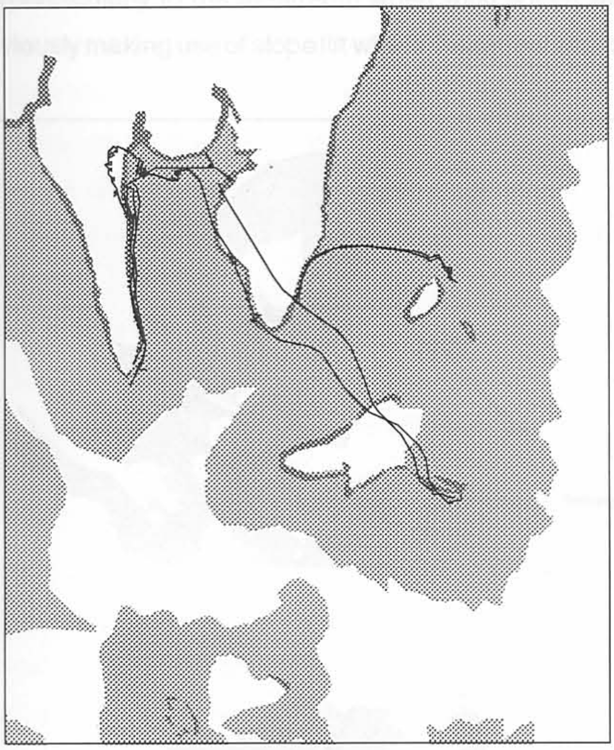


Figure 56a. Flight paths of the Kortkloof eagles on two still days. Mountains in grey, escarpment in dark grey.

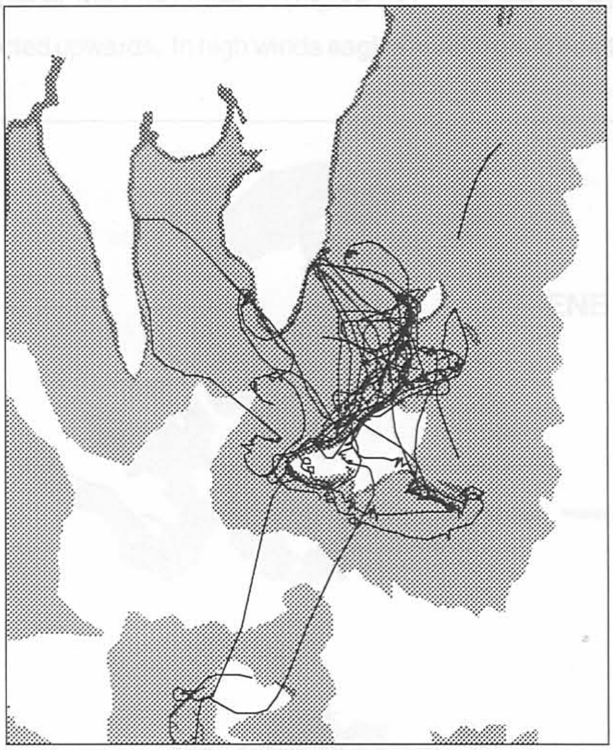


Figure 56b. Flight paths of the Kortkloof eagles on two windy days

Short-term influences on black eagle behaviour

Early observations of the Kortkloof pair suggested a strong link between flying time and wind speed on particular days (Figure 56). However, with increased coverage of behaviour from observations of different pairs, this relationship became progressively obscure and there was no significant correlation between daily flying time and mean wind speed for the entire database of 40 observation days. Coverage of behaviour varied greatly between pairs and between days, and this may have hidden any relationship. I calculated the daily ratio of flight time to perch time to overcome some of these biases, and obtained a significant relationship between flight:perch ratio and average daily wind speed for all observation days (r=0,38; p=0,014). Eagles had no problem getting airborne in winds greater than 2 msec^{-1}, so the difficulty in obtaining correlations with flight time may have been due to the infrequency of still conditions. Mean flight:perch ratio was 0,447 on still days (s.d.=0,527; n=9) and 0,726 on windy (>2msec^{-1}) days (s.d.=0,972; n=31). A Kruskal-Wallis test did not detect a significant difference between flight:perch ratios on still and windy days, but it did demonstrate that eagles launched significantly (K^2=5,52; d.o.f.=1; p<0,05) **more** flights on windy days (mean=19,3; s.d.=9,0) than on still days (mean=10,6; s.d.=8,2). There was no correlation between the distance or duration or speed of flights and wind speed recorded actually during those flights.

Wind direction had a more obvious influence on black eagle flying. Eagles clearly favoured slopes orientated perpendicularly to the air-stream when wind speed was greater than two msec^{-1} (Figure 57). The eagles were obviously making use of slope lift where the airflow was deflected upwards. In high winds eagles rose to great heights

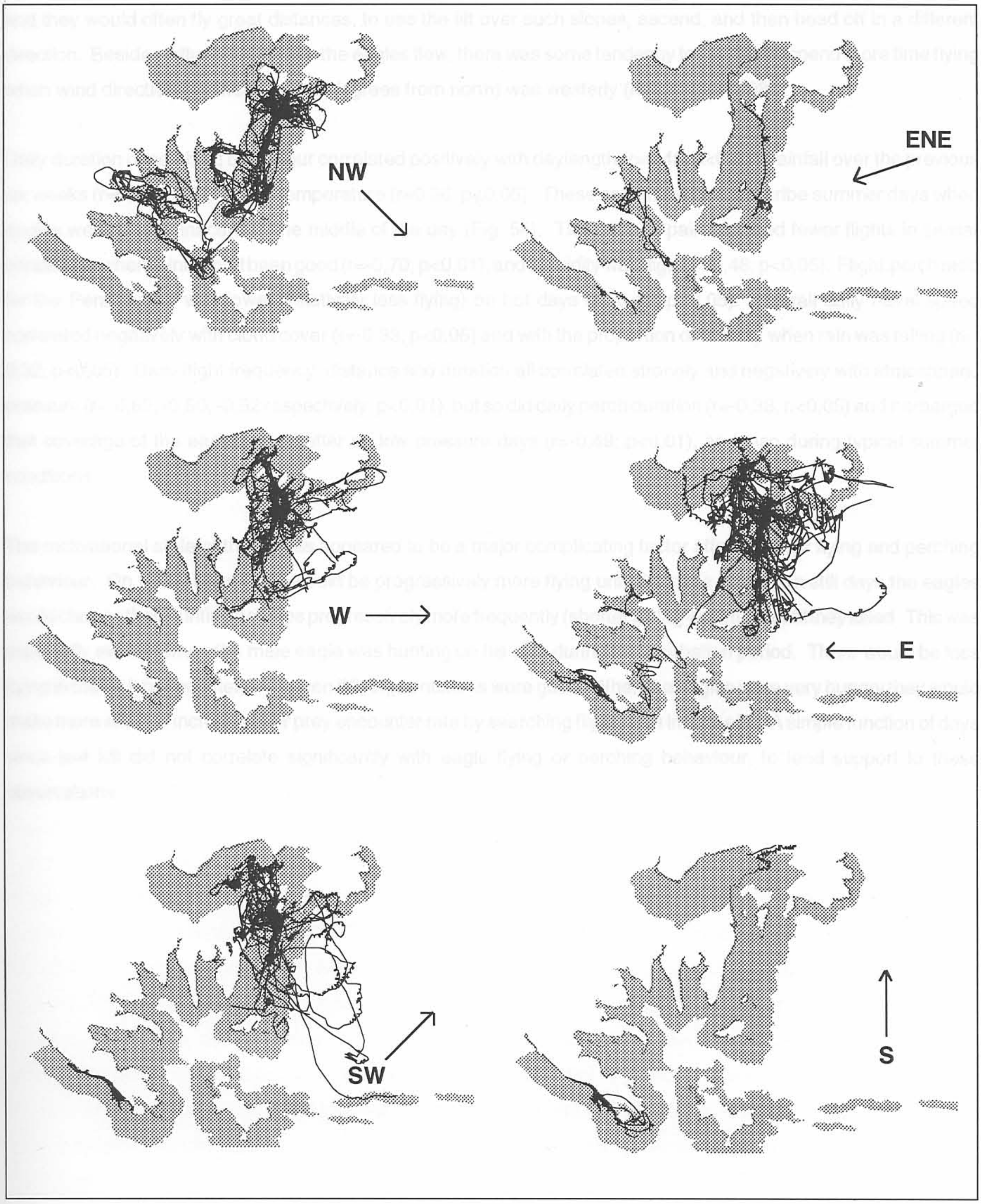


Figure 57. Flight paths for all eagle pairs for different wind directions, when wind was greater than 2msec^{-1}. Mountains in grey, escarpment in dark grey. Consult TIN-model on page 17 for 3-D topography.

above and beyond such slopes, apparently using 'wave' airflow. Black eagles can fly in the strongest of gales. On one occasion wind speed over the Penberi ridge was recorded at 157kph and the eagle pair were hanging motionless overhead, with a slight adjustment of wingshape the eagles moved steadily headlong into the gale without any obvious loss of height. Bowls or amphitheatres facing the airflow were particularly favoured by slope-soaring eagles, and they would often fly great distances, to use the lift over such slopes, ascend, and then head off in a different direction. Besides influencing where the eagles flew, there was some tendency for eagles to spend more time flying when wind direction (as measured in degrees from north) was westerly (r=0,314; p=0,08).

Daily duration of perching behaviour correlated positively with daylength (r=0,48; p<0,01), rainfall over the previous six weeks (r=0,61; p<0,01), and temperature (r=0,36; p<0,05). These conditions best describe summer days when eagles were largely inactive in the middle of the day (Fig. 54). The Penberi pair launched fewer flights in similar conditions: when rainfall had been good (r=-0,70; p<0,01), and humidity was high (r=-0,48; p<0,05). Flight:perch ratio for the Penberi pair was lower (relatively less flying) on hot days (r=-0,45; p<0,05). Overall daily travel speed correlated negatively with cloud cover (r=-0,33; p<0,05) and with the proportion of the day when rain was falling (r=-0,32; p<0,05). Daily flight frequency, distance and duration all correlated strongly and negatively with atmospheric pressure (r=-0,62, -0,50, -0,52 respectively; p<0,01), but so did daily perch duration (r=-0,38; p<0,05) and it emerged that coverage of the eagles was better on low pressure days (r=-0,49; p<0,01), and also during typical summer conditions.

The motivational state of the eagles appeared to be a major complicating factor affecting their flying and perching behaviour. On windy days there would be progressively more flying until the birds killed. On still days the eagles would change their hunting perches progressively more frequently (shorter giving-up times) until they killed. This was especially evident when the male eagle was hunting on his own during the incubation period. There would be less flying in the 24 h period after a kill, even if flying conditions were good. When the eagles were very hungry they would make more effort to increase their prey encounter rate by searching flight even in light airs. A simple function of days since last kill did not correlate significantly with eagle flying or perching behaviour, to lend support to these observations.

DISCUSSION

Distribution and abundance

Regular territorial spacing in raptors can usually be attributed to an even, predictable and defensible prey base, and has the effect of minimizing interference in the hunting and breeding behaviour of neighbouring conspecifics (Newton 1979). The G-value of 0,79 calculated from nearest neighbour distances between active nests of black eagles in the Nuweveld Mountains at Beaufort West suggests that this population is regularly spaced, and this corresponds to a relatively even distribution of hyrax groups within the rocky habitats that the eagles defend (Chapter 4).

Spacing patterns of golden eagle pairs are often more regular than this (G-values range between 0,84 and 0,94: Tjernberg 1985; Watson & Rothery 1986). The lower G-value obtained in the present study can mainly be attributed to the closer nest spacing between upper escarpment pairs than between lower escarpment pairs, but higher variability in black eagle nest spacing has also been ascribed to patchy distribution of nesting habitat within relatively small ranges (Gargett 1990), and the spacing of other *Aquila* eagles has been found to be more variable in arid regions (Murphy 1975; Beecham & Kochert 1975; Ridpath & Brooker 1987). Less regular spacing of black eagle nest sites may also be related to patchy distribution of the refuge microhabitats used by hyrax in some areas.

On the basis of a nearest neighbour analysis of nest spacing, black eagle pairs in the Nuweveld Mountains at Beaufort West approach the same proximity recorded for black eagle pairs in the Matobo Hills, Zimbabwe (Table 16). This similarity might be an artefact produced by differences in the two dispersion patterns for the estimates of density in the two study areas are markedly different (Table 16). The black eagle population in the Matobo Hills, with an overall average territory size of 10,5km^2, remains the highest nesting density recorded for a large eagle species anywhere in the world, excluding the piscivorous *Haliaeetus* spp. (Newton 1979; Gargett 1990). Unlike the Matobo population, the study population at Beaufort West can be considered as linearly distributed along two escarpments. Spacing of sequential pairs along these escarpments is compared with other similar populations distributed linearly along mountain ranges in Table 16. Black eagle pairs evidently nest closer together along the upper escarpment at Beaufort West than along any other escarpment or ridge investigated to date.

A wider spacing between black eagle pairs nesting at lower altitude has also been noted by Brown (1988) for the Drakensberg escarpment and foothills. The wider spacing of sequential pairs along the lower escarpment at Beaufort West was similar to that recorded by Boshoff & Palmer (1988) for a population about 80km west along the Nuweveld range at Fraserberg, but both these populations are still more closely spaced than any other populations along linear mountain features in southern Africa. Nest sites are unlikely to be limiting along such escarpments so one might surmise that closer nesting along the Karoo escarpments is permitted by a greater abundance of rocky habitats and associated hyrax populations. Each kilometre of upper escarpment was associated with 3,5 km of other linear rock outcrops (mainly sandstone lenses), 35 ha of screes and 7,1 hyrax groups on the upper slopes; each kilometre of lower escarpment was associated with 2km of linear outcrops, 12 ha of screes and 4,7 hyrax groups on the lower slopes (Chapters 3 & 4). By defending four times as much escarpment, lower escarpment pairs evidently enjoy greater quantities of rock outcrop and hyrax groups, but they must cope with less convenient flying conditions.

TABLE 16
NEST-SPACING AND DENSITY OF BLACK EAGLE PAIRS IN THIS AND OTHER STUDIES
consult Fig. 3 for locations of mountain ranges

LOCATION	NO. PAIRS	MEAN (km)	Std. Dev.	Coeff. Var. (%)	RANGE	SOURCE
nearest neighbours analysis of nest-spacing:						
Matobo Hills 1979	38	2,6				Gargett (1990)
Matobo Hills (park)		2,0				Gargett (1990)
Nuweveld, Beaufort West	20	2,7	1,0	37	1,3 - 4,5	present study
Nuweveld, Fraserberg	13	3,5	0,6	17	2,8 - 4,7	Boshoff & Palmer (1988) from figure
Drakensberg	8	6,2	1,5	24	4,9 - 8,8	Brown (1988) from figure
sequential pairs analysis of nest-spacing:						
Magaliesberg	13	9,5	4,5	47	3,0 - 19,5	Tarboton & Allan (1984)
Waterberg, Transvaal	11	13,3	6,5	49	5,0 - 12,0	Tarboton & Allan (1984)
Soutpansberg	8	6,8	4,0	59	2,0 - 14,5	Tarboton & Allan (1984)
Drakensberg escarpment	5	5,8			4,8 - 6,5	Brown (1988)
Drakensberg foothills	3	8,6			8,3 - 8,9	Brown (1988)
Waterberg, Namibia	7	9,8				Brown & Cooper (1987)
Nuweveld, Fraserberg	13	4,3	1,4	33	3,0 - 7,5	Boshoff & Palmer (1988)
Nuweveld, BW upper esc.	8	2,7	1,0	37	1,5 - 4,3	present study
Nuweveld, BW lower esc.	11	4,6	1,5	33	3,0 - 7,1	present study
density analysis						
Matobo Hills (park)	39	varied from 8,8 - 11,3 km2/pair				Gargett (1990)
Matobo Hills (communal)	26	35,0 km2/pair				Gargett (1990)
Nuweveld, Fraserberg	13	@15,0 km2/pair (probably 23,3)				Boshoff & Palmer (1988)
Nuweveld, Beaufort West	18	24,0 km2/pair				present study
Magaliesberg	13	35,0 km2/pair (probably larger)				Allan (1988)
Drakensberg	8	65,0 km2/pair				Brown (1988)
Karoo		65,0 km2/pair				Siegfried (1968)
Kenya	1	65,0 km2/pair				Rowe (1947)

Aquila eagles can subsist at relatively high densities in unstable environments by relying on periodic abundances of food such as carrion (Watson & Langslow 1989) and rabbits (Ridpath & Brooker 1987); but both these studies revealed that breeding is always more successful in regions where a suitable and predictable prey base exists. The tall cliffs and huge boulders encompassed by the small territories of the upper escarpment pairs are probably havens for hyrax when populations are not depressed by drought. But these territories offer little in terms of alternative prey when the hyrax population crashes as occurred in the KRNP between 1981 and 1984 (Chapters 1 & 4). Despite their appearance as optimal black eagle habitat - harbouring high densities of usually more dominant pairs, the upper escarpment territories can be considered inferior and less reliable in terms of the prey base, and this is borne out by the greater breeding effort and success of the lower escarpment pairs.

Black eagles are considered to be more territorial in the Matobo Hills where they occupy small defensible ranges (Gargett 1990), than in the Drakensberg where widely-spaced patches of rocky habitat lead to large areas of overlap and unused space between neighbouring pairs (Brown 1988). The present study indicated minimal overlap between pairs (5,5%), especially between their foraging ranges. There was very little evidence of unused space by the pairs. On this basis it seems fair to assume that the average territory size of 18 well-known pairs within the 435 km^2 study area would be 24,2 km^2. The indications of greater incidence of territorial intrusions on the upper escarpment may be associated with frequent use of the upper escarpment as a 'flyway' by non-breeding birds, and/or small prey populations in the upper escarpment territories.

Study pairs with access to plains within their territories often ranged several kilometres away from the mountainous areas. For this reason, the assumption that black eagles only occupy mountainous terrain probably led to significant under-estimation of territory size in the very similar Fraserberg terrain by Boshoff & Palmer (1988), and perhaps along the Magaliesberg range by Allan (1988), see Table 16. Territory sizes given for the Fraserberg pairs were probably further underestimated by the assumption of circular non-overlapping ranges. Neatly interlocking territories were observed in the present study and also in the Matobo (Gargett 1990).

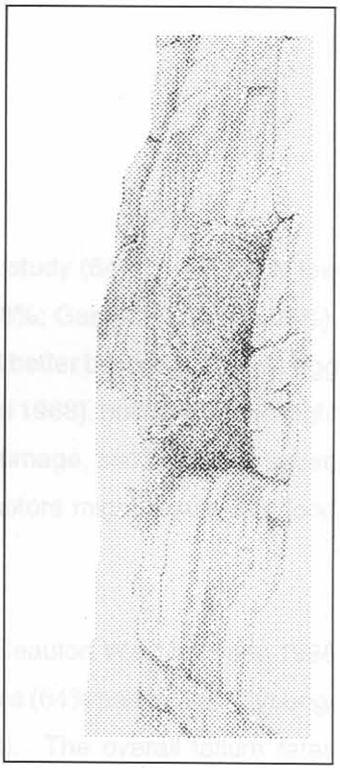
The nesting distribution of the Fraserberg birds within the area searched (about 303km^2) actually suggests a density of 4,3 pairs/100km^2 and an average territory size of 23,3 km^2 (assuming interlocking territories with no overlap and no unused space). The similarity of this nesting density with that of the Beaufort West population (4,1 pairs/100km^2) suggests that estimation of the total population in the Nuweveld Mountain range (152 pairs) by extrapolation is valid.

Using the same density estimate to predict population sizes for the other stretches of continental escarpment in the Karoo may be criticized on the grounds that rainfall and productivity vary between these ranges. But topography of the Roggeveld range is highly similar, and the Sneeuberg and Winterberg ranges are about twice the width of the Nuweveld range so the total population estimate of 600 resident pairs along the Karoo escarpments is likely to be very conservative. These ranges represent just over one quarter of the mountainous regions in the Cape. Other Cape mountain ranges, the Cape fold mountains (comprising 68% of remaining mountain regions) and the Drakensberg (9% remainder), probably accommodate black eagles at lower density than the Karoo escarpments. Black eagles also occur on scattered isolated koppies throughout the Karoo which would not have been incorporated into the calculated area of the mountainous regions. So it seems likely that the black eagle population in the Cape Province greatly exceeds the estimate of 487 pairs (range 280-730) predicted from a questionnaire survey by Boshoff & Vernon (1980). If black eagles occur at the lowest recorded nesting density (60km^2/pair) in the remaining mountain ranges of the Cape Province (90305km^2), this would yield a minimum population estimate of nearly 2000 pairs in the Cape (excluding any pairs nesting outside major mountain ranges).

The increment to include the non-breeding population is probably also conservative because of a very probable bias towards territorial birds in the flight-frequency ratio. However it probably represents a minimum increment. Non-breeders would be much more abundant in mountainous areas lacking nest cliffs. Immatures often comprise about 30% of eagle populations (Brown & Watson 1964; Boeker & Ray 1972; Watson 1990). In the present study they comprised up to 40% of the non-breeding population. Following the incidents of adult mortality, mate-replacement took place in relatively short periods of time. This indicates a healthy floating population and adequate recruitment. Such is not the case for tawny and martial eagles on farmland in Namibia (Brown 1991). The healthy status of the black eagle population in the Cape can be ascribed to a few factors: black eagles rarely scavenge so they are less susceptible to strychnine poisoning (Allan 1989); they inhabit remote areas so direct persecution is difficult; and farmers in the Cape are changing their attitudes towards these birds thanks to major conservation efforts such as the postal survey conducted by Boshoff & Vernon (1980).

Choice of nest-site

Usually, an abundance of alternative nest sites is taken to indicate that a particular population is not limited by the availability of suitable sites. The correlation established in the present study and put forward by Gargett (1990), between abundant alternative sites and high failure rate indicates that this can be far from the case, and that failure stimulates 'frustration' nest-building at other sites.



Unlike other eagle populations where breeding failure usually occurred at the egg stage (Hustler & Howells 1986, 1987; Allan 1988; Gargett 1990), the Beaufort West black eagles were mainly failing at the small chick stage (55-64% all failures). Various lines of evidence suggest that much of this failure was caused by terrestrial predators. First, nests were preferentially located on tall cliffs no doubt since small cliffs experienced a higher failure rate (lower siting of nests on very tall cliffs may be to reduce risk of injury to fledging eagles). Secondly, the eagles avoided nesting on sandstone cliffs which also experienced higher failure rate. This substrate is richer in crevices (200ha^{-1}) than dolerite cliffs (78 crevices ha^{-1}) (Chapter 3), and thus can be considered more accessible to terrestrial predators. These factors would not influence accessibility to avian predators.

But most conclusively, the time-lapse cameras actually revealed predation by the small grey mongoose *Galerella pulverulenta* on black eagle nestlings, two years in a row at one very accessible site. It is anomalous to consider that a top predator such as the black eagle is at risk of predation to one of its prey species, but small grey mongooses are known to be very rapacious and have been observed to kill ostrich chicks (D. Conroy pers. comm.) and to challenge a female kori bustard on her nest (Allan 1987 unpubl., pers. comm.). Baboons are also considered to be a threat to nesting black eagles (Gargett 1990) and it may be relevant that the destruction or disintegration of two nests in the KRNP occurred on the more accessible sandstone cliffs which are favoured by baboons as roost sites.

Black eagles might be expected to be more prone to nest predation than other large eagles through low nest attendancy due to their preferential habit of tandem hunting, especially when prey is scarce. Watson (1988) considered that active, time-consuming foraging methods were responsible for low nest attendancy and high risk of nestling predation in the bateleur. However, there was no obvious indication in the present study from time-lapse photography at nests that attendancy was low in comparison with other eagles or black eagles elsewhere (Chap. 8).

Selection of certain cliff aspects by nesting black eagles was not associated with any differences in failure rate, suggesting that this factor may not be of vital importance. Avoidance of east-facing cliffs might be due to inferior flying conditions (important for birds laden with prey). Strong winds from the west and south-west may create difficult down drafts over east-facing cliffs. The preferred south-facing cliffs enjoy good flying conditions and cooler temperatures. Nest-attendancy was greatly prolonged on one sunny, north-facing nest site (Chapter 8), presumably while an adult was shading the chick from the sun.

Upper escarpment pairs enjoyed fewer nesting failures (16% attempts) than lower escarpment pairs (27% attempts), probably on account of the availability of tall inaccessible nest cliffs. But the effects of this were more than compensated for by the enhanced breeding effort of lower escarpment pairs.

Breeding success

The proportion of double egg clutches recorded for black eagle eyries in the present study (64%) is relatively low compared with other studies (Siegfried 1968 viz. 92%; Tarboton & Allan 1984 viz. 78%; Gargett 1990 viz. 85%). Furthermore, my observations were of lower escarpment pairs which were confirmed better breeders. Single egg clutches may be produced by females breeding for the first time (Visser 1963; Siegfried 1968), but none of the eight single egg clutches observed in the present study were laid by females in sub-adult plumage, and two of the seven females involved were suspected to be old. Alternatively, reduced clutch size in raptors might result from food shortage (Newton 1979; Jenkins & Joseph 1984).

Overall breeding effort and productivity of black eagles in the Nuweveld mountains at Beaufort West between 1986 and 1990 (61% pairs/yr; 0,46 young/pr/yr), were very similar to the corresponding figures (64% pairs/yr; 0,47 young/pr/yr) for black eagles in the Matobo Hills between 1967 and 1984 (Gargett 1990). The overall failure rates experienced by the pairs in both studies were also very similar (25% of Nuweveld attempts; 27% of Matobo Hills attempts). However, most of the Matobo failures occurred at the egg stage, and many of these cases could be attributed to human depredation; remaining losses were probably due to a healthy population of other predators in the Matobo Hills National Park: outside the park, on communal land where other predators were considered to be rare, failure rate of nesting eagles was lower (Gargett 1990). In the Magaliesberg range between 1981 and 1983, (Allan 1988), black eagles made more breeding effort (81% pairs/yr), suffered heavy failure rate (30% attempts), but still raised more chicks (0,57 chicks/pr/yr). Again, most nest failure in this study occurred at the egg stage and productivity was greatly reduced by human interference. The relatively low occurrence of nest failure at the egg stage in the present study might be due to minimal human disturbance within the KRNP.

Only 79% of eggs laid by the study pairs actually hatched, but inviability of eggs caused only one breeding failure (the majority of inviability occurred in double egg clutches). In the Matobo Hills by contrast, as much as 42% of single egg clutches didn't hatch (Gargett 1990). It is apparent that laying two eggs can be very advantageous to black eagle breeding success. Breeding failure at the small chick stage has already been discussed. Large chicks suffered far lower mortality, the death of the large chick from an impacted crop might have resulted from low provisioning rates at this nest (Chapter 8) and a long preceding period without food. A similar occurrence was recorded by Tuer (1969) where the chick lost weight but survived.

In other *Aquila* species, breeding can be delayed or severely disrupted by the immediate effects of adverse climatic conditions such as heavy rains (Hustler & Howells 1986) or snow storms (Phillips, Wheeler, Lockhart, McEneaney & Forrester 1990). The only instance of sudden climate-induced failure in the present study was a small chick blown out of the nest by gale-force winds. The Beaufort West region is known to experience highest average wind and gust speeds (up to 175kph) in South Africa (Milford 1987).

In compliance with most raptor studies (as reviewed by Newton 1979), there was evidence from this survey that the pairs which initiated nesting early in the season enjoyed a greater degree of nesting success. Early breeding and successful breeding was probably encouraged by richer food supplies in lower escarpment territories, and in territories with more farmland.

Peak laying during June as recorded in this study is later than that recorded (usually May) for black eagles in the Transvaal (Tarboton & Allan 1984) and in the Matobo Hills (Gargett 1990). Later breeding can be expected for most African raptors at more southerly latitudes (Maclean 1985). However, delayed breeding can also be caused by food shortage (Newton 1979), and the early breeding of pairs nesting on farmland suggests that this may be more responsible. Black eagles are known to feed on lambs of domestic stock (Boshoff *et al.* 1991; Chapters 9 & 11). Whether lambs are scavenged or killed, they comprise a highly available food supply for eagles over relatively short periods of time. This is because eagles only normally pose a threat to very small lambs, and because most non-violent lamb mortality occurs in the first few weeks after birth (see Chapter 11). So the peak lambing season in March/April would be well timed to bring local eagles into breeding condition, but it does not necessarily confer an abundant food supply later in the year. Despite the variation most young fledged just prior to the hyrax birth pulse. Fledging times of other raptors has also been noted to coincide with peak prey abundance (Olsen & Georges 1993).

Breeding effort of the study pairs was linked to the size of their territories and to the areas of certain habitats within those territories. Pairs with more bottom plains, more lower slopes, more farmland and less upper plateau made more breeding attempts. This might suggest that pairs with more alternative prey available after the hyrax decline would be more likely to breed, but this hypothesis was not reflected by a more catholic diet among more determined breeders. Neither the proportion of red rock rabbit or domestic lamb in the diet, nor the number of species taken were associated with greater breeding effort. On the contrary, pairs with a greater proportion of hyrax in their diet were those that made more effort, and there was some indication that these pairs were also

more successful. There is the possibility of bias here since greater amounts of prey remains were recovered after a successful breeding attempt, and hyrax remains tend to accumulate disproportionately in such collections (Chapter 9). But better breeding can be expected in black eagle territories with greater availability of their staple prey, and the significant and positive correlation between breeding effort and estimates of hyrax numbers in the territories suggests that this is so. Large areas of bottom plains, lower slopes and sometimes farmland encompassed by lower escarpment territories support good populations of hyrax as well as a wide spectrum of alternate prey leading to a stable and diverse prey base which encourages breeding. Indeed, breeding pairs with more lagomorphs in their diet proved to be better providers (Chapter 8).

Despite earlier breeding by pairs with access to large areas of farmland and with a high proportion of lamb in their diet, a link between breeding success of black eagles and the extent of farmland in their territories or the proportion of lamb in their diet could not be demonstrated statistically. It would appear that young domestic lambs are a timely food resource which can dramatically induce breeding condition in farm eagles and lead to greater breeding effort, but that later in the season the availability of this resource is reduced such that breeding outcome is more influenced by other factors such as the proportion of hyrax in the diet.

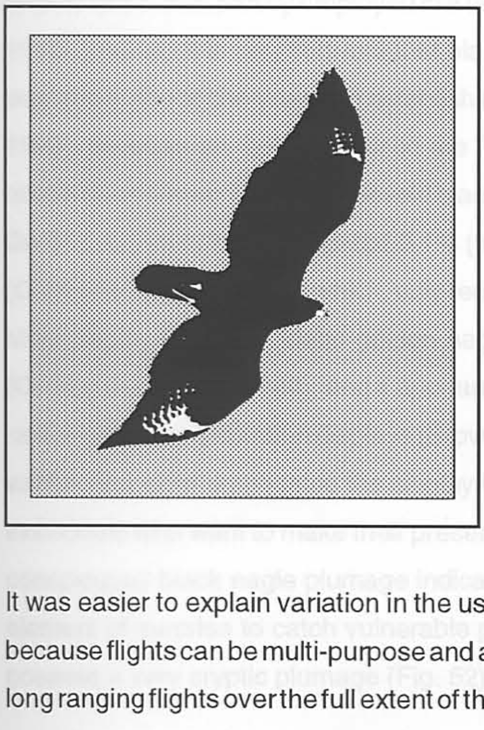
The effects of the early 1980's drought, following good rains in the late 1970's (see Chapter 2), were widespread throughout the summer rainfall regions of southern Africa and probably accounted for the observed declines in hyrax populations in many areas including the Matobo Hills where 1984 was the worst breeding season recorded for the black eagle population there (Gargett 1990). Dips in productivity of eagle populations at this time, as far afield as wedge-tailed eagles in Australia (Robertson 1987), and golden eagles in North America (Phillips *et al.* 1990), may have been caused by adverse weather conditions resulting from the far-reaching teleconnection effects (Philander 1983) of the same El Nino event. The present study was carried out during a recovery phase after major drought and it is likely that the karoo biota were more responsive to rainfall than usual. Rock hyrax population structure was found to be very dynamic in the Karoo National Park over the study period, with recruitment and survival rates varying markedly with the timing and amounts of rainfall (Chapter 4)

Poor breeding performance might also have been expected for the Beaufort West black eagle population at the end of the hyrax population decline in 1983-84. Good rains in 1985 and to a lesser extent 1986 should have had a beneficial effect on the highly depressed hyrax population, and this may have resulted in improved eagle breeding performance as recorded for 1986. The subsequent breeding pattern (Fig. 45) suggested alternate good and poor breeding for three to four years, which may have resulted from synchronized breeding following the drought event. Breeding in alternate years is common for other large eagles where prey is less available (Skorupa 1986; Hustler & Howells 1987). Any statistical evidence of breeding in alternate years however, was probably over-shadowed by the predominance of consistently successful and consistently unsuccessful breeding pairs. This character has been recorded for black eagles elsewhere (Gargett 1990), and is a regular feature of raptor populations (Newton 1979).

A large-scale breeding effort during 1988 tallies with the highest prey capture rates recorded for this year which may have been due to high hyrax vulnerability in dry conditions as defined by a trough in summer rainfall (Chapter 8). Heavy predation in 1988 may have been partly responsible for the observed hyrax decline in that year (Chapter 12). Subsequently breeding effort appeared to be linked to prey abundance the previous December as indicated by total counts at 16 hyrax colonies within the study area (Fig. 45). It is likely that breeding should be enhanced in good prey years, but continued monitoring will reveal whether this relationship was not somewhat fortuitous. The same pattern was not evident for breeding success on account of variable failure rate. Breeding failures were minimal in 1989 when very heavy rains fell September to November, suggesting that well-timed rains may have a rapid effect on the prey base. Red rock rabbit numbers reached a peak at this time (Chapter 5). Hyrax recruitment during the study period was enhanced by early summer rains (Chapter 4). High failure rates were associated with dry conditions in the years of 1987 and 1988, but there was no obvious indication of poorer nest attendancy or reduced prey delivery rates in those years (Chapter 8).

The influence of rainfall on the breeding performance of large eagles has been found to vary between predominantly wet and dry periods. The breeding performance of tawny eagles responded positively to rain in a dry spell (presumably through effects on the prey base) but was disrupted by the immediate effects of heavy rains during the wet 1970's (Hustler & Howells 1986). Up till the late 1970's black eagle breeding in the Matobo Hills was negatively affected by heavy rains the previous season, and enhanced after dry years; in the 1980's this pattern was reversed (Gargett 1990). It has been hypothesised (Allan 1988) that during wet periods and high hyrax densities good rains actually reduce hyrax availability to black eagles by leading to increased vegetation cover and by reducing the need for hyrax to move far from rocky shelter to forage; when the hyrax population is depressed by drought however, the beneficial effects of good rains on prey abundance may lead to improved black eagle breeding performance (this aspect of the predator/prey relationship is considered in more detail in Chapter 12). As the present study was carried out during a recovery phase of the Karoo after a major drought, these effects must be borne in mind, and overall prey availability was probably a function of both changes in prey abundance and changes in prey vulnerability. However by contrast to the above studies karoo rainfall is erratic and very limiting, and it is likely that the short karoo scrub and the prey populations that it supports would always respond positively to rainfall in this water-limited environment.

Use of space and territoriality



Black eagles fly mainly over mountain slopes where their staple prey is most concentrated and where air currents suit their flight design. Strong updraughts over certain slopes are strategically used by flying eagles, as has been observed for golden eagles in North America (Dixon 1937). Although superior performers to other large eagles in slope lift, black eagles also soar in thermals over flat country and they must lift prey weighing as much as themselves up to their nest sites. Their unique and very characteristic wingshape is probably a compromise solution between these opposing demands of efficiency in slope lift (narrow wings), slow turning ability in thermals and the ability of generating powerful lift to get airborne with prey (broad wings).

It was easier to explain variation in the use of areas by perching eagles than that by flying eagles. This is probably because flights can be multi-purpose and are greatly influenced by weather conditions. Black eagles frequently made long ranging flights over the full extent of their ranges but they preferred to forage closer to the nest. During the nesting season most prey was conveyed directly from capture site to the nest, and in this way black eagles behave as 'single-prey loaders' (Orians & Pearson 1979). Foraging nearer to the nest reduces transport costs but it is doubtful that these eagles would truly comply with the predictions of Central Place Foraging Theory and turn down rare opportunities of prey capture on the basis of prey size and distance from the nest. But there were not sufficient data to demonstrate this. Black eagles delivered even tiny prey (200-300g) to their nests if they were not too hungry themselves (and they also have the ability of dismembering large prey into transportable portions).

Black eagles allocated as much flying time (if not more), to keeping other conspecifics out of their foraging range as they did to actually harvesting prey. They also regularly used energetically-costly flapping flight to repel intruders, and risked injury by grappling and cartwheeling with persistent offenders. Territoriality is evidently of major importance in the daily activity of resident black eagle pairs, and largely essential for successful breeding. Black eagle pairs nest in close proximity for such a large eagle and often in open country, so it is not surprising that most of their 'spacing' behaviour is based on visual rather than auditory cues (olfactory communication is rare in birds). Crowned eagles and African fish eagles nest in densely vegetated habitats and make more use of vocal communication in spacing behaviour.

The highly conspicuous black and white plumage of black eagles is used to maximal advantage during their pendulum display which was mostly employed in a territorial context and sometimes to signal to mates in this and other (Gargett 1990) studies. It is very relevant that black eagles nesting at the highest recorded density probably display in this way every day of the year and establishing pairs were observed to display up to 16 times in a single day (Gargett 1990), whereas an isolated pair in the Rift Valley performed the pendulum display only once during 1013 h of observation (Rowe 1947). Nuweveld black eagles allocated 3,33% of flight time and 0,81% of daytime to this display. Golden eagles in Idaho allocated 0,1% (females) and 0,4% (males) of their day time to a similar undulation display (Collopy & Edwards 1989) which, only recently has been held to serve primarily a territorial function (Harmata 1982). Most display flights by Idaho golden eagles were conducted near the nest sites and along territorial boundaries (Collopy & Edwards 1989), and it appeared as if Nuweveld black eagles behaved likewise. Many eagles and other raptors perform undulation displays (Brown & Amadon 1968) but these other species are not as conspicuous as black eagles and most emphasise the display by shallow, rapid wing beats at each rise. This display is clearly used by individuals who want to make their presence known to other conspecifics ('a desire to be noticed'). Evolution of the conspicuous black eagle plumage indicates that crypsis has not been essential for this hunter which uses a high element of surprise to catch vulnerable prey away from refuge. Non-territorial juvenile black eagles however do possess a very cryptic plumage (Fig. 52).

It is not obvious why black eagle display flights were more apparent during the post-fledging period in the present study (Fig. 55). One would expect that eagle pairs would have more time available for territorial behaviour prior to breeding in May. Gargett (1990) observed the same phenomenon and thought that it might be due to observation effort or possibly to particular weather conditions prevailing at that time of the year (the formation of thermals and massive cumulus clouds) which encouraged high altitude soaring and display flights. High altitude soaring has been associated with a territorial function in other raptors (Ballam 1984). On several occasions during the present field study, black eagle pairs appeared to suddenly switch from conventional foraging behaviour within strict ranges to far-ranging, high altitude display flights which covered the entire territory and sometimes strayed across boundaries. These observations tally with Gargett's (1975) concept of a black eagle territory as an inverted cone, where overlap is greater at high altitude. But overlap in the present study was not extensive, and mostly occurred when the motive of high-flying eagles did not appear to be foraging. At such times, all neighbouring pairs would often ascend together and up to four pairs were observed to interact over the corners of their territories, so it sometimes became difficult to keep track of focal pairs. It was not clear whether this synchronised activity was triggered by the sight of neighbours as has been inferred elsewhere (Gargett 1990) and for other *Aquila* species (Brooker 1974; Collopy & Edwards 1989), or by some climatic change. Measures of flight behaviour showed very strong negative correlations with atmospheric pressure. Much of this relationship was probably due to better coverage of the pairs on low pressure days, but the correlation with perching behaviour was not as strong, and it is possible that high altitude flights were stimulated by ascending airflow which can be associated with a drop in pressure. Closer investigation will show whether this was the case.

The total ranges of neighbouring lower escarpment pairs of black eagles overlapped by less than 10% and usually followed clear, well-defined boundaries, often along topographical features as has been observed for the ranges of other raptors and birds (Watson & Miller 1971; Village 1982). Neighbours largely respected these boundaries and this must have reduced interference between pairs (which can, under very high density conditions, lead to breeding failure - Gargett 1990). Most truly aggressive behaviour (chasing and grappling) was directed at non-breeding intruders. Overlap in the foraging ranges of neighbouring pairs was further reduced on account of the eagles' preference for hunting near the nest area. These observations concur with the findings of Gargett (1975) that black eagles do defend territories. Brown (1988b) ascribed greater overlap (16%) between black eagle pairs in the Drakensberg to the difficulty of maintaining large ranges and to the presence of large areas of unpreferred habitat. Total exclusion of conspecifics is not a pre-requisite for territoriality, and on the basis that most of the overlap between Drakensberg neighbours occurred over the unpreferred habitats and may have involved non-foraging eagles (as indicated in the present study), I would argue that these eagles are still territorial.

The size of bird territories is often found to vary inversely with the density of certain desired habitat characteristics, such that most territories often contain similar total values for these commodities. In the case of wrens *Troglodytes troglodytes* it can be the area of rock faces (Cody & Cody 1972); for pileated woodpeckers *Dryocopus pileatus* it may be forest log and stump volumes or overstory canopy cover (Renken & Wiggers 1989); and for golden eagles it might be good jackrabbit habitats (Collopy & Edwards 1989). These habitat characters are all related to the food of the territory holders. In the case of black eagles, the key habitat character appears to be the extent of rocky habitats, the refuge resource for their staple prey (Gargett 1975, 1990; Brown 1988b). The total extent of lineal rock outcrops (the more preferred hyrax refuge habitat - see Chapter 4) defended by black eagle pairs was astonishingly similar for the first three territories mapped which varied widely in size. The fourth territory mapped had 15% more lineal outcrops than the others, but it also had 34% less screes (less preferred habitat) so these effects may have been compensatory in terms of overall prey refuge within the territory. Quality-related compensatory effects between the extent of different habitat types in territories have been noted for wrens (Cody & Cody 1972) and golden eagles (Collopy & Edwards 1989). But the parameter which showed noticeably less variability than the number of hyrax groups across territories was the area safely accessible to hyrax from their rock outcrops. This safe feeding area is the closest measure of carrying capacity for the prey base (Chapter 12). It is tempting to conclude from this that black eagles may appraise and defend their territories on the basis of the extent of rocky habitats, which might be more easily assessed than hyrax numbers. The fixed extent of these refuge habitats might also provide the eagles with a good long-term indication of prey numbers despite the short-term fluctuations that do characterise hyrax populations (Chapters 1 & 4). This would be in keeping with Smith & Shugart's (1987) 'structural cue hypothesis'. If black eagle territories did not change with time this might be plausible. Large eagles are generally considered to maintain more stable territories than other raptors (Newton 1979), and some nest sites have a long history of use. Although there was no evidence of territory change during fieldwork in the present study an investigation of nest age and nest dispersion patterns in the KRNP did not lend any supporting evidence for long-term stability of black eagle territories in the Nuweveld Mountains, and initial observations on the marked stability of black eagle territories in the Matobo Hills between 1965 and 1972 (Gargett 1975) have not stood the test of time. Matobo territories increased from 58 to 65 between 1972 and 1977, and then declined to 37 by 1992 (Gargett 1993 unpubl.). These changes correlate with a major fluctuation in the prey base predicted by a hyrax population model (Chapter 12) using the Matobo rainfall pattern for this period, and supported by field observations (Gargett & Barry pers. comm.). This change may have been brought about by an unusual climate change, but the indication is that black eagle territories do not remain as permanent as the rocky habitats within them but do change somewhat with temporal variation in the prey base. Black eagles occupying small territories in high density hyrax habitats such as the Matobo Hills are probably more susceptible to changes in this prey base than elsewhere. The increased demand for both foraging time and territorial behaviour must lead to conflict at low prey density. It is not clear whether territories fell vacant in the Matobo because of the inability of the eagles to find sufficient food, or because of increased territorial behaviour by neighbours, or because of a combination of these factors. Gargett (1993 unpubl.) considers that poor recruitment to the population was contributory. Geographical variability in eagle territory size in relation to productivity and the prey base (e.g. Hustler & Howells 1990) is better known than temporal variability. It is clear that despite pronounced spacing behaviour in these long-lived eagles, territory size, as with most raptors (Newton 1979) is primarily related to food supply.

Foraging behaviour and success

In the literature, hunting black eagles are reputed to fly close against rock outcrops, and capture their prey by surprise. Extensive observation indicates that black eagles in the Matobo hunt their hyrax prey in just such an opportunistic manner (Gargett 1990). Although subject to certain observer bias, extensive observations in the Matobo suggested that eagles did most of their hunting late morning, early afternoon and Gargett (1990) concluded that hyrax are probably usually captured by surprise when they are basking near their rocks. Synchronicity between seasonal rhythms of hyrax and eagle foraging behaviour suggests that this does not hold true for black eagles in the Karoo. Hyrax are furthest from shelter when foraging (Chapter 4) and this is when black eagles launched most of their hunting flights and made most of their strikes at prey (Figure 58). Hyrax and eagles avoid activity in the heat of the day in summer, and concentrate their activity over midday and early afternoon in winter. Tri-modal peaks in eagle activity every 3-4h may reflect motivational change in the hunter, but there was some indication that the peaks coincided with times when hyrax were most likely to initiate and terminate group foraging expeditions.

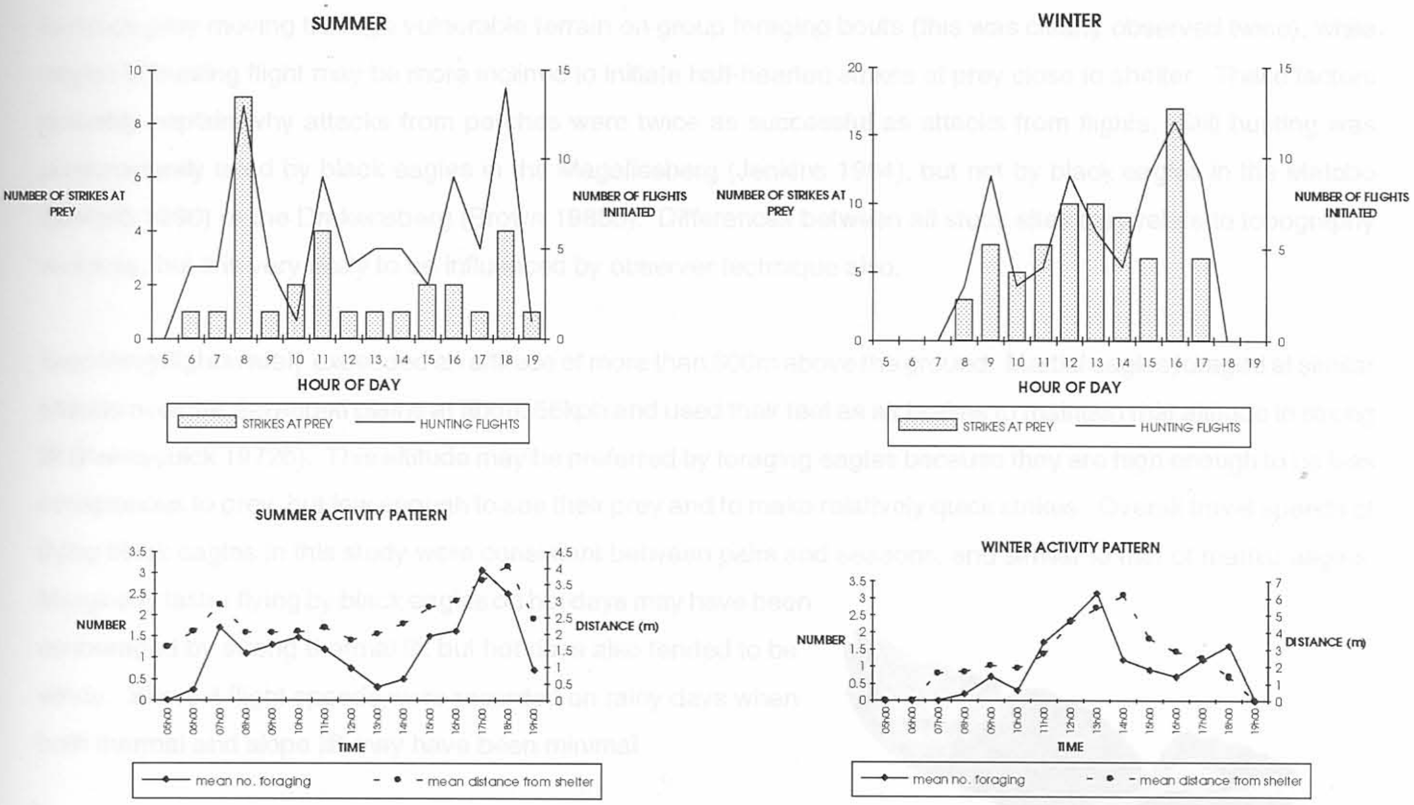


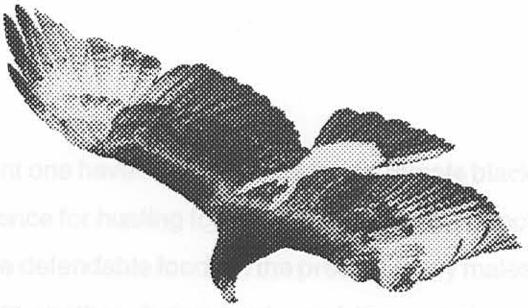
Figure 58. Seasonal synchronicity (summer on the left; winter on the right) in the daily foraging behaviour of black eagles (above) and hyrax (below).

The timing of hunting flights in winter correlated with patterns of mean distance from shelter that hyrax move on winter days (r=0,57; p<0,05). The timing of strikes by eagles in winter also correlated with distance from shelter (r=0,52; p<0,05) and with daily foraging pattern of hyrax in winter (r=0,72; p<0,01). Hourly statistical analysis did not confirm relationships between hyrax and eagle activity patterns in summer, but there was a tendency for eagles to launch more hunting flights at times of the day in summer when hyrax were furthest from shelter (r=0,46; p=0,085), and synchrony is evident for summer in Figure 58 although the activity peaks of hyrax and eagles may differ by an hour either way.

The timing of hyrax foraging behaviour is determined by other factors besides predation risk such as their need to raise their body temperature on cold winter mornings and to gather sufficient forage every day. Synchronicity in activity patterns suggests that hyrax behaviour is largely predictable in this regard and eagles can adjust their foraging behaviour accordingly although they may also face some constraints imposed by daily change in flying conditions. However the overall synchronicity may also relate to environmental factors affecting both species, and hyrax were observed to minimise synchronicity in the shorter-term, for instance during windy conditions (Chapter 4).

Eagles can evidently greatly increase their prey encounter rate by active hunting rather than still hunting, but at some extra energetic cost. One consequence of the flight:perch time ratio in this study was that hyrax experienced approximately equal numbers of attacks from perching and flying eagles, but this was probably fortuitous. Use of either method was evidently greatly influenced by weather conditions and motivational state of the eagles. Hyrax are probably less aware of perching eagles than flying eagles. Perching eagles may time their strikes more accurately to attack prey moving through vulnerable terrain on group foraging bouts (this was clearly observed twice), while eagles in hunting flight may be more inclined to initiate half-hearted strikes at prey close to shelter. These factors probably explain why attacks from perches were twice as successful as attacks from flights. Still hunting was predominantly used by black eagles in the Magaliesberg (Jenkins 1984), but not by black eagles in the Matobo (Gargett 1990) or the Drakensberg (Brown 1988b). Differences between all study sites may relate to topography and prey, but it is very likely to be influenced by observer technique also.

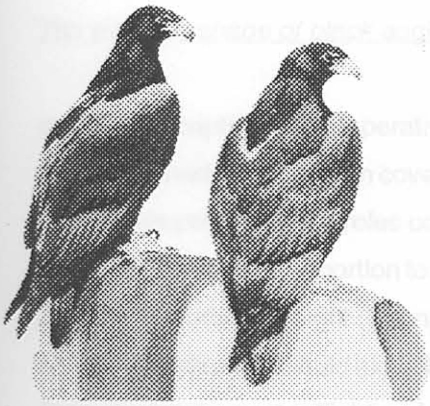
Searching flights rarely exceeded an altitude of more than 600m above the ground. Martial eagles foraged at similar altitude over the Serengeti plains at about 55kph and used their feet as air brakes to maintain that altitude in strong lift (Pennycuick 1972b). This altitude may be preferred by foraging eagles because they are high enough to be less conspicuous to prey, but low enough to see their prey and to make relatively quick strikes. Overall travel speeds of flying black eagles in this study were consistent between pairs and seasons, and similar to that of martial eagles. Marginally faster flying by black eagles on hot days may have been encouraged by strong thermal lift but hot days also tended to be windy. Slowest flight speeds were recorded on rainy days when both thermal and slope lift may have been minimal.



There was very little indication in the present study that black eagles flew randomly around rocky habitats in the hope of catching prey opportunistically, as has been described for black eagles hunting in the Matobo (Gargett 1990). Nearly all observed foraging behaviour involved extensive search from a high altitude perch or flight, and attacks were then launched at sighted prey. In other words, black eagles in the Nuweveld Mountains hunted by observation rather than expectation in keeping with Steyn (1982). A different approach by Matobo black eagles may be favoured in this more densely-vegetated habitat, but I would propose that hunting by expectation rather than observation is probably only successful at relatively high prey densities (such as the Matobo Hills during the 1970's), and the search hunting favoured by Nuweveld black eagles maybe in response to the difficulty in catching hyrax after a major decline in this prey base. If black eagles are hunting high density prey by expectation then time since last visit to a particular rock outcrop may be an important measure by which to judge foraging technique but it was not appropriate in the present study. Overall hunting success in the present study (8,5% of 106 strikes) was far lower than that reported for black eagles hunting in the Magaliesberg (viz. 40% of 30 strikes, Jenkins 1984) and in the Drakensberg (viz. 29% of 14 strikes, Brown 1988b). Some of this difference may have resulted from observer technique and the definition of what comprises a strike. Hunting success was not appraised in the Matobo but much greater prey capture rates in this region than in the present study (Chapter 8) indicate that hyrax were probably easier to catch during the Matobo study.

Both the Matobo and the present study concurred however that foraging behaviour of black eagles is highly 'state-dependent' with more flights preceding a kill and less flights thereafter. State-dependent hunting has been noted for other raptors (Mueller & Berger 1970). Much greater rates of prey capture observed in the Matobo (see Chapter 8) may have been due to greater frequency of capture opportunities while the eagles were not specifically foraging. Black eagles in the present study were catching prey approximately every other day, so days since last kill was not really a good measure for judging the motivational state of the eagles. Patterns in the foraging behaviour of black eagles are hard to evaluate because they result from a complex interaction of motivation, climate and prey density.

Whether black eagle attacks at prey are preceded by observation of the prey or not, they very often surprise the prey when approach paths are hidden from view. In the present study black eagles often used obvious tactics to conceal their approach paths from intended prey until the last seconds. Concealed attacks are more likely to be successful for prey which spend 96% of their time within five metres of shelter (Chapter 4). Obvious surprise tactics were employed by black eagles observed by Thompson (in Gargett 1990, p. 67), Brown (1988b) and Steyn (1982), but they are not always used (Gargett 1990). Hunting by surprise may have evolutionary consequences for the prey (Rudebeck 1950, 1951; Kenward 1978a). The selective nature of black eagle predation can be expected to act primarily against individuals whose behaviour places them in vulnerable situations more frequently, rather than primarily against individuals who are less well-equipped to flee. Because black eagles hunt by surprise, different components of the hyrax population should be caught in accordance with their vulnerability and not in any 'prudent' fashion (Slobodkin 1968)



Most studies, including the present one have shown that male and female black eagles have a very strong preference for hunting together, that they may select the same prey and that they share defendable food. In the present study males and females also monitored one another during hunts and they employed division of labour on nearly half of their tandem strikes and on 4/5 tandem kills. In these ways, black eagles fulfil five of the six conditions for co-operative hunting listed by Hector (1986). There was no indication that black eagle pairs used a coordinating signal during hunts, but monitoring one another may have been sufficient communication to coordinate moves. Hunting success recorded in this study provides the first indication that cooperative hunting by a large eagle may increase the success of strikes (improved success is not necessarily a pre-requisite for cooperative hunting - Bertram 1978). It is difficult to obtain sufficient data on eagle kills to demonstrate statistically significant differences in this regard. Collopy (1983a) showed that attacks by male golden eagles were twice as successful as those by females, but could not confirm this difference statistically on account of small sample size (23 kills). He could however, demonstrate that solo hunts by golden eagles were surprisingly significantly more successful than tandem hunts. Hector (1986) demonstrated that tandem hunts of bird prey by Aplomado falcons *Falco femoralis* were significantly more successful than solo hunts (37 kills), but this difference did not hold for all attacks at prey (including insects). To date, only one investigation of raptors (Harris hawks, *Parabuteo unicinctus*) has shown that cooperative foraging consistently yields improved success in attacks at prey, and more energy per individual raptor involved (Bednarz 1988).

Cooperative hunting by raptors, especially desert falcons chasing birds, usually takes place when the intended prey make use of vegetative cover and from which they can sometimes be flushed (Hector 1986). Raptors will generally make successive strikes at their prey and often the prey is secured after the first strike (pers. obs.). A single black eagle hunting hyrax which spend 96% of their time within 5m of refuge is unlikely to have the opportunity of repeated strikes at individual prey. By keeping close together in a tandem attack, black eagle pairs can make two strikes at the same prey in quick succession. Division of labour became apparent when prey took cover in vegetation rather than rock crevices: an adult hyrax, a juvenile hyrax, a suricate and a karoo korhaan were all taken in this situation when one bird flushed the prey at ground level and the second bird caught the prey from a 'waiting-on' position. The same approach has been observed for Aplomado falcons (Hector 1986), red-necked falcons *Falco chicquera* (Ali & Ripley 1969; Osborne 1981; Malan 1991), and black eagles catching guinea fowl (Porter 1984). A different type of cooperation has been suggested for black eagles preying on vulture chicks and hyrax, where one bird serves to distract attention from the other (Bowen 1970; Steyn 1982; Mundy, Robertson, Komen & O'Connor 1986). But the use and success of cooperative hunting (specifically division of labour) by raptors probably depends mostly on the frequency at which prey take cover in a refuge from which they can be flushed, and on the resolve of the raptors to enter that refuge. Rock hyrax may be able to avoid these situations in the Magaliesberg and the Matobo because observers did not witness division of labour by attacking black eagle pairs in these habitats (Jenkins 1984; Gargett 1990). But there was evidence to suggest that hyrax were easier to catch during both these studies, so alternatively, like search hunting, cooperative hunting may be employed more often by black eagles when prey are especially hard to catch.

The size and shape of black eagles

In most descriptions of cooperative hunting by raptors where division of labour was clearly apparent, the female usually flushed the prey from cover while the male waited on (Osborne 1981; Hector 1986; Malan 1991; the present study). Adoption of these roles complies with certain morphological differences between the sexes. If females are the same shape and proportion to the smaller males then one can expect a concordant increase in wing loading and power requirement in flight (Pennycuick 1972a). In the case of black eagles, females are 13% heavier than males and from scaling one would expect a 6% increase in flight area for females if they were to be the same shape as males. Proportionately greater flight surface area of females (15% greater than males) may offset greater expected wing-loading with increased mass, but this would tend to reduce agility and create more drag. This may explain why females were observed to flap more in light airs. Superior flight performance of males is offered to explain why males 'wait-on' to catch prey which is flushed by the more heavily built and powerful females.

Reversed sexual dimorphism in raptors is clearly linked to diet with raptors taking large, fast prey being more dimorphic, but the evolutionary processes behind this phenomenon are still being debated and speculated upon (see Newton 1992). I believe there are two key factors involved in this process - dispersion patterns and agility. Because males have the capacity to mate with many females whereas females are restricted to a few offspring at a time, there is a tendency for large males to arise in social animals where males can interact and dominate one another over access to females (Clark 1978). Males cannot dominate one another or monopolise harems if individuals in the population are spaced too widely by territorial behaviour related to food supplies. In many small territorial antelopes, for instance, females are somewhat larger than males (see average masses for all small antelope species in Skinner & Smithers 1990). I would argue that normal sexual dimorphism cannot arise in most raptors because of their dispersion patterns. Only in the gregarious vultures is there some indication of normal sexual dimorphism (Newton 1992). In the case of carnivores, being large does not necessarily disadvantage the males in terms of hunting, but it would certainly disadvantage male raptors because of flight constraints operating against large size in birds (Pennycuick 1972a). Male raptors need to do more hunting than female raptors especially when they are provisioning food to a female with chicks. Thus one can expect stronger selection to operate on the foraging ability of males than on the foraging ability of females. Males often demonstrate their abilities to females by accelerated provisioning prior to nesting (Simmons 1989). In the case of raptors hunting elusive prey there must be strong selection forces favouring agility, and smaller birds tend to be more agile. I think this explains why males are much smaller than females in these species of raptor.

In the case of black eagles, smaller males do appear to be endowed with a more efficient and agile form for flight, and it is not surprising that when hunting as a pair the greater agility of males is used to full advantage. Despite their moderate/large size dimorphism, male and female black eagles cooperate to catch exactly the same prey, and it is relevant that males have almost as large feet as females and a longer tarsus. There were no data in the present study to suggest that the larger females captured larger prey, nor that they conveyed larger food items to the nest. Adult hyrax can weigh as much, and sometimes even more than adult black eagles. They have an extremely tough skin, a strong skeletal structure and they can be formidable adversaries. Average prey size taken by black eagles in this study was almost twice the prey size normally captured by larger golden eagles (see Chapter 8), despite the fact that golden eagles hold most of the records for the largest prey captured by eagles (see Table 26, p. 178). I suggest that disproportionately large feet in female and especially male black eagles have evolved due to specialised hunting for rock hyrax, sometimes involving cooperative behaviour.

Besides the observed differences in flight pattern and plumage between adult and juvenile black eagles, there were subtle differences in posture: adults generally flew on perfectly outstretched wings while juveniles often wobbled and had a hunched appearance somewhat resembling a skier on the snow slopes for the first time (see photo). High performance wings with reduced control surfaces are often unstable (Pennycuick 1972a), and the juvenile plumage of birds with such flight designs such as the bateleur (Watson 1987), and various falcons (Cramp & Simmons 1980; W. Clark pers. comm.) often endows young birds with greater control surfaces and more stability until they moult into the adult, 'high-performance' plumage. The long square tails of juvenile black eagles probably enhance stability and manoeuvrability and so assist early flying experiences. The characteristic 'leaf shape' of black eagle wings is not so evident in the juveniles - more conventional rectangular wings may assist young black eagles which are excluded from mountainous terrain by resident breeding eagles and are forced to fly great distances through more variable flying conditions over plains as well as mountains.

Adult black eagle, possibly male, bearing down on juvenile at high speed (upper escarpment, January 1989). Note the outstretched wings of the adult and the hunched, 'survival stance' of the juvenile.

The cryptic juvenile plumage would also assist these young birds at catching prey and evading territorial birds during a period which is normally associated with very heavy mortality in eagles (Brown 1976). Because black eagles are very long-lived and occupy territories in probably all the breeding, mountainous habitat south of the Sahara, it must be very difficult for young eagles to survive the sub-adult period and to become established as breeding adults. This scenario has been offered in explanation of the highly conservative reproductive strategy shown by black eagles, which involves obligate siblicide, and presumably results in the production of high quality offspring (Simmons 1991). In support of this hypothesis, breeding opportunities for black eagles can be expected to occur less frequently than for other species such as golden eagles which subsist on relatively less stable prey bases (see synthesis) and which show more opportunistic reproductive output (e.g. Jenkins & Joseph 1984).