A STUDY OF THE BLACKSHOULDERED KITE

ELANUS CAERULEUS

by

John Martin Mendelsohn

Submitted in partial fulfilment of the
requirements for the degree of

Doctor of Philosophy

in the
Department of Zoology
University of Natal
Pietermaritzburg
1981

This thesis, unless specifically indicated to the contrary in the text, is my own original work. It has not been submitted for a degree to any other University

FRONTISPIECE

♀74 about to take the partly-eaten remains of a _Rhabdomys_ _pumilio_ from ♂15

ACKNOWLEDGEMENTS

Many people helped me during this study and their assistance did much to enhance the scope of the work. The enthusiasm, too, of many friends helped and I thank these people sincerely.

Farmers at Settlers kindly gave unrestricted access to the whole area. The staff and pupils of the Settlers Agricultural High School were helpful in many ways, not least for making our stay at Settlers pleasant. The Transvaal Museum loaned rodent traps and sound recording equipment. The Director of the Durban Museum, Dr. P.A. Clancey, gave me the opportunity to write up the study.

Dr. N. Passmore kindly organised the sonagraphic analysis of kite calls. Tony Harris and Dr. J. Gulledge were helpful in providing calls of Whitetailed Kites. Nico Dippenaar performed the laborious and specialised task of identifying shrew remains. Adrian Craig gave many useful ideas and pointed me towards some helpful literature.

I benefited greatly from discussions and correspondence with many people and in particular I thank Rod Baxter, Harry Biggs, the late Dr. Leslie Brown, Dr. T. Cade, Nigel Collar, Jeremy David, Dr. J. Koplin, John Ledger, Prof. J. Meester, Prof. J. Nel, Naas Rautenbach, Manfred Schmitt, Frank von Maltitz and Robbie and Craig Weir. Dr. Ian Newton kindly came to Settlers and gave me a "crash" course on some interesting problems. Two computer "boffins", Dale Schultz and Derek Charlton were very helpful in sorting out many problems.

Warwick Tarboton and Alan Kemp were strong guiding forces in this study. Both gave me much help, advice and information concerning kites. Warwick introduced me to studying kites in the field and his work provided a very helpful background to this study. Alan Kemp showed me the light in becoming a raptor-phile and did much to separate my bad from acceptable ideas on the biology of raptors.

Prof. Gordon Maclean, my supervisor, taught me to write English, to be concise and to try and be critical. His help and advice throughout were most useful. He also assisted in generating the all-important funds for the study through the University of Natal and Council for Scientific and Industrial Research. I thank these institutions for their generosity.

Celia, my wife, helped watch kites, provided support and assistance at all stages, and gave moral encouragement necessary to see the study through. My parents gave me the right kind of genes and stimulation to be interested in kites. Their help has given me a healthy introduction to life and for this I thank them.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

GENERAL INTRODUCTION, STUDY AREA AND METHODS

The bird

The Blackshouldered Kite *Elanus caeruleus* (Desfontaines) is a small accipitrid (Jollie 1976-77) measuring about 30 cm in length and standing about 18 cm high. The adult plumage (Frontispiece) is predominantly white below and pale grey above. The lesser, median and greater wing coverts and ventral surfaces of the primaries are largely black. The irides are bright red and the rectrices are grey and white. Young birds in their first plumage differ in having brown feathering on the breast and white edging to most feathers of the upperparts. Fuller plumage descriptions are available in Brown & Amadon (1968), Cramp & Simmons (1980), Swann (1945) and Chapter 6. In general terms, Blackshouldered Kites (hereafter called kites) have short, thick tarsometatarsi, medium length toes and claws, long, broad and pointed wings, square-ended tails, large heads and small raptorial bills.

The species was first described from near Algiers, North Africa by Desfontaines in 1789 as *Falco caeruleus*. Several synonyms (listed by Swann 1945) were later proposed, both from North Africa and elsewhere in the species' range. The genus *Elanus* was erected by Savigny in 1809 for his synonym, *Elanus caesius*. While *Elanus* is closer to the monotypic *Gampsonyx* and *Chelictinia* than to other accipitrids (Jollie 1976-77), nobody has recently contested the limits of *Elanus*. It is today widely agreed to contain four taxa: the Blackshouldered Kite *E. caeruleus* of Africa, Europe and Asia, the Whitetailed Kite *E. leucurus* of America and the Blackwinged Kite *E. notatus*, and Letterwinged Kite *E. scriptus* of Australia.

There has been disagreement concerning the specific rank of caeruleus, leucurus and notatus. The three taxa are allopatric (Fig. 1.1) and could be considered geographic variants of one species (Husain 1959; Parkes 1958). The three populations differ most notably in the plumages of juveniles. In this study I have followed general custom (Brown & Amadon 1968, Stresemann & Amadon 1979; Swann 1945) in treating caeruleus, leucurus and notatus as species.

The Blackshouldered Kite is widely distributed in the Afrotropical, Palaearctic and Oriental regions (Fig. 1.1). Stresemann & Amadon (1979) recognise five subspecies: caeruleus from Africa and Europe, vociferus from India, Sri Lanka, southern China and the Malay Peninsula, sumatranus in Sumatra, hypoleucus from Java, Borneo, Phillipines, Celebes, Kalao and Lesser Sunda Islands, and wahgiensis for kites in New Guinea. In many areas the species is very common, particularly in fairly dry areas (400-800 mm rain/year) where open savanna and grassland have been partly cleared for the cultivation of cereal crops. Elsewhere in deserts and densely wooded areas kites are irregular, being either localised or sporadic visitors.

Scope of the study

This study grew out of an interest that developed while ringing kites in the early 1970's. Much of the effort at that time was devoted to ringing as many kites as possible and studying the moult of kites. The species was particularly abundant in the Transvaal (where most ringing took place), Orange Free State and Western Cape. In spite of this abundance, there appeared then to be little published information on their biology. The limited literature, however, did suggest several interesting aspects of the bird. Kites were reported as being multibrooded on occasion (Malherbe 1963), eruptive in great numbers into some areas (Brown & Amadon

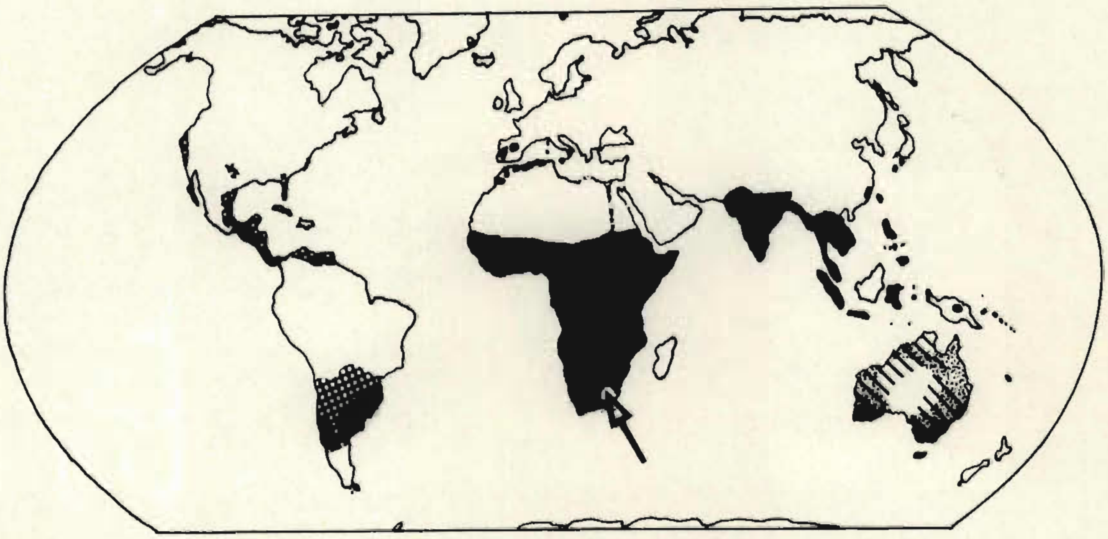


FIGURE 1.1 The world distribution of Elanus; Blackshouldered Kite E. caeruleus - black areas, Whitetailed Kite E. leucurus - white stippling, Blackwinged Kite E. notatus - fine stippling, Letterwinged Kite E. scriptus - hatching (based on Brown & Amadon 1968; Eisenmann 1971; Hollands 1979; Slater 1971; Snow 1978). The Settlers study area is arrowed.

1968; Skead 1974), communally roosting (Brooke 1965; Morgan-Davies 1965), and largely dependent on rodent prey (Siegfried 1965; Tarboton 1977). While none of these features is unique among raptors, they are sufficiently unusual to attract attention and merit study. Several authors had speculated that multiple-brooding and eruptiveness were related to high prey densities (Brown & Amadon 1968; Malherbe 1963), but little else was either known or suggested.

The objectives of the present study were 1) to describe the basic biology of kites, and 2) to examine the proximate and ultimate effects of prey on predator. It soon became clear that a large population could not be studied effectively because changes in social, spatial and breeding behaviour occurred too rapidly and unpredictably to be monitored accurately in many birds. My approach therefore became one of trying to study in detail one small group of kites, with the emphasis often placed on the individual. Large samples and comparisons between different areas have thus been sacrificed to a degree. However, it is hoped that the study will offer some insight into the factors, particularly those related to food, that mould a kite's performance.

Study area

From March 1977 to September 1978 kites were studied in a 6900-ha area near Settlers (24 57S; 28 33E) in the Springbok Flats, Transvaal (Figs. 1.1 & 1.2). The area was roughly 12 km long and 5,5 km wide. The topography was flat with a 60-m drop over 12 km from north to south. Several drainage lines (Fig. 1.2) produced a gentle rolling landscape from west to east.

Most of the Springbok Flats and the whole of the study area consists of black turf soil and red clay (Fig. 1.2). Black turf (64,4% of the study

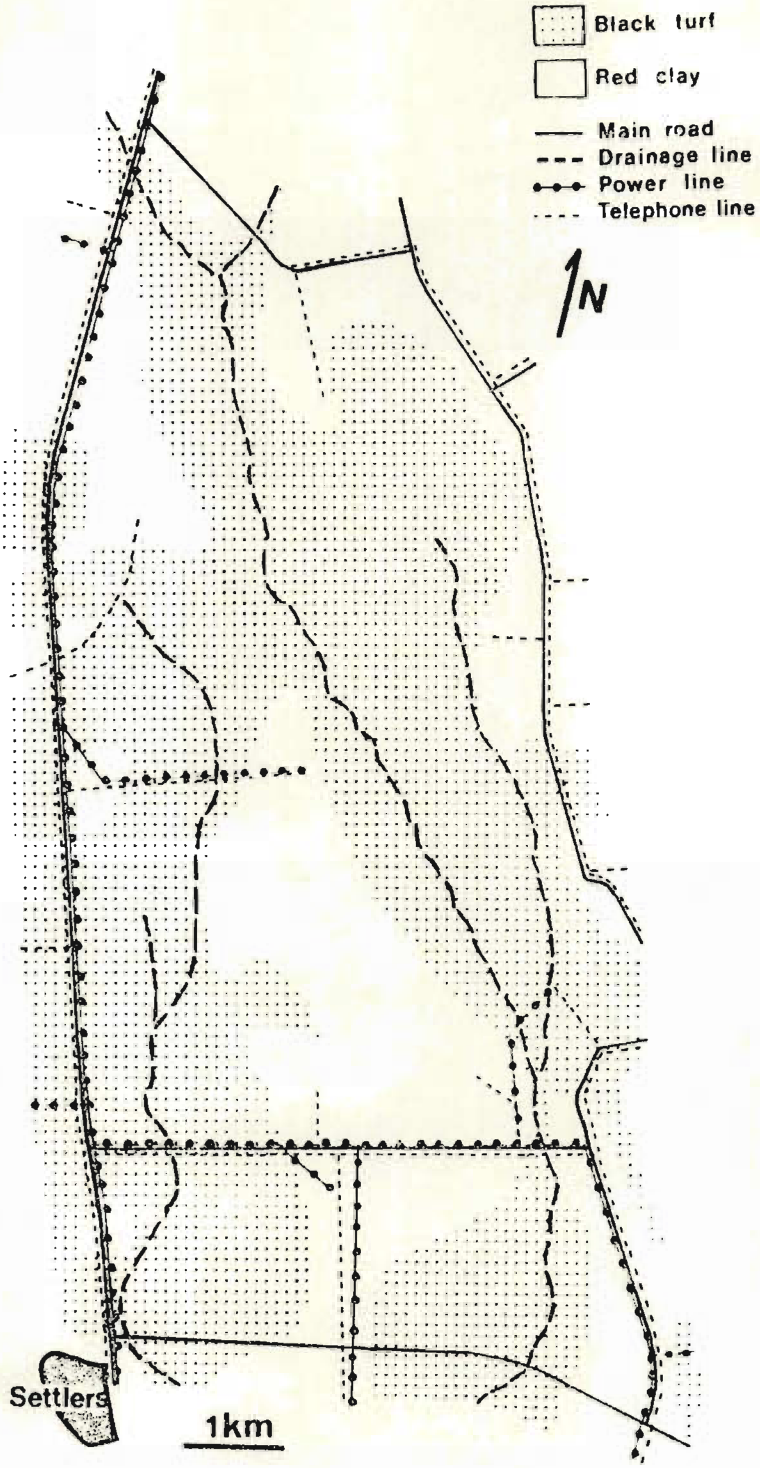


FIGURE 1.2 The study area at Settlers (24 57S; 28 33E - 1048 m a.s.l. - stippled area). The boundaries of the 6900-ha study area (Table 1.1) were placed 500 m beyond the peripheral roads shown on the map.

FIGURE 1.3 The study area at Settlers showing the main habitats. Lines represent road or field verges or contour strips.

area) predominated near drainage lines while red clay (35,5%) largely formed the intervening ridges. There were four main categories of land use (Fig. 1.3; Table 1.1). Cultivation accounted for 71,5% of the area, with six predominant crops: wheat (38%), sunflowers (33%), maize (9%), millet (9%), sorghum (7%), and manna (5%). These percentages are for 1978 but the same crops were grown in similar proportions in 1977. All crops, except wheat, were planted between September and November after the first substantial summer rains, and harvested between April and August. Wheat was usually planted in February or March and harvested between July and September.

The distinction between grasslands and woodlands (Fig. 1.3) was often somewhat arbitrary. Grassland areas had been cleared of trees but often held a re-growth of small shrubs. Both habitats were grazed by cattle. There were roughly 370 km of road verges, field verges and contour strips in the area (Fig. 1.3) varying in width between 3 and 20 m. For Table 1.1, an average width of 10 m has been used, giving about 370 ha of verge. Farmhouses, and therefore farmyards, were usually sited on red clay. Several farmyards were surrounded by small fields of planted pasture. These pastures of Cenchrus ciliaris have been included in the grassland areas of Table 1.1.

Power and telephone lines were frequently used as perches by kites. There were about 29,5 km of power lines and 44 km of telephone lines in the area (Fig. 1.2). Power lines averaged 9 m while telephone lines varied between 5 and 7 m in height.

The indigenous plant communities varied according to soil conditions. On black turf Acacia tortilis, A. nilotica, A. flecki and Rhus pyroides accounted for about 98% of the trees, while grasses consisted mainly of Setaria woodi, Ischaemum glaucostachyum, Bothriochloa insculpta, Sorghum

TABLE 1.1 The areas and percentages of major habitats in the Settlers study area.

Habitat	Area (ha)	%
Black turf:		
Cultivation	3369	48,8
Grassland	162	2,3
Woodland	677	9,8
Road verge	238	3,4
Subtotal	4446	64,4
Red Clay:		
Cultivation	1563	22,7
Grassland	213	3,1
Woodland	469	6,8
Farmyards	77	1,1
Road Verge	132	1,9
Subtotal	2454	35,6
TOTAL	6900	100,0

versicolor and *Sehima galpini*. There was a more diverse flora on red clay where *Acacia tortilis*, *A. nilotica*, *A. robusta*, *A. caffra*, *A. karroo* and *Zizyphus mucronata* formed woodlands. *Themeda triandra*, *Hyparrhenia hirta*, *Bothriochloa insculpta*, *Eragrostis* spp., *Heteropogon contortus*, *Fingerhuthia africana* and *Panicum coloratum* were the commonest grasses.

Meteorological data in Figures 1.4 and 1.5 were obtained from the nearest weather station at Towoomba (24 54S; 28 20E — 1173 m a.s.l.). The mean annual rainfall at Settlers was 601 mm, but this figure was based on fewer years than at Towoomba. About 90% of the rain fell between October and April, with the highest monthly totals in December, January and February. A large proportion of the rain fell in localised afternoon thunderstorms, often resulting in marked differences in the extent of a fall between areas. Temperatures in winter seldom reached freezing point but frost could be expected on about 20% of the days in June and July. Maximum temperatures in summer often rose to 35-38°C. Wind was predominantly from ENE, except during the middle of winter when SW winds were most frequent. Wind speeds seldom exceeded 8 m/s. Daylength averaged 12,6 h (range 10,5-13,75 h). For most calculations I added 1 h of twilight to give 13,6 h of active time.

General methods

I attempted to catch, ring and colour mark all kites in the study area at Settlers. Most birds were caught on Bal-chatri traps (Berger & Mueller 1959) baited with wild *Praomys natalensis* or *Rhabdomys pumilio*. Two mice were normally placed in a trap. Some kites, however, were trap-shy after being caught previously. Four of these were trapped in small (1 x 2 m) mist nets placed around either two tethered mice or a captive kite. The mice were tethered to the ground while the kite was placed on a perch 0,3-0,5 m off the ground. The wild kites became entangled in the nets when they swooped down to attack the mice or the intruding captive kite. Two

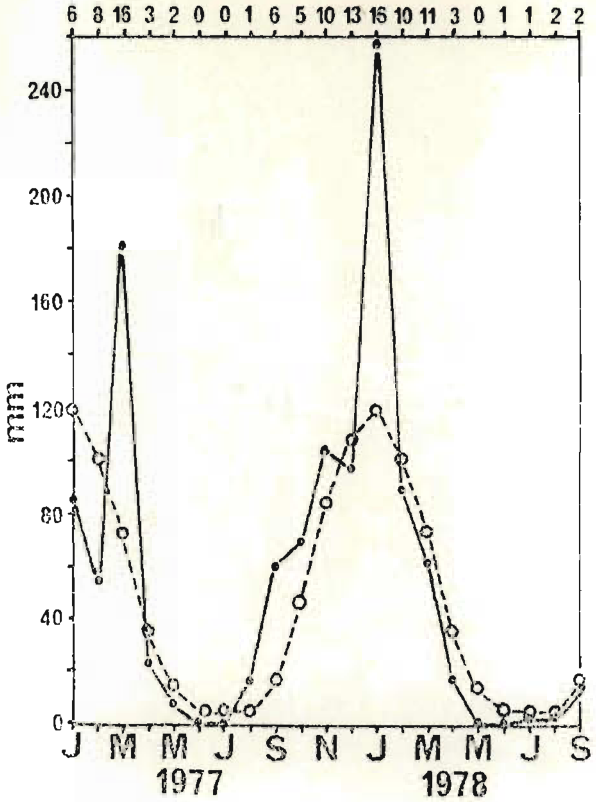


FIGURE 1.4 The observed (———) and average (-----) rainfall at Towoomba weather station. The average annual rainfall at Towoomba was 621 mm. Figures above each month show the number of days on which rain was recorded at Towoomba during 1977 and 1978. Data from Towoomba weather station and the South African Weather Bureau (WB 20).

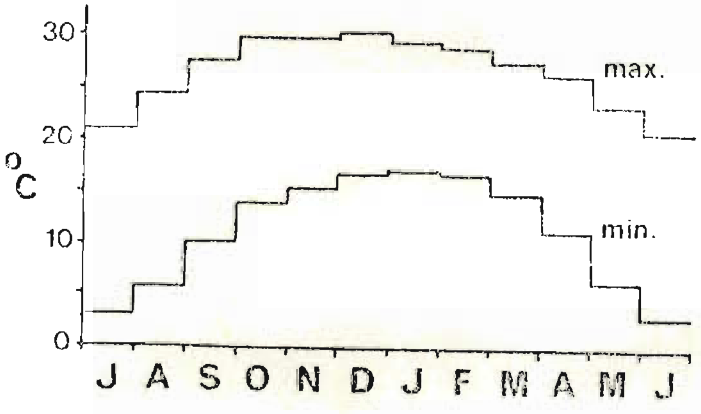


FIGURE 1.5 The average minimum and maximum daily temperatures at Towoomba weather station. From South African Weather Bureau (WB 19).

other kites were caught on a modified pole-trap. The trap basically consisted of a 2,5-m pole stuck in the ground with a platform that formed a suitable perch for kites. As soon as a kite landed on the platform, a sprung noose closed rapidly round its legs. The trap was placed near a tethered captive kite which helped to attract wild kites to the immediate area.

Kites were ringed with serially numbered rings supplied by the South African Bird Ringing Unit. Coloured patagial tags (Kemp 1977; Picozzi 1971; Fig. 1.6) were also fitted to kites. Individual identities were determined by marking the left or right wing, and by colour and shape combinations (Fig. 1.6). The tags were made of "Sterkolite" produced by Kahn & Kahn Plastics, Johannesburg. Five suitable colours were available: red, yellow, green, blue and white. The colours remained fast after being on some birds for 19 months.

The methods used to attach the tags were generally those described by Kemp (1977). However, I found that nine birds lost their tags after between four weeks and ten months. These kites were recaptured, and in one case the nylon rod through the patagium (Fig. 1.6) was found to have broken. The other eight tags were lost after the ventral washers had cut into and through the patagium. To remedy this I inserted an oval disc of "Sterkolite" between the ventral washer and patagium. The pliable "Sterkolite" prevented damage to the patagium and no further losses were recorded.

Observations during the study were made mostly from a car or motor cycle. The 370 km of roads and verges could all be easily negotiated by these vehicles. 10 x 35 binoculars and a 50 power telescope were used to view the birds. Observations on kites were often confined to the first and last three or four hours of the day. The intervening period was

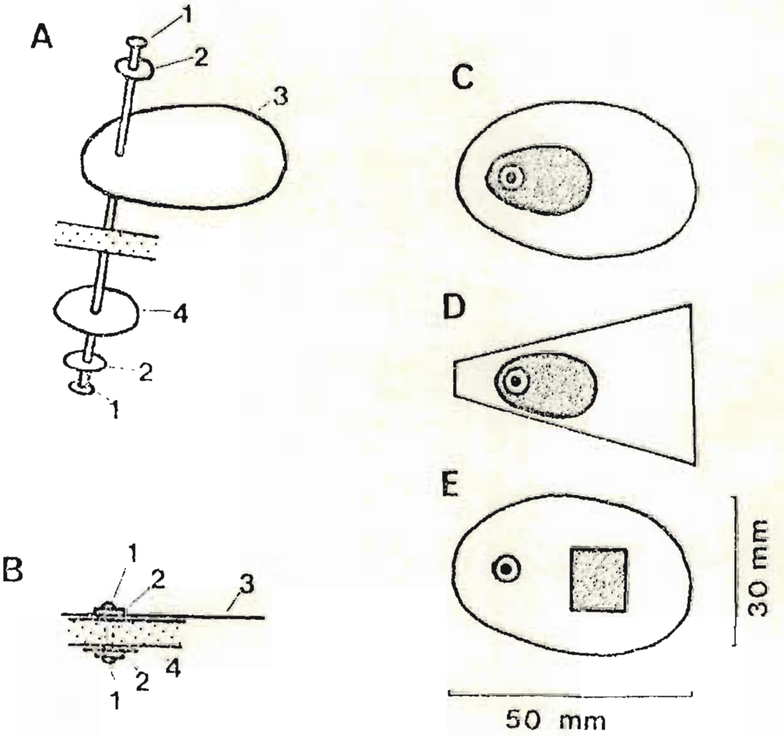


FIGURE 1.6 Patagial tags used on kites. (A) - exploded view showing (1) the flattened ends to the 1-mm diameter nylon rod, (2) the 10-mm diameter nylon washers, (3) the "Sterkolite" tag, the patagium (stippled), and (4) the protective disc of "Sterkolite". (B) - the tag shown *in situ*. (C) and (D) - different tag shapes with two colours to each tag; the overlying piece is held in place by the nylon rod. (E) - pattern formed by glueing two pieces of "Sterkolite" together, and then removing a square from the upper layer to reveal the underlying colour.

usually hot and few kites were seen; the birds normally perched inactive in the shade of trees. As a result I often spent the middle of the day checking nests, roosts and setting or inspecting rodent traps (Chapter 2).

Every sighting of a kite in the study area was noted, the time, locality, identity and activity of the bird when first seen being recorded. These records provided a form of "instantaneous sampling" of activity (Altmann 1974). The following activity categories were used: Inactive, Intense perched-hunting, Preening, Casual search, Feeding, Directional flying, Soaring, Flying with prey, and Hovering. Most of these categories are self-explanatory and are those used by Tarboton (1978a). Casual searching kites occasionally glanced at the ground, preened or looked around. During Intense perched-hunting, in contrast, kites searched the ground continuously.

Each tagged kite was identified by a number and a "♂" or "♀" preceding the number indicated its sex, for example ♂15 or ♀74. Males and females were identified by their behaviour (Chapter 4) or by a discriminant analysis of certain body measurements (Chapter 6). Unmarked birds were named according to the areas they occupied or, where possible, their marked mates, for example Clev. chick, ♀30x or ♀30y (first and second unmarked mates of ♂30).

Time was recorded in relation to sunrise. Each week I adjusted my watch to read 00h00 at sunrise. A time therefore given as, e.g. 05s45 indicated that the observation was made 5 hours and 45 minutes after sunrise. Observations made at different times of the year are thus comparable, at least relative to the start of each day. For several analyses, the day was divided into three periods: morning, midday, and afternoon. The lengths of these periods were calculated for each week of the year by dividing the day into four quarters. The "morning" period was then taken as the first quarter in addition to 30 min before sunrise. The second and third quarters formed the "midday" period, while the "afternoon" consisted of the final quarter and any activity observed after sunset.

Chapter 2

FEEDING ECOLOGY

INTRODUCTION

Intensive studies of raptor feeding ecology are seldom practical. Most raptors either catch prey rarely (e.g.large eagles) or hunt within closed habitats (e.g. accipiters). In addition, many factors influence the total feeding strategy of a bird and it is seldom possible to monitor these simultaneously. Our knowledge of raptor feeding ecology consists mostly of lists of prey species and strike success rates. Exceptions are studies by Balgooyen (1976) of American Kestrels Falco sparverius, Warner & Rudd (1975) of Whitetailed Kites, Tarboton (1977; 1978 a) of Blackshouldered Kites, and Wakeley (1978 a, b, c) of Ferruginous Hawks Buteo regalis.

For raptors, information is especially lacking on 1) changing relationships between factors such as prey size, hunting method and food values, which influence feeding success, 2) how these factors vary diurnally and seasonally, 3) energy budgets, and 4) differences in feeding ecology between birds of different sex and status. In focusing on the proximate relationship between a predator and its prey, I aimed in this chapter to investigate some of these poorly understood subjects. Basic descriptions are first given of hunting behaviour and performance, rodent behaviour and population dynamics, and the prey caught by kites. These variables are then compared for different habitats, seasons and groups of kites. An analysis of activity and energy budgets is offered for non-breeding kites. Finally, the results are discussed in terms of foraging theory (Krebs 1978; Schoener 1971) in an attempt to understand the relationships between time, energy and hunting behaviour.

METHODS

The feeding ecology of kites was studied in three ways: by observing hunting performance, by trapping rodents and by analysing pellets. Hunting behaviour was recorded during observation periods (n = 648) which lasted a maximum of 30 min. The periods were shorter if kites under observation were lost to view or stopped hunting. The variables, most of which follow Tarboton (1978 a), noted during hunting observations were:

1) individual identity of kite, date, locality and habitat (see Chapter 1 — Table 1.1)
2) hunting strategy (perched-hunting or hovering. Intense scanning of the ground distinguished perched-hunting from other activity. Hovering never formed part of a display and was assumed to be only for hunting)
3) the number of perch changes
4) duration of hovering bouts (a bout ended when a kite landed or started soaring)
5) the number of hovers in each bout (a hover occurred when a kite hovered above one position and ended when the kite moved elsewhere)
6) duration of each hover
7) number of descents towards prey during each hovering bout
8) strikes (continuous dives towards prey; either full-strikes if the kites hit the ground, or half-strikes if they pulled out of dives just above the ground. These criteria were the same for perched-hunting and hovering, except that all flights from perches towards prey were called strikes)
9) wind speed (estimated at ground level and scored 0-5; 0 indicating no wind and 5 a wind stronger than about 16 m/s)
10) hovering height (scored 1-5, with 1 = 5-10 m and 5 > 100 m).

Details of all full-strikes seen incidentally were also recorded. Total samples of full-strikes and kills are therefore larger than those recorded within hunting periods.

Small mammals were trapped at three-month intervals from April 1977 to September 1978. At five sites, 20 trap-stations were fixed 10 m apart along a line, with one hardboard live-trap (Meester 1970) and two break-back snap traps set at each station. At a sixth site, started in October 1977, 30 live-traps were placed 10 m apart along a line. These traps were carefully set in runways to catch as many *Otomys angoniensis* as possible. This species was not normally attracted to baited traps (Taylor & Green 1976; pers. obs.). All traps were baited with a peanut butter-syrup-oatmeal mixture (Dippenaar 1974). Trapping sessions lasted three days and nights. All catches were removed and bait renewed if necessary late in the morning of each day. Specimens were weighed on a triple-beam balance, and from June 1978 all rodents were examined for reproductive activity. Trapping success at different sites was compared per 100 trap-nights (total no. traps x no. of nights).

Pellets were collected below roost trees and other favoured perches. All pellets were dried to constant weight and weighed to the nearest 0,1 g on a triple-beam or electronic scale. They were then soaked and dissected to identify prey remains. Rodent skulls were identified using a key (Coetzee 1972) and reference collection. For non-mammalian prey and pellets with no skull fragments, the following characters were used: lizards - scales together with large insect fragments; birds - feathers and skeletons; shrews - fine fragments of insect cuticle and a characteristic odour; *Otomys angoniensis* - long hair with dark grey and brown proximal and distal ends respectively, also the presence of large bones; *Rhabdomys pumilio* - short, stout hair, none of which was white; *Lemniscomys griselda* - as for *R. pumilio*, but with much white hair; *Praomys natalensis* - fine short hair (< 10 mm in length); *Saccostomus campestris* - fine hair, but with a large quantity of white hair. These features were checked against specimens and pellets of known identity. Although *P.natalensis* has been found to consist of two sibling species with different karyotypes (Hallet 1979; Taylor & Gordon 1978), the karyotype(s) of these rodents at Settlers has not been determined; I shall therefore continue using the name natalensis. The full names of rodents are given when the species are first introduced, but the generic names only are used thereafter.

RESULTS

Hunting behaviour

Most hunting occurred during the first and last 2-4 daylight hours (Chapter 5, p. 204). The hunting activity of five kites during dawn-to-dusk watches is shown in Figure 2.1. On four days no hunting occurred during the middle of the day. Morning hunting normally stopped after prey had been caught and kites then spent the heat of the day (above about 25° C) perched in the shade of trees. It was often possible to drive 50-60 km between 05s00 and 09s00 without seeing an active kite. Tarboton (1978 b) showed that the number of kites seen during road-counts was 2-4 times lower in the middle of the day than in the morning or late afternoon.

During the five full-day watches the kites hunted for 148, 256, 260, 264 and 549 min respectively ($\bar{x}$ = 296,4 min) and made three kills during 1077 min of perched-hunting (359,0 min/kill) and seven kills in 400 min of hovering (57,1 min/kill). These rates of prey capture were lower than average rates (see p. 27 & Table 2.4) for the population, and the five kites therefore hunted for longer periods than usual to catch their daily food requirements. Further estimates of the duration of hunting are made elsewhere (see Activity and energy budgets, p. 60).

Table 2.1 gives three sets of data showing the overall proportions of hovering and perched-hunting. Tarboton's (1978 a) data are biased in favour of perched-hunting because his samples include little afternoon hunting (see below). My Settlers hunting observations also favour perched-hunting because perched kites were more readily spotted, and then watched, than hovering ones. Data for full-day watches are unbiased but the samples

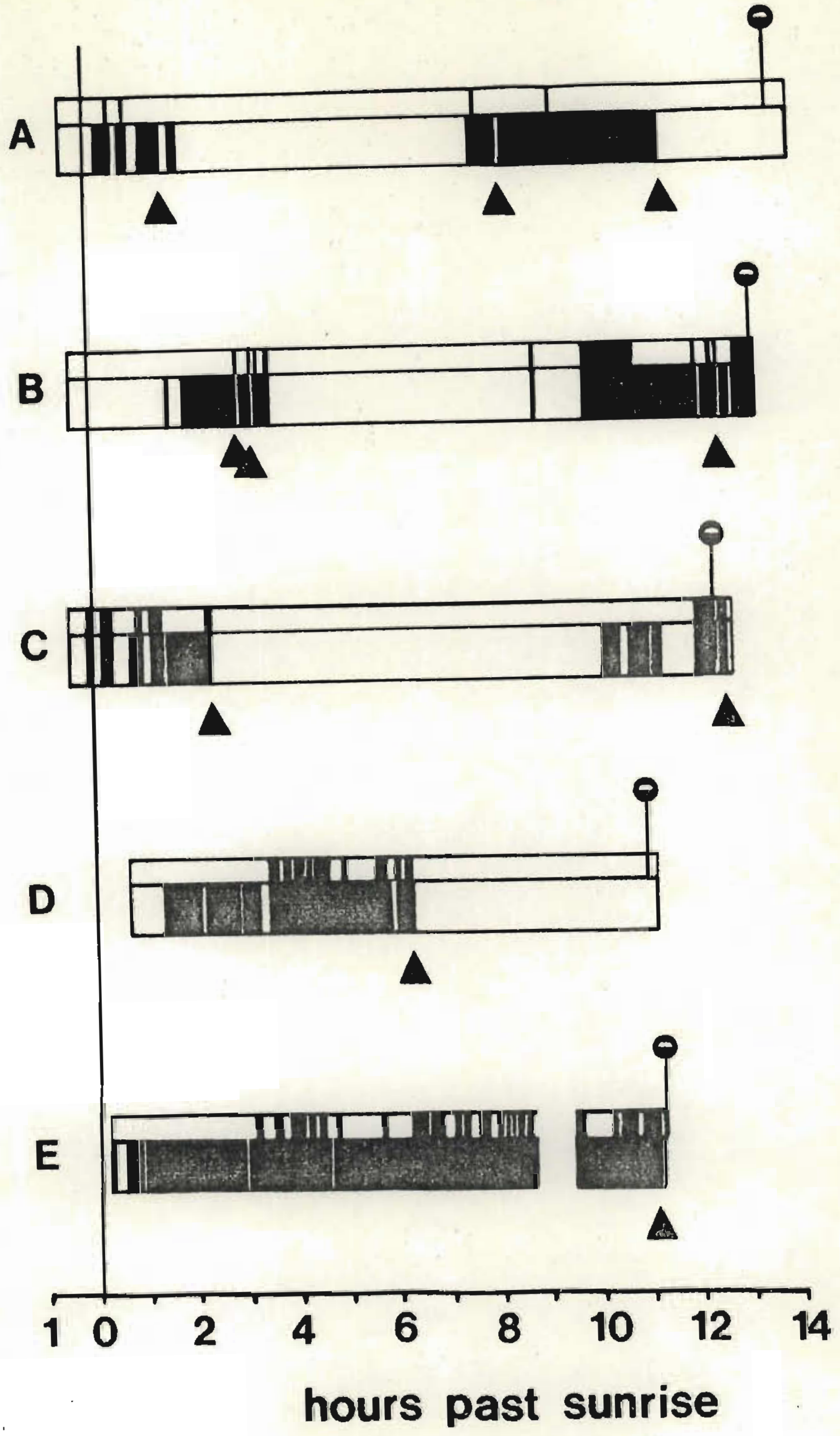


FIGURE 2.1 The hunting and non-hunting activity of five kites during dawn-to-dusk watches. Time spent hunting is shaded - upper bar for hovering, lower bar for all hunting. Sunset (●) and kills (▲) are indicated. (A) - 20 Jan 1978, paired female; (B) - 9 Feb 1978, unpaired male; (C) - 16 Mar 1978, breeding male; (D) - 4 Aug 1975, female; (E) - 17 Aug 1975, same female as in (D). (D) and (E) from W.R. Tarboton (pers. comm.). See Chapter 5 (p. 204) for details of these kites' other activities.

TABLE 2.1 Observed proportions of hovering and perched-hunting. Two full-day watches from Tarboton (1978a) are included with data from Figure 2.1.

Data source	Total time observed hunting (min)	Percentage hovering
Tarboton (1978a) excluding two full-day watches	3514	28,7
Hunting observations at Settlers	11384	25,2
Five full-day watches (Fig. 2.1)	1477	27,1
TOTAL	16375 (272,9 h)	26,3

are small. Figures of 30% hovering and 70% perched hunting are probably close to the mean proportions. However, these proportions were highly variable as shown by the percentage hovering (3,5-37,3%) during the five full-day watches (Fig. 2.1).

Kites hovered least often in the morning and most often in the afternoon (Table 2.2 & Chapter 5 — Fig. 5.2 b). Hovering was the usual hunting strategy in the hour before dark, and indeed it was rare to see perched-hunting at this time. The data in Table 2.2 suggest slightly more hovering at midday than in the morning; Tarboton (1978 a) found a similar trend.

Hovering usually started after a period of perched-hunting or soaring. After leaving a perch a kite gained height to a hovering position by direct flight or soaring. After successful or unsuccessful attempts at prey capture the kite usually returned to perch. Hovering bouts lasted an average 4,2 min (n = 435; range 1-26 min). This is substantially lower than Tarboton's (1978 a) average of 7,8 min and Warner & Rudd's (1975) 6,1 min for the Whitetailed Kite. These authors took a bout as having ended once the bird landed on a perch; they thus excluded bouts ending when soaring started. At Settlers bouts ending when soaring started lasted an average 3,3 min (n = 85). Bouts ending with a kill lasted 4,8 min (n = 49), while bouts ending unsuccessfully lasted 4,1 min (n = 386). Morning bouts lasted 3,7 min (n = 113), midday bouts 3,2 min (n = 161), and afternoon bouts 5,7 min (n = 112). Afternoon bouts were significantly longer than the others ($\chi^2_8 = 24{,}8$; $p < 0{,}01$). Wind conditions apparently did not affect the duration of hovering bouts; in wind rated 0-1 bouts averaged 4,5 min (n = 75) and in stronger wind of 2-4 averaged 4,1 min (n = 83).

A hovering kite maintained position above a site by rapidly flapping its wings. It remained in this position until it either flew to another

TABLE 2.2 Indices showing the frequency of hovering and perched-hunting at different times of the day. Day periods defined in Chapter 1 (p.13).

Data source	Time of day		
	Morning	Midday	Afternoon
% hovering of all kites seen (total no. seen)	$5{,}8^{a}$ (342)	$10{,}9^{ab}$ (339)	$18{,}0^{b}$ (372)
% perched-hunting kites to start hovering during observation (total no. watched perched-hunting)	$36{,}1^{c}$ (144)	$38{,}4^{cd}$ (172)	$53{,}1^{d}$ (128)

$^{aa}p < 0{,}05$; $^{bb}p < 0{,}01$; ^{cc}N.S.; $^{dd}p < 0{,}05$.

hovering position or started a descent towards prey. Excluding hovers ending with descents, each hover lasted a mean 11,6 s (n = 447, range 1-67,8 s). Kites thus searched for an average 11,6 s without seeing prey, or without seeing prey warranting an attempt at capture (i.e. a descent). The considerable variation in search time suggests that in some cases kites quickly assessed that potential for prey capture was poor, while in other places they searched longer. Hovers in the morning (12,8 s; n = 72) and afternoon (12,6 s; n = 250) were significantly longer than those at midday (8,9 s; n = 125) (X^2_9 = 17,7; $p < 0,05$). Hovers low over the ground (rated 1-2; 9,85 s; n = 235) were shorter than higher ones (rated 3-5; 13,8 s; n = 209) (X^2_9 = 31,8; $p < 0,001$). Wing beat depended on wind speed and was shallowest during strong winds. Wind also influenced the angle of the body; normally this was horizontal but during light wind the body was held obliquely. During wind rated 0-1 hovers were shorter ($\bar{x}$ = 9,65 s; n = 209) than in stronger wind rated 2-4 ($\bar{x}$ = 13,9 s; n = 237) (X^2_9 = 42,3; $p < 0,001$)

Descents were either vertical or at a steep angle. The wings were held above the body and used parachute-like to control the rate of descent; during a slow descent they were held far apart, and during a rapid drop clo together. Some descents were uninterrupted with the kites reaching the ground after a single long dive. In others, kites checked their descent several times by pausing to hover. One kite spent 7 min hovering during a descent. Most descents (65,4%) did not end in strikes or final dives towards prey, presumably because prey often disappeared. Hovering was usually resumed elsewhere after a descent was abandoned.

During a final strike at prey the wings were first held above the body to control its speed, and then the bird tilted forwards to approach 'head-first' over the last few metres. Each strike was either a half-strike or a full-strike, and each full-strike was either successful (a kill) or unsuccessful. The proportions of these alternatives are given in Table 2.3

TABLE 2.3 Proportions of half-strikes, full-strikes and kills made by hovering and perched-hunting kites. Numbers of kills and 'total' numbers of full-strikes were determined from all observations (see METHODS, p. 16). Day periods are defined in Chapter 1 (p.13).

Variables	Morning	Midday	Afternoon	Total
Hovering				
No. (%) full-strikes	34 (40,0)[a]	44 (56,4)	91 (54,8)[a]	169 (51,4)[d]
No. (%) half-strikes	51 (60,0)	34 (43,6)	75 (45,2)	160 (48,6)
Total no. full-strikes from all observations	40	64	115	219
% full-strikes successful (no. kills)	37,5[b] (15)	39,1 (25)	44,3[b] (51)	41,6[e] (91)
Estimated % of all strikes successful	15,0	22,1	24,3	21,4
Perched-hunting				
No. (%) full-strikes	48 (35,0)[c]	63 (48,5)[c]	42 (52,5)	153 (44,1)[d]
No. (%) half-strikes	89 (65,0)	67 (51,5)	38 (47,5)	194 (55,9)
Total no. full-strikes from all observations	82	93	71	246
% full-strikes successful (no. kills)	47,6 (39)	45,2 (42)	47,9 (34)	46,3[e] (114)
Estimated % of all strikes successful	16,6	21,9	25,1	20,4

[aa] $p < 0,025$; [bb] N.S.; [cc] $p < 0,025$; [dd] $p < 0,05$; [ee] N.S.

Of all strikes from hovers, 51,4% were full-strikes and 21,4% resulted in kills. Fewer full-strikes were made in the morning than at other times of the day (Table 2.3). Grass cover and speed made it impossible to see actual details of prey capture. However, observations on captive kites and a study by Harris (1978) indicate that at the last moment the pelvis and feet are thrown forward and the prey grabbed. The method seems gener for raptors (Goslow 1971).

Perched-hunting kites spent most of the time scanning the ground, on glancing up and around at 5-20-s intervals. Hunting perches characteristically provided a clear view of the ground below and it appeared that kites selected such perches. Resting and feeding perches were usually more robust than hunting perches. Thus, kites hunted from telephone wires and insulators, but perched on telephone poles while resting. In order of frequency, kites hunted from telephone lines (6-8 m above ground), electricity lines (10-11 m), trees (2-20 m), and fence posts (1,3 m).

The availability of perches varied between territories. Trees and fence posts served as perches in areas without telephone or electricity lines (see Chapter 1 — Fig. 1.2). Kites also showed individual preferences. While some kites used any perch, others consistently avoided available telephone and electricity wires. This was obvious where the male and female of a pair differed in their choice of perches. Several birds also changed their use of perches, e.g. one female hunted fr trees and fence posts only when she arrived in the study area but three months later used all the artificial perches.

Hunting kites made frequent perch changes, usually flying 10-50 m to new sites where they resumed hunting immediately. Birds hunting from telephone and electricity wires moved along the lines and often moved 1-2 within 0,5-1,0 h. Perch changes were made on average every 7,0 min (n = 1220), but the rate changed significantly during the day ($X_2^2 = 13,6$; $p < 0,01$); in the morning it was 6,4 min, at midday 6,8 min, and in the afternoon 8,6 min.

Perched-hunting kites often TAIL WAGGED (see Chapter 5 — Fig. 5.3), especially while watching prey intently and after making a strike, regardle of success. This display probably served to repel other kites away from the immediate area in which the kite was hunting, since their flight may have alerted rodents which had moved into positions where they were expose to capture.

Three perched-hunting kites made clucking and grating calls unlike any of their usual whistles and screams (Chapters 4, p. 154 & 5, p. 214) W.R. Tarboton (pers. comm.) heard the same call from a perched-hunting kite Some of these calls were made from perches, but most were made during perc changes and strikes. In each case hunting seemed to be particularly intense. There were no other kites nearby, suggesting that the calls were not directed at particular conspecifics. It is not clear what function these calls performed.

Most strikes consisted of direct dives at prey within 5 m of perches. There were initial horizontal flights in strikes over greater distances and at the end of such flights kites often hovered and then either dived or flew back to perch. One successful strike was over 130 m across a plough field. In steep dives the wings were held above the body, whereas kites dived "head-first" at shallow angles. The proportions of half- and full-strikes are given in Table 2.3. Fewer full-strikes were made in the morning than at midday and in the afternoon. Of all strikes 44,1% were full-strikes and 20,4% resulted in kills. Compared to strike performances from hovering, only the proportion of full- and half-strikes differed significantly (Table 2.3).

Tarboton (1978 a) observed 125 strikes by perching kites; 66 (52,8%) were full-strikes and 11 (16,7%) of these were kills. These percentages differ significantly from Settlers data in Table 2.3 (full-strikes/all strikes, z = 1,7; p < 0,05; kills/full-strikes, z = 4,3; p < 0,001). He also recorded 127 strikes by hovering kites; 90 (70,9%) were full-strikes and 24 (26,7%) of the full-strikes were successful. These proportions, to differ from those in Table 2.3 (full-strikes/all strikes, z = 3,8; p < 0,00 kills/full-strikes, z = 2,5; p < 0,01).

Hunting performance

Table 2.4 summarizes hunting performance. Hovering resulted in 3,2 times more kills and 2,8 times more strike opportunities per unit time than perched-hunting. Highly variable and skewed distributions of time intervals between successive prey captures (Fig. 2.2) suggests that although most prey was obtained quite rapidly, kites often had to hunt for long periods before catching prey.

Hovering in the afternoon was more successful than at other times of the day, and both hovering and perched-hunting were least successful at midday (Table 2.4). While these conclusions were shown by only several statistically significant differences, many rodents are less active during the middle of the day than at other times (Brooks 1974; Choate 1972; Davi 1973).

Tarboton (1978 a) recorded 1250 min of hovering with the following rat of success: 52,08 min/kill, 9,84 min/all strike, and 13,89 min/full-strike Only the rate of full-strikes differed from the rate observed at Settlers (χ^2_1 = 3,02; p < 0,1), probably because of the different proportions of full- and half-strikes observed by Tarboton (see above). During 3077 min of perched-hunting he observed the following success rates: 279,7 min/kill, 24,6 min/all strike, and 46,62 min/full-strike. Only the rate of kills differed from Settlers data (χ^2_1 = 6,24; p < 0,025) and this, too, was due

TABLE 2.4 Aspects of hunting success for hovering and perched-hunting kites at different times of the day. Day periods are defined in Chapter 1, p.13.

Variables	Morning	Midday	Afternoon	Total
Hovering				
Time observed (min)	651	783	1430	2864
Minutes/kill (no.kills)	40,7^{a} (16)	48,9^{a} (16)	35,8^{a} (40)	39,8^{i} (72)
Minutes/all strike (no. all strikes)	7,7^{b} (85)	10,0^{b} (78)	8,6 (166)	8,7^{j} (329)
Minutes/full-strike (no. full-strikes)	19,1^{c} (34)	18,2^{c} (43)	16,4^{c} (87)	17,5^{k} (164)
Hovers/descent (no. descents)	8,1 (145)	8,2^{d} (137)	6,3^{d} (354)	7,1 (636)
Perched-hunting				
Time observed	2734	3807	1979	8520
Minutes/kill (no. kills)	109,4^{e} (25)	152,3^{e} (25)	116,4^{e} (17)	127,2^{i} (67)
Minutes/all strike (no. all strikes)	20,0^{f} (137)	29,3^{fg} (130)	24,7^{g} (80)	24,6^{j} (347)
Minutes/full-strike (no. full-strikes)	57,0^{h} (48)	60,4^{h} (63)	47,1^{h} (42)	55,7^{k} (153)

$^{aa}{}_{NS}$; $^{bb}{}_{+}$; $^{cc}{}_{NS}$; $^{dd}{}_{+++}$; $^{ee}{}_{NS}$; $^{ff}{}_{+++}$; $^{gg}{}_{NS}$; $^{hh}{}_{NS}$; $^{ii}{}_{++++}$; $^{jj}{}_{++++}$; $^{kk}{}_{++++}$

+ $p < 0{,}1$; +++ $p < 0{,}01$; ++++ $p < 0{,}001$

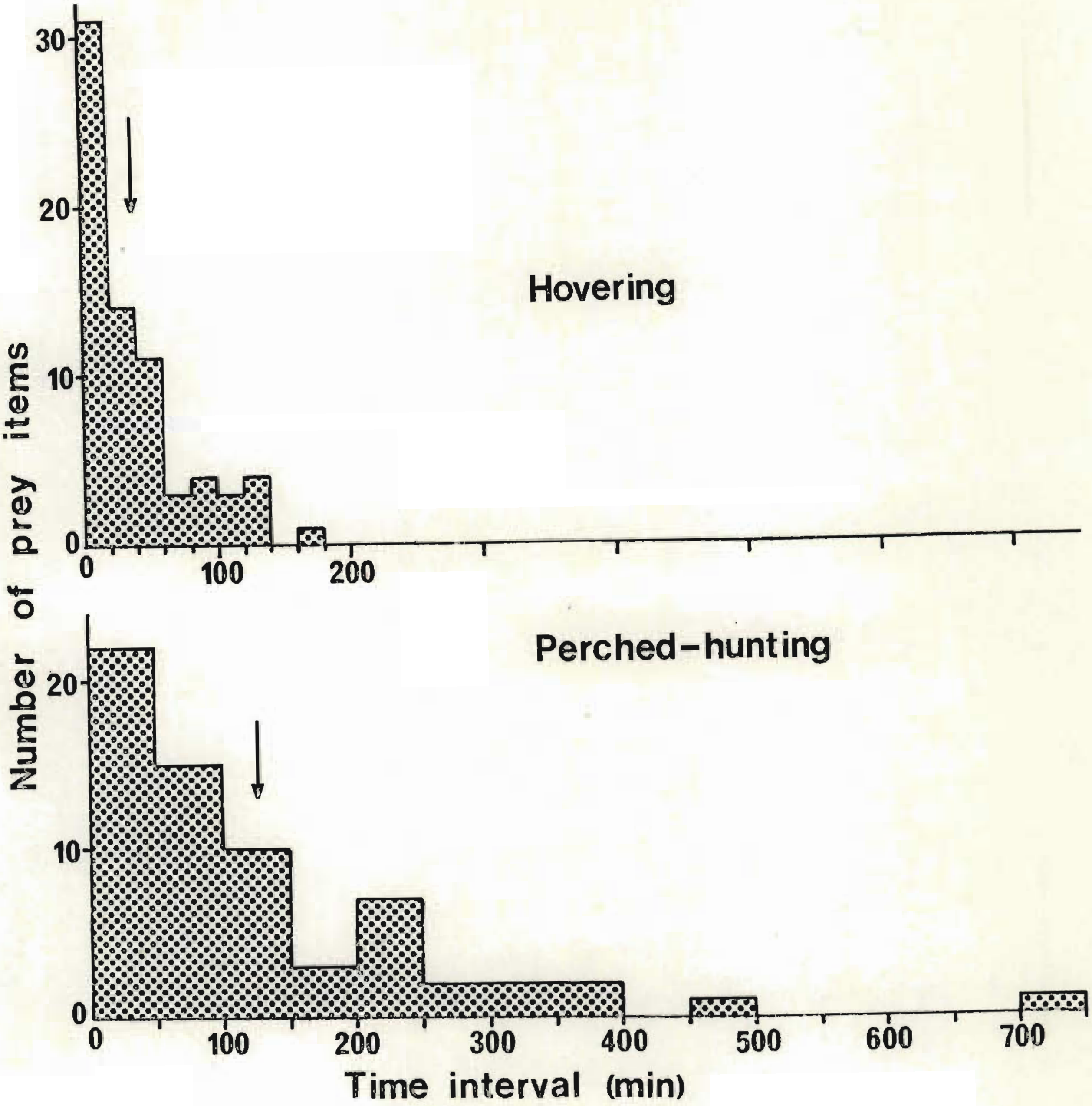


FIGURE 2.2 Frequencies of intervals of time spent hunting between successi prey captures. The intervals were those that I recorded betweer observed consecutive kills and they therefore approximate to the intervals that hunting kites had to wait before capturin prey. Mean rates of prey capture (arrows) from Table 2.4.

to a difference in strike success. The hunting performance of kites in Tarboton's study and mine therefore differed mainly in strike performances; the kites found and attacked prey at similar rates.

Feeding behaviour

Of 205 prey items I saw caught, 185 (90,2%) were immediately taken to a feeding perch (or if breeding, to females or chicks). Prey was carried in the feet. Three (1,5%) tiny items were swallowed whole in flight, and three (1,5%) were eaten where they were caught in bare ploughe fields. Fourteen (6,8%) very large rodents (13 Otomys, 1 Praomys) were not carried away and feeding started at the capture site in dense cover. In each case I flushed the kite after it had failed to fly up after a full-strike. Eleven of these rodents weighed an average of 114,9 g (S.D. = 18,0 g; range 91-153 g). The kites later returned to their prey, fed on them some more, and carried them to a perch. The kites could have carrie these rodents away initially but by eating part of them first, reduced the to a more manageable size (see below). I observed a kite carry a 105-g rodent and Forbes Watson (1977) recorded a 210-g kite flying with a 164-g load.

Stout perches such as telephone poles, fence posts and thick branche (> 3-4 cm diameter) were used for feeding. One breeding female regularl fed on the ground in a bare ploughed field in spite of other feeding perche nearby.

Prey smaller than about 10 g was either swallowed whole or torn into two or three pieces. Larger prey was torn into small pieces and the intestines and embryos were discarded. The heads of Otomys heavier than about 60 g were also discarded because kites were unable to swallow them or tear them into smaller pieces. The body parts that kites would not ha eaten were removed from 25 rodents to get an indication of weight loss (Ta 2.5). These data show substantial percentage weight losses which increas in proportion to rodent weight.

TABLE 2.5 Prey weight (g) reduction resulting from removal of heads (h), intestines and stomachs (i) and embryos (e).

Weight class	Species	Whole weight	Reduced weight (part removed)	% reduction
15 - 30	Praomys	19,0	15,5 (i)	18,4
	"	19,0	15,5 (i)	18,4
	"	21,5	17,5 (i)	18,6
	"	22,0	18,0 (i)	18,2
	"	22,0	18,0 (i)	18,2
	"	23,0	18,0 (i)	21,7
	"	24,5	21,0 (i)	14,3
	"	25,0	19,5 (i)	22,0
	"	25,5	22,0 (i)	13,7
	"	27,5	19,5 (i)	29,1
			(Mean reduction =	19,3%)
31 - 50	Otomys	36,5	28,5 (i)	21,9
	Praomys	35,5	29,0 (i)	18,3
	"	38,0	30,5 (i)	19,7
	"	39,0	26,5 (i)	32,0
	"	40,0	24,5 (i)	38,7
	"	43,0	34,5 (i)	19,8
			(Mean reduction =	25,1%)
51 -70	Otomys	60,5	38,0 (ih)	37,2
	Rhabdomys	62,0	46,5 (ie)	25,0
			(Mean reduction =	31,1%)
71 -160	Otomys	78,5	47,0 (ih)	40,1
	"	92,5	54,5 (ih)	41,1
	"	97,5	53,0 (ih)	45,6
	"	104,5	71,0 (ih)	32,1
	"	107,0	53,5 (ih)	50,0
	"	111,0	61,0 (ih)	45,0
	"	153,0	82,0 (ihe)	46,4
			(Mean reduction =	42,9%)

While feeding, the two inner claws (II) pinned the prey between the legs. The head of the prey pointed forwards with its tail hanging down behind the kite. Feeding started at the head and neck, the head being removed whole after several pieces of skin and muscle had been torn away. Feeding proceeded posteriorally from the neck. Some fur was plucked from large rodents, but this was only after the kite had already eaten a substantial meal. Remiges and rectrices were plucked from bird prey. Once the muscles had been eaten, some limb bones and the vertebral column of large *Otomys* were discarded. The tail of the prey was usually last to disappear.

Nestlings and kites recently out of the nest did not feed as competently as adults. They were often unable to tear the skin, remove the head and separate bones at the joints. They also often started eating intestines and then tried to dislodge them from the beak.

Continuous feeding seldom lasted more than 20 min, after which kites showed a full crop. Any food remaining was occasionally abandoned, but usually carried to a perch in the shade. There feeding resumed sporadically and may have ended only several hours later. Prey was never cached.

Feeding kites frequently glanced around, probably to watch for pirates such as Black Kites *Milvus migrans* and Steppe Buzzards *Buteo buteo*. I saw a Blackshouldered Kite drop an *Otomys* while being pursued by a buzzard. Feeding kites also did not tolerate the close presence of conspecifics. Approaching birds were threatened and the prey covered by mantling. Threat consisted of TAIL WAGGING, TAIL FANNING and several calls (Chapter 5).

Pellets, prey composition and size

Pellets consisted largely of hair, a few fragments of the large limb and jaw bones, and teeth. Some pellets contained no bones or teeth; these had probaly been digested away. The bone content of a pellet may reflect the bone hardness and time interval between consumption and regurgitation.

Normally, a pellet was produced each morning either just before or just after the kite left the roost. Captive kites followed this pattern although I often fe them several meals at different times of the day. Pellets from captive kites held remains from the previous day's feeding only. Most pellets therefore probably reflected feeding success on the previous day, but several observations suggested variability in pellet production. On five occasions I saw wild kites regurgitate pellets later in the day. One was at 12s20 and this pellet probably came from prey eaten earlier that same day rather than the previous day. However, most pellets were collected below roosts (79%) or at nest areas (20%), suggesting that most of those analyzed reflected the previous day's intake.

Pellets had a mean weight of 1,28 g (S.D. = 0,63; range 0,1-4,5 g; n = 1990). This sample excludes abnormally large pellets that came from females feeding small chicks. Chicks younger than about 10 days were fed little skin, this being eaten by the female parents. Figure 2.3 shows that pellet weights were normally distributed with a small tail in the higher range of values. The heaviest pellets were probably abnormal as a result of high bone content.

I identified 3408 prey items in 2573 pellets, or 1,32 animals/pellet. This is a minimum figure because although two items of the same species might have been eaten, only one could be identified if either or both heads had been discarded or digested away. This error was potentially present in all pellets.

Prey composition is shown in Table 2.6 in terms of the frequency and contribution by weight of each species. *Otomys*, *Rhabdomys* and *Praomys* formed 86,8% of prey numbers and 92,3% of prey weight. Mammals accounted for 96,5% of prey weight. More *Otomys* were identified from hair than other species because their large heads were often discarded. No arthropod prey remains were found except for a scorpion *Opisthophthalmus* sp. cheliped.

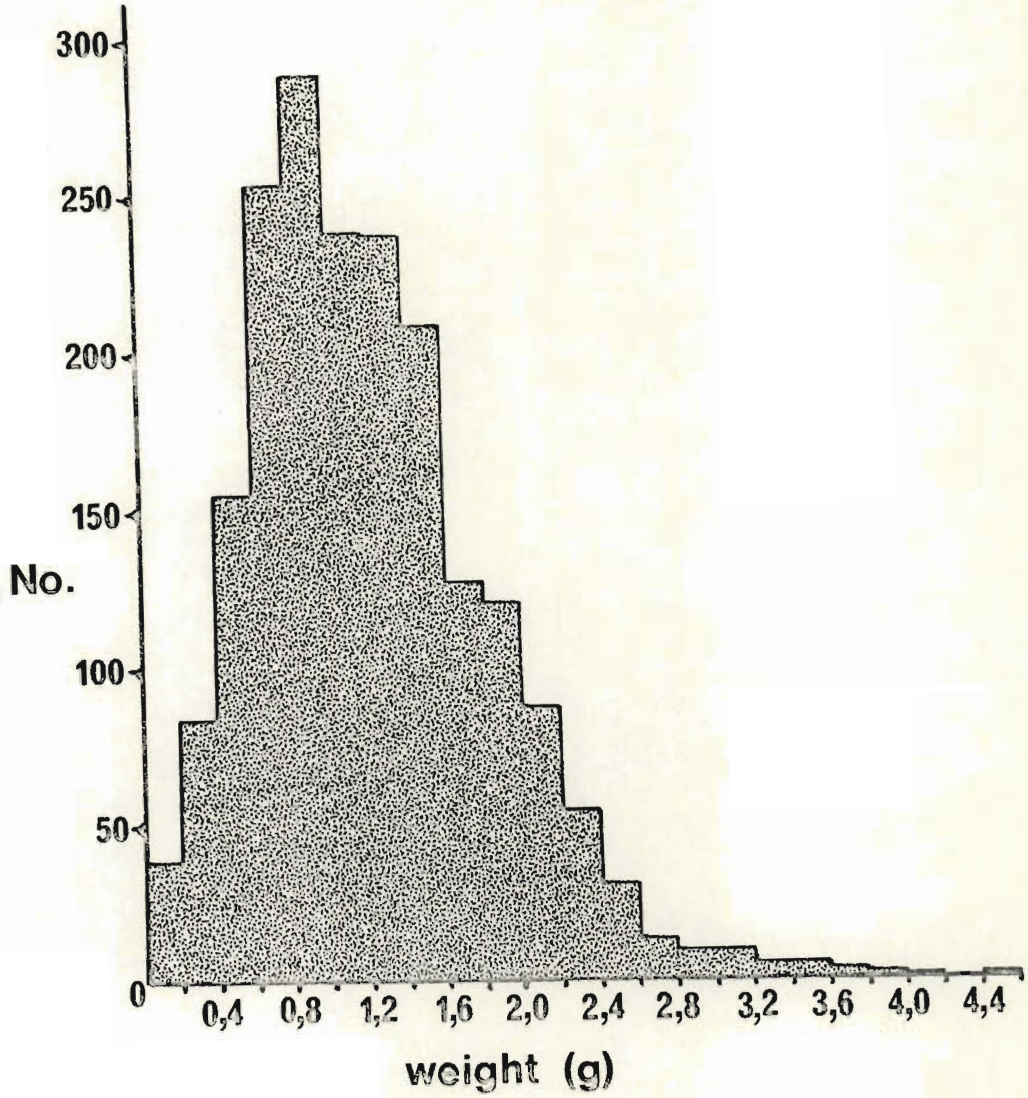


FIGURE 2.3 Frequency distribution of the weights of 1990 pellets.

TABLE 2.6 Prey composition in terms of frequency and weight. Species weights are given in Table 2.7. Shrew species are shown in Table 2.8.

Prey species	No. identified by:		Total	%	% weight of total diet
	Hair (%)	Skull			
Otomys angoniensis	386 (41)	554	940	27,6	43,4
Rhabdomys pumilio	270 (27)	734	1004	29,5	25,6
Praomys natalensis	288 (28)	726	1014	29,8	23,3
Lemniscomys griselda	21 (23)	70	91	2,7	3,4
Dendromus melanotis	0 (0)	11	11	0,3	0,1
Saccostomus campestris	2 (29)	5	7	0,2	0,2
Steatomys pratensis	0 (0)	6	6	0,2	0,1
Shrews	45 (20)	179	224	6,6	2,1
Birds	-	-	68	2,0	1,4
Lizards	-	-	43	1,3	0,4
Total	1012	2285	3408	100	100

TABLE 2.7 Average weights of prey species and the weights consumed after discarding heads, guts and embryos. Discarded percentages were estimated from Table 2.5.

Prey species	Average weight (g)	Sample size	% discarded	Average weight eaten (g)	[a]Mean weight in one prey item
Otomys angoniensis	83,2	128	40	49,9	13,77
Rhabdomys pumilio	34,4	240	20	27,5	8,11
Praomys natalensis	31,0	503	20	24,8	7,39
Lemniscomys griselda	54,0[b]	-	25	40,5	1,09
Dendromus melanotis	8,2[b]	-	0	8,2	0,02
Saccostomus campestris	49,0[b]	-	25	36,7	0,07
Steatomys pratensis	23,0[b]	-	15	19,5	0,04
Shrews	10,0[c]	-	0	10,0	0,66
Birds	20,0[d]	-	10	18,0	0,36
Lizards	10,0[d]	-	0	10,0	0,13

a - calculated by (average weight eaten)(% frequency - from Table 2.6)

b - estimated from Rautenbach (1978)

c - estimated average for different species (Table 2.8)

d - general estimate

The origin of the cheliped is obscure since other fragments should have been found if the scorpion had been eaten. Most bird remains were those of seed eaters and seven Redbilled Queleas *Quelea quelea* were identified. A Fantail Cisticola *Cisticola juncidis* was seen being caught. Most pellets with reptile scales also held insect remains, indicating lizard prey. An intac lizard *Mabuya striata* (W.D. Haacke pers. comm.) was found in a nest.

Shrews were identified using size, rather than structural, characters of the skull because structural features are not species-specific within *Crocidura* and *Suncus* (Meester 1963; N.J. Dippenaar pers. comm.). Identification was nevertheless often uncertain because of size-overlap between species. Probable names were assigned to 148 of the 179 skeletal remains (Table 2.8). The presence of shrews in 45 other pellets was established by smell and the presence of small arthropod fragments; identification to species level using hair cuticle patterns is not possible (H. Keogh pers. comm.).

Average weights for prey species (Table 2.7) have been corrected using wastage factors estimated from Table 2.5. Table 2.7 lists the calculated mean contribution of each species per prey item. Adding these contribution yields a value of 31,6 g for an average prey item.

A further measure of prey size comes from estimates of the size of each item seen caught. Estimates were based on observations of how long captive kites took to eat certain sized items, and on the prey size relative to the size of the kite. Perched-hunting kites caught significantly larger prey than hovering birds (Table 2.9). A greater number of large *Otomys* were probably caught from perches since this species favoured dense cover over which perched-hunting predominantly occurred (see p. 46). The data in Tabl 2.9 suggest the heaviest prey was caught at midday. Lumping prey sizes for hovering and perched-hunting gives an average prey mass of 26,4 g or 19,7% lower than the previous estimate.

TABLE 2.8 The frequencies and weights of shrews identified in kite pellets.

Species	Frequency	Weight (g) and source
Crocidura hirta	82	13,6 - this study, n = 52
Crocidura cyanea	37	9,0 - Rautenbach (1978)
Crocidura bicolor	6	4,0 - Rautenbach (1978)
Suncus infinitesimus	23	2,0 - Rautenbach (1978)
Unidentified	31	-
TOTAL and Average weight	179	10,3

TABLE 2.9 The numbers of prey of different weights seen caught at different times of the day by hovering or perched-hunting kites. The difference in prey weight between hovering and perched-hunting was significant ($X^2_2 = 10{,}8$; $p < 0{,}01$).

Prey weight (g)	Morning	Midday	Afternoon	Total
Perched-hunting				
10	13	12	10	35
30	21	20	16	57
60	5	10	7	22
Mean prey weight	27,2	31,4	30,3	29,6
Hovering				
10	7	10	28	45
30	7	12	18	37
60	0	3	4	7
Mean prey weight	20,0	25,6	21,2	22,2

Rodent trapping

General features of the six trap lines are described in Table 2.10. Lines 1-4 on black turf soils were in climax communities, and these were seldom disturbed by grazing. In contrast, cattle grazed heavily on more palatable grasses in red clay communities. Most red clay areas were overgrazed with either pioneer (unpalatable) communities (Line 5), or a sparse grass cover (Line 6).

The soil at Line 6 was slightly sandy, unlike other parts of the study area. There was an associated greater plant diversity in the vicinity of this line, and certain species, *e.g.* *Acacia karroo* and *A. gerrardii*, were found only in this area. This diversity was linked to a more varied rodent community (Table 2.10). Most pellets containing *Lemniscomys*, *Steatomys*, *Dendromus* and *Saccostomus* were obtained from kites that hunted around Line 6 or in sandy areas just outside the study area (Chapter 1 — Fig. 1.2). Clay and turf soils generally supported fewer plant species than sandy soils (Galpin 1926; Van der Riet 1974) and only three rodents (Table 2.10).

Otomys and *Rhabdomys* were more abundant in black than in red soil areas. (Table 2.10). Both species were active diurnally and favoured the dense plant cover on black turf (Brooks 1974; Choate 1972; Davis 1973; pers. obs.). The two soils differed only marginally in overall rodent abundance with better trapping success on black turf ($\chi^2_1 = 3{,}70$; $p < 0{,}1$). This difference, together with good *Praomys* populations (*i.e.* high abundance of all three main prey species), suggests that black turf areas offered better hunting potential than red clay areas.

Capture rates of *Otomys* were low (Table 2.10) because they fed on grass stalks and leaves and were not attracted to the bait I used (Taylor & Green 1976; pers. obs.). Thus, of the 1065 mammals trapped, only 89 (8,4%) were *Otomys* compared with a frequency of 27,6% in pellets (Table 2.6).

TABLE 2.10 Habitat features and rodent trapping successes at six trap-lines. Grass species listed in order of dominance were *Ischaemum glaucostachyum*, *Setaria woodi*, *Cynodon dactylon*, *Hyparrhenia hirta*, *Bothriochloa insculpta*, *Themeda triandra* and *Panicum coloratum*.

Trap line	1	2	3	4	5	6
Soil type	Black turf	Black turf	Black turf	Black turf	Red clay	Red clay
Habitat	Woodland edge	Woodland	Woodland	Field verge	Road verge	Woodland edge
Dominant grasses	*Ischaemum* *Setaria*	*Setaria* *Ischaemum*	*Setaria* *Ischaemum*	*Ischaemum* *Setaria* *Cynodon*	*Hyparr.* *Bothrio.* *Themeda*	*Themeda* *Bothrio.* *Panicum*
No. of trap-nights	360	1080	1080	1080	1080	1080
No. of captures	107	236	186	167	203	166
NO. CAPTURES/ 100 TRAP-NIGHTS						
All species	29,7	21,8	17,2	15,5	18,8	15,4
Otomys angoniensis	5,6	1,3	1,7	2,2	0,6	0,6
Rhabdomys pumilio	8,1	10,9	7,4	4,3	1,2	2,1
Praomys natalensis	12,8	8,1	6,9	8,0	15,9	10,9
Crocidura spp.	3,3	1,4	1,2	1,0	0,8	0,6
Dendromus melanotis	0	0	0	0	0,3	0
Lemniscomys griselda	0	0	0	0	0	0,4
Saccostomus campestris	0	0	0	0	0	0,7
Rattus sp.	0	0,1	0	0	0	0
Mus minutoides	0	0	0	0	0	0,1

Praomys and Rhabdomys were largely granivorous (Curtis & Perrin 1979; Hanney 1965; Taylor & Green 1976) and greater numbers were caught (Table 2.10). The proportion of Praomys trapped (54,9%) was higher than their incidence in pellets (29,8%), probably because, as nocturnal rodents (Choate 1972), they were under-represented in the prey of diurnal kites.

Seasonal changes in the percentage of juveniles in trapped samples of Otomys, Rhabdomys and Praomys are shown in Figure 2.4. Specimens weighing less than 50 g (Otomys), 20 g (Rhabdomys) and 15 g (Praomys) were considered juvenile and less than a month old (Brooks 1974; Coetzee 1967; Davis 1973). Otomys samples were small and suggested that young were produced year round. For Rhabdomys and Praomys greater numbers of juveniles trapped during spring and autumn suggested that there were two peaks of breeding activity (Fig. 2.4). Between October 1977 and February 1978 there were no juveniles in a relatively large sample of 104 Praomys. Similarly, between November and March only one juvenile Rhabdomys was caught in a sample of 33. Figure 2.4 shows an increase in breeding activity for all three species with the onset of the 1978 spring.

While samples of Otomys and Rhabdomys showed no marked seasonal changes in weight, Praomys were heaviest in summer samples (Fig. 2.5), corresponding with the absence of young individuals.

Habitats and hunting

Kites hovered mainly over areas with sparse cover (Fig. 2.6). This was obvious at dusk when hovering increased over harvested wheat and bare ploughed fields, probably in response to the onset of Praomys activity. Day-time hovering over fields with sparse cover was also recorded, but to a lesser extent and only in dry months. Large crevices (25-100 cm deep and 5-10 cm wide) formed in black turf during dry periods, and these attracted rodents by providing cover and refuge. Rodents were absent from

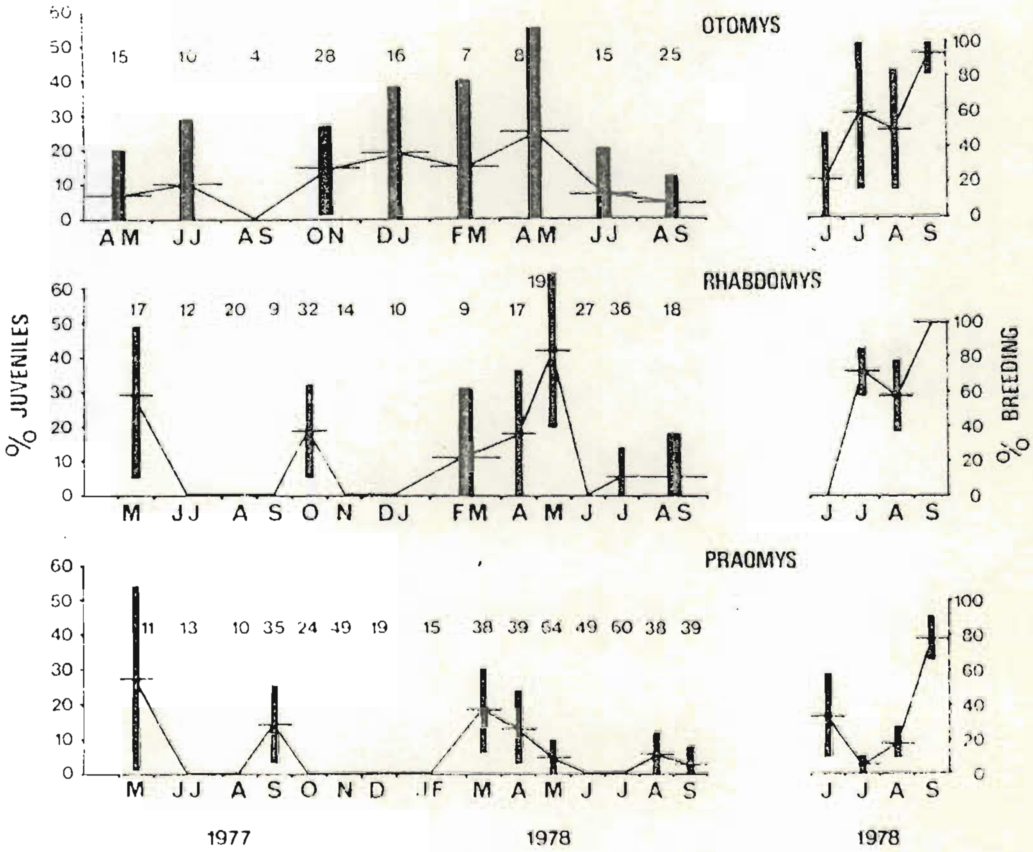


FIGURE 2.4 Seasonal distribution of breeding activity in Otomys, Rhabdomys and Praomys, as determined by the frequency of juveniles and reproductively active animals in trapped samples. Horizontal lines are means and vertical bars are 2(SE$\bar{x}$) above and below means. Small samples were pooled into two-month periods. Reproductive activity in late 1978 was identified by scrotal males and pregnant or lactating females.

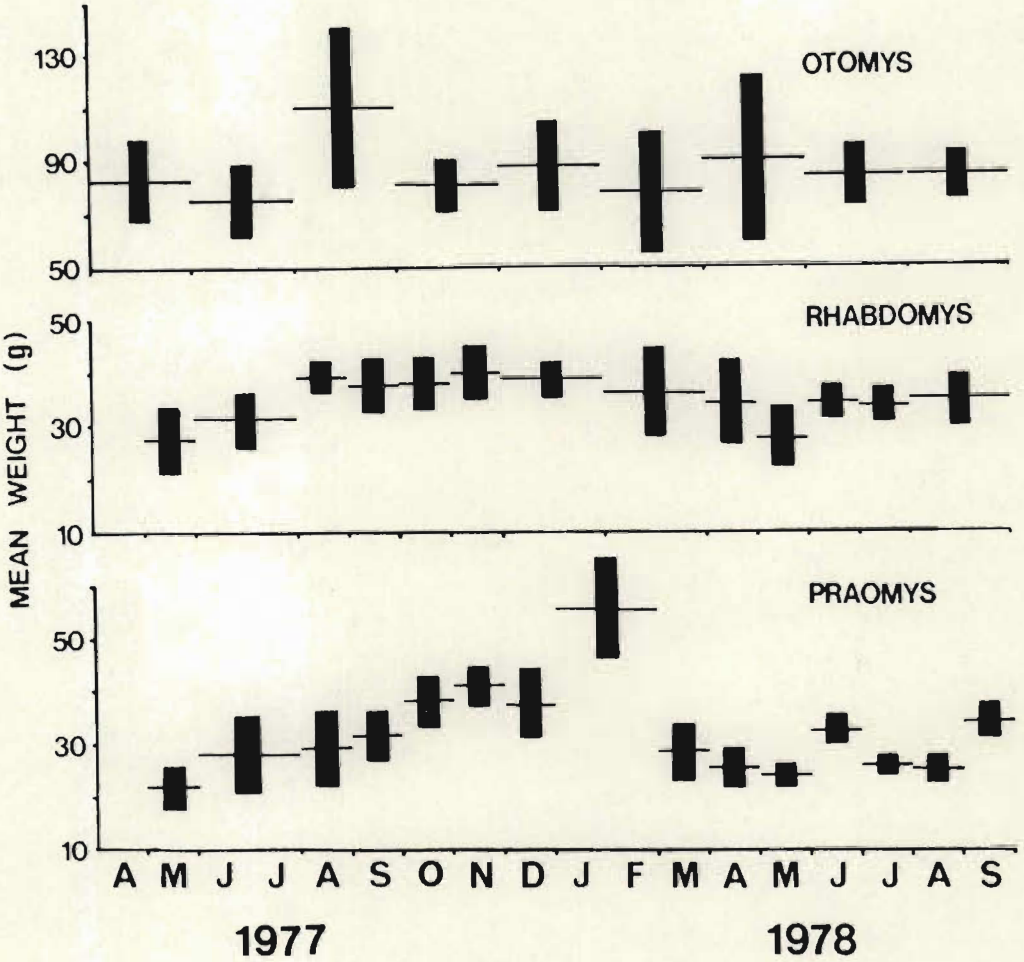


FIGURE 2.5 Mean weights of monthly or two-monthly samples of Otomys, Rhabdomys and Praomys. Horizontal lines are means and vertical bars are 2(SE$\bar{x}$) above and below means.

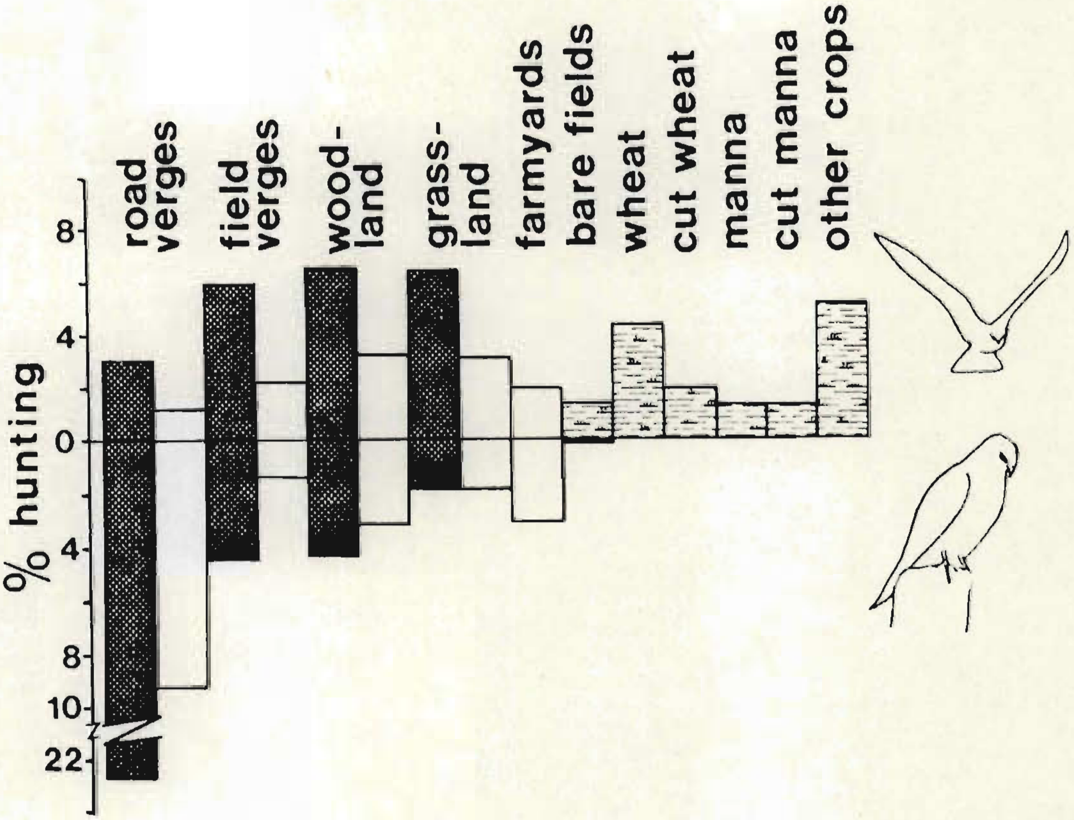


FIGURE 2.6 Percentage frequencies with which kites were observed hovering and perch-hunting over different habitats on black turf (shaded), red clay (unshaded) and croplands, for which the two soils are shown pooled. Habitats with the densest cover are on the left, those with sparse cover on the right.

fields during the wet summers when there were no crevices. There were no burrowing small mammals (*e.g.* *Tatera* sp., *Cryptomys hottentotus*, *Amblysomys hottentotus*, *Pedetes capensis*) in the clay soils at Settlers. The soils were probably too hard when dry, and too clayey when wet for burrowing. Burrowing species mentioned above were all common in surrounding sandy areas (Dean 1973 a; Jacobsen 1977; pers. obs.).

Perched-hunting occurred predominantly over areas with dense grass cover (Fig. 2.6). Road verges, in particular, attracted hunting kites because they held high rodent densities in climax grass communities which were seldom disturbed (grazed, burnt *etc*.). Their attractiveness was shown by the high percentages of hunting over road verges compared with low percentages over field verges (Fig. 2.6). Fences below electricity and telephone lines separated similar widths of road and field verge, and kites perched on the utility lines therefore had equal access to the two habitats. Field verges were often disturbed (including regular use by farm vehicles) and cover was poorer with less developed grass communities.

It was suggested (see *Rodent trapping*, p. 42) that different prey species composition and abundance might affect the food supply of kites in red and black soil areas. Table 2.11 compares several aspects of hunting success on the two soils, but these data do not reveal any consistent differences. A greater number of descents and half-strikes on red clay suggests that kites spotted prey more frequently on red than on black areas. Apart from more frequent descents, the data in Table 2.11 suggest that hovering was less successful, and perched-hunting more successful on red clay than on black turf. This is contrary to the expected poorer hunting on red clay where *Otomys* and *Rhabdomys* were less abundant (Table 2.10).

Prey sizes, estimated from prey seen caught, were similar on red and black soil ($\bar{x}$ red = 29,8 g; n = 52; $\bar{x}$ black = 28,9 g; n = 108). Prey caught in fields was significantly smaller than prey in other habitats

TABLE 2.11 A comparison of hunting performance of kites over black turf and red clay. Chi-squared and binomial tests were used.

Variables	Black turf	Red clay	Difference
HOVERING			
Minutes/kill (no. kills)	37,89 (64)	54,88 (8)	NS
Minutes/all strike (no. all strikes)	8,33 (291)	11,55 (38)	$p < 0,1$
Minutes/full-strike (no. full-strikes)	16,84 (144)	21,95 (20)	NS
Hovers/descent (no. descents)	7,32 (523)	6,22 (113)	$p < 0,05$
% success of full-strikes (no. full-strikes)	43,37 (83)	38,46 (39)	NS
% half-strikes of all strikes (no. half-strikes)	50,52 (147)	47,37 (18)	NS
PERCHED-HUNTING			
Minutes/kill (no. kills)	144,90 (41)	99,19 (26)	NS
Minutes/all strike (no. all strikes)	28,84 (206)	18,29 (141)	$p < 0,001$
Minutes/full-strike (no. full-strikes)	54,50 (109)	58,61 (44)	NS
% success of full-strikes (no. full-strikes)	42,94 (163)	51,39 (72)	NS
% half-strikes of all strikes (no. half-strikes)	47,09 (97)	68,79 (97)	$p < 0,001$

($\bar{x}$ fields = 20,0 g; n = 43; $\bar{x}$ other habitats = 29,2 g; n = 160; χ^2_2 = 11,64; p < 0,005). This difference in prey size was attributable to the absence of Otomys from fields.

Seasonal food changes

Rodent trapping success varied during the study, with similar changes from month to month at the six trap-lines (Fig. 2.7). Assuming that trapping success reflects rodent density, these data suggest that prey densities varied 2-4 times during the study. The six curves in Figure 2.7 a have been combined to give a mean curve (Fig. 2.7 b) which compares well with other measures (Fig. 2.8 a & b) of seasonal food change. There were good correlations between these measurements of food supply: rodent trapping vs. pellet weights (Spearman's Rank r_{15} = +0,78; p < 0,001); rodent trapping vs. % kites spotted with prey (Spearman's Rank r_{15} = +0,58; p < 0,025); % kites spotted with prey vs. pellet weights (Spearman's Rank r_{17} = +0,47; p < 0,05). A mean index of food supply each month (Fig. 2.8 c) has been calculated by averaging rank values for these three indicators of food supply. Aspects of social behaviour, dispersion (Chapter 3), breeding (Chapter 4) and weight (Chapter 6) are compared with this index.

The proportion of hovering and perched hunting also varied seasonally. Two independent measurements of hovering activity (Fig. 2.9 a & b) are highly variable and not significantly correlated with each other (Spearman's Rank r_{15} = +0,19; NS). In spite of the variability the data independently show that least hovering occurred in summer. This trend is highly significant if the same data are combined into summer and non-summer periods (Table 2.12). The monthly values in Figure 2.9 a & b have been ranked and the ranks averaged to give a mean curve (Fig. 2.9 c). There was little variation in the percentage time spent hovering during autumn, winter and spring.

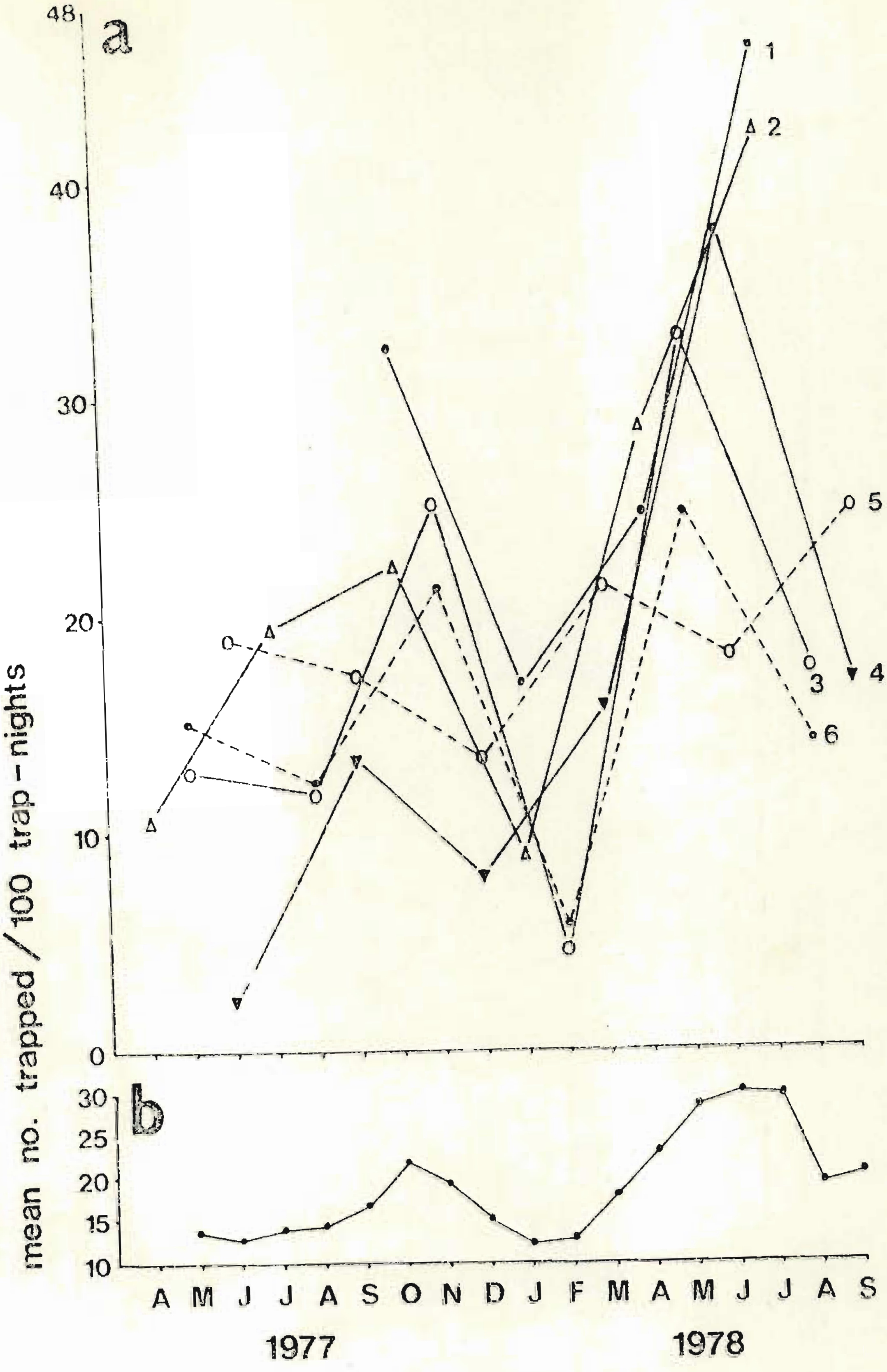


FIGURE 2.7 Observed (a) and mean (b) trapping success rates at six rodent trap-lines, numbered as in Table 2.10. The mean value for each month (b) was calculated by averaging monthly observed trapping rates and interpolated rates (read off the curves in (a) for trap-lines at which there was no trapping).

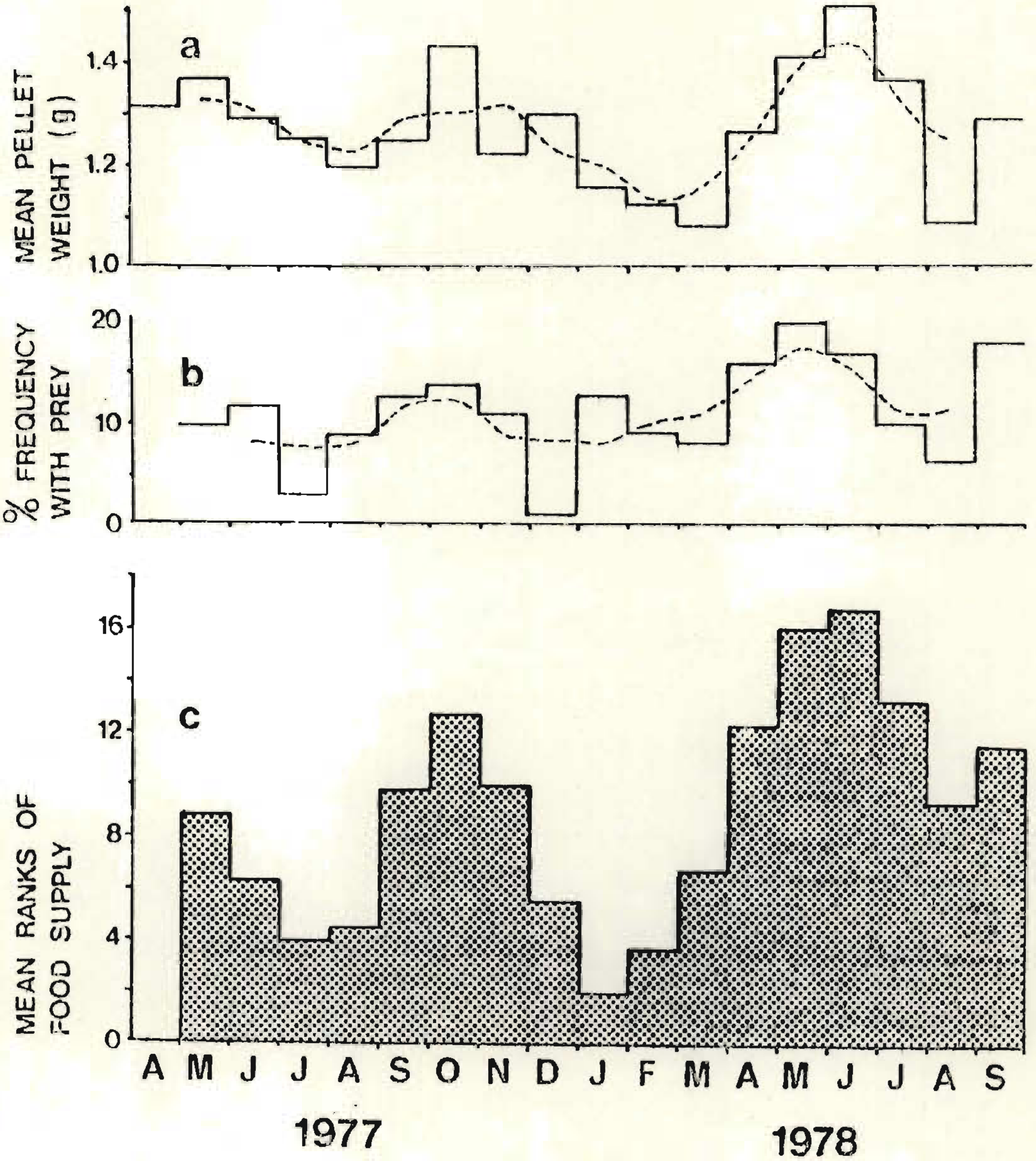


FIGURE 2.8 Seasonal changes in the food supply of kites. a) Percentage kites seen perched or flying with prey ((no. seen with prey/ no. seen hunting)(100)); b) mean pellet weights; c) mean ranked food supply values for data in Figure 2.7b and three-point moving averages in (a) and (b) (broken lines).

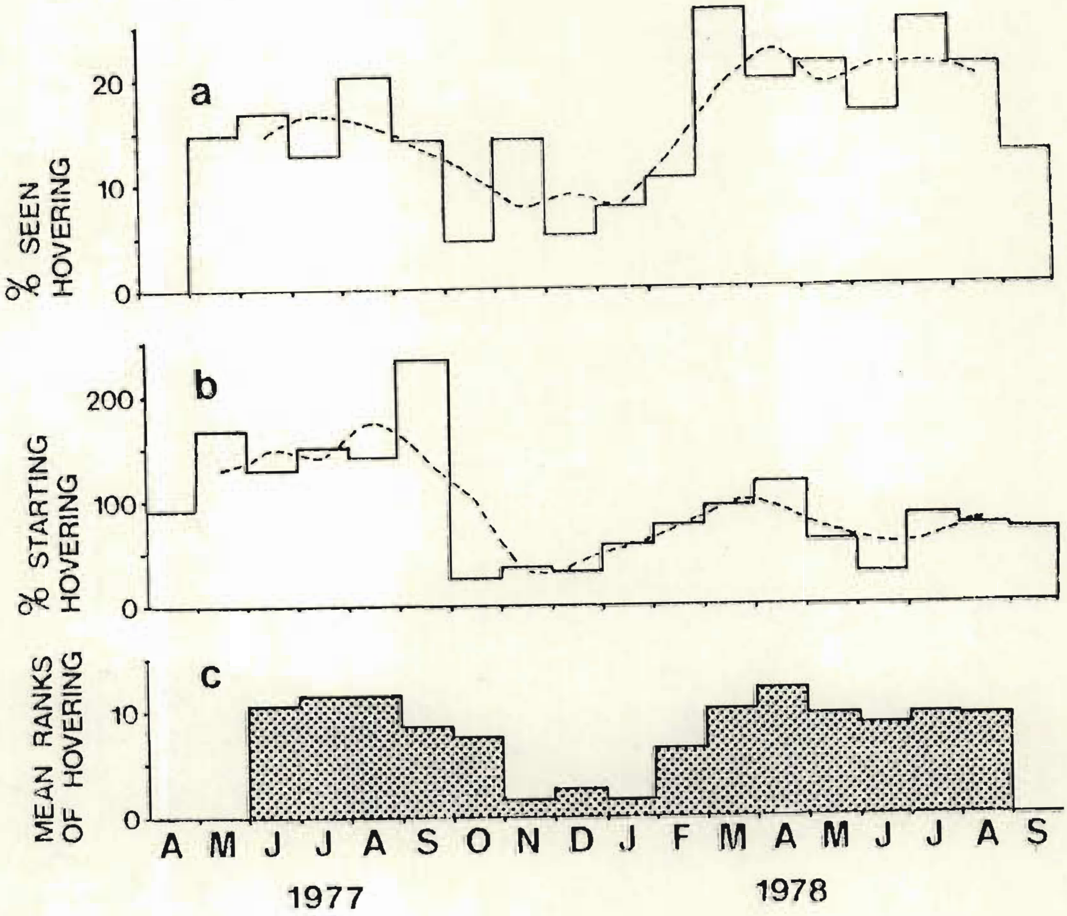


FIGURE 2.9 Seasonal changes in proportions of hovering and perched-hunting. a) Percentage frequency of kites seen hovering ((no. seen hovering/total no. seen hunting)(100)); b) percentage frequency of perched-hunting kites to start hovering during hunting observations ((no. starting to hover/total no. observed perched-hunting)(100)); c) mean ranked values for the three-point moving averages in (a) and (b) (broken lines).

TABLE 2.12 Differences in the proportion of hovering and hunting success in summer (October 1977 - February 1978) and non-summer months (April - September 1977 & March - September 1978).

Variables	Non-summer	Summer	Difference
% hovering of all kites seen hunting (no. seen hunting)	17,75 (907)	7,79 (475)	$p < 0{,}001$
% perched-hunting kites to start hovering during observation (no. observed perched-hunting)	47,40 (289)	29,17 (144)	$p < 0{,}001$
Hovering			
Minutes/kill (no. kills)	37,06 (62)	56,60 (10)	N.S.
Minutes/all strike (no. all strikes)	8,42 (273)	10,48 (54)	N.S.
Perched-hunting			
Minutes/kill (no. kills)	140,62 (42)	104,56 (25)	N.S.
Minutes/all strike (no. all strikes)	24,92 (237)	24,20 (108)	N.S.

Overall, hovering gave an average prey capture rate 3,2 times greater than perched-hunting (Table 2.4). During summer this difference in capture rate was only 1,8 times (Table 2.12), suggesting that hovering was less frequent because of lower returns. Poorer hovering success during summer was probably because the grass cover was denser.

Average prey size did not vary significantly from month to month (Fig. 2.10) despite a possibly greater number of small prey during rodent breeding seasons. The lack of agreement between the two measures in Figure 2.10 is probably because seasonal changes were slight and prey varied greatly in size. Only relatively few animals ($\bar{x}$ = 10,15) were seen being caught each month.

There were marked seasonal changes in prey composition (Fig. 2.11) and, for each species, certain trends were distinguishable. Otomys featured most prominently during summer, probably because perched-hunting over dense grass increased. After the summer the proportion of Otomys decreased to a minimum in the following spring. Rhabdomys was most numerous in late winter and spring. Praomys was caught least frequently in late summer but featured prominently in October-November 1977 and in the autumn and winter of 1978.

One may expect that if kites had caught sufficient prey during the day they would not have needed to hunt at dusk; i.e. diurnal prey would be caught before nocturnal prey. If this is correct, trapping success and proportion in the diet should be more closely related in diurnal Rhabdomys than in nocturnal Praomys. However, Praomys showed a highly significant correlation between abundance in traps and pellets (Fig. 2.11) (Spearman's Rank r_{16} = +0,66; $p < 0,005$), while Rhabdomys showed no correlation (Spearman's Rank r_{16} = +0,33; NS). One explanation for this may be that the correlation tests did not reflect the relatively small changes in Rhabdomys numbers, compared with the great fluctuations shown by Praomys

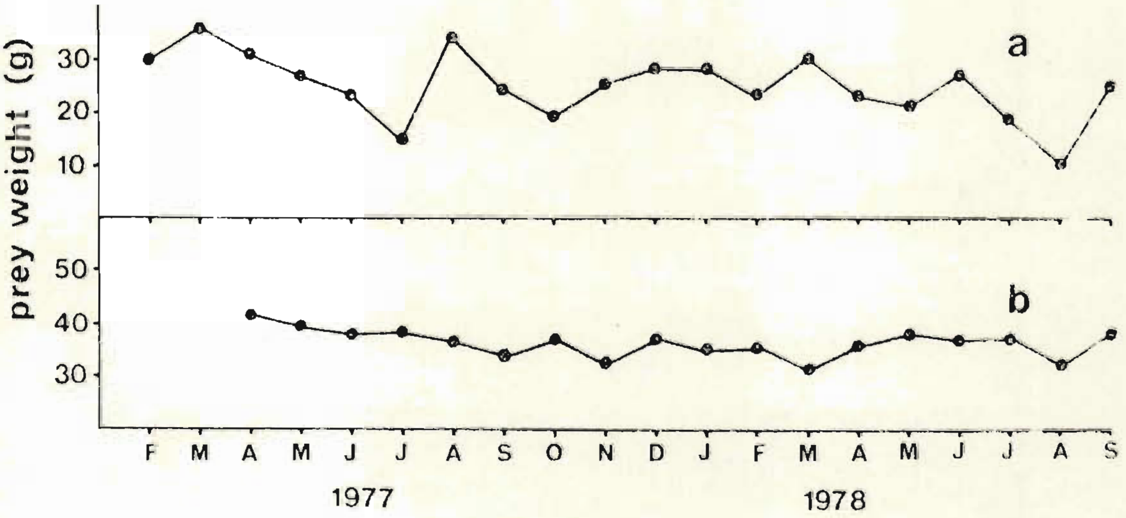


FIGURE 2.10 Seasonal changes in prey weight. a) Mean weight of prey seen caught; b) mean weight of prey items in pellets (weight of prey represented in pellet/mean no. of prey items per pellet).

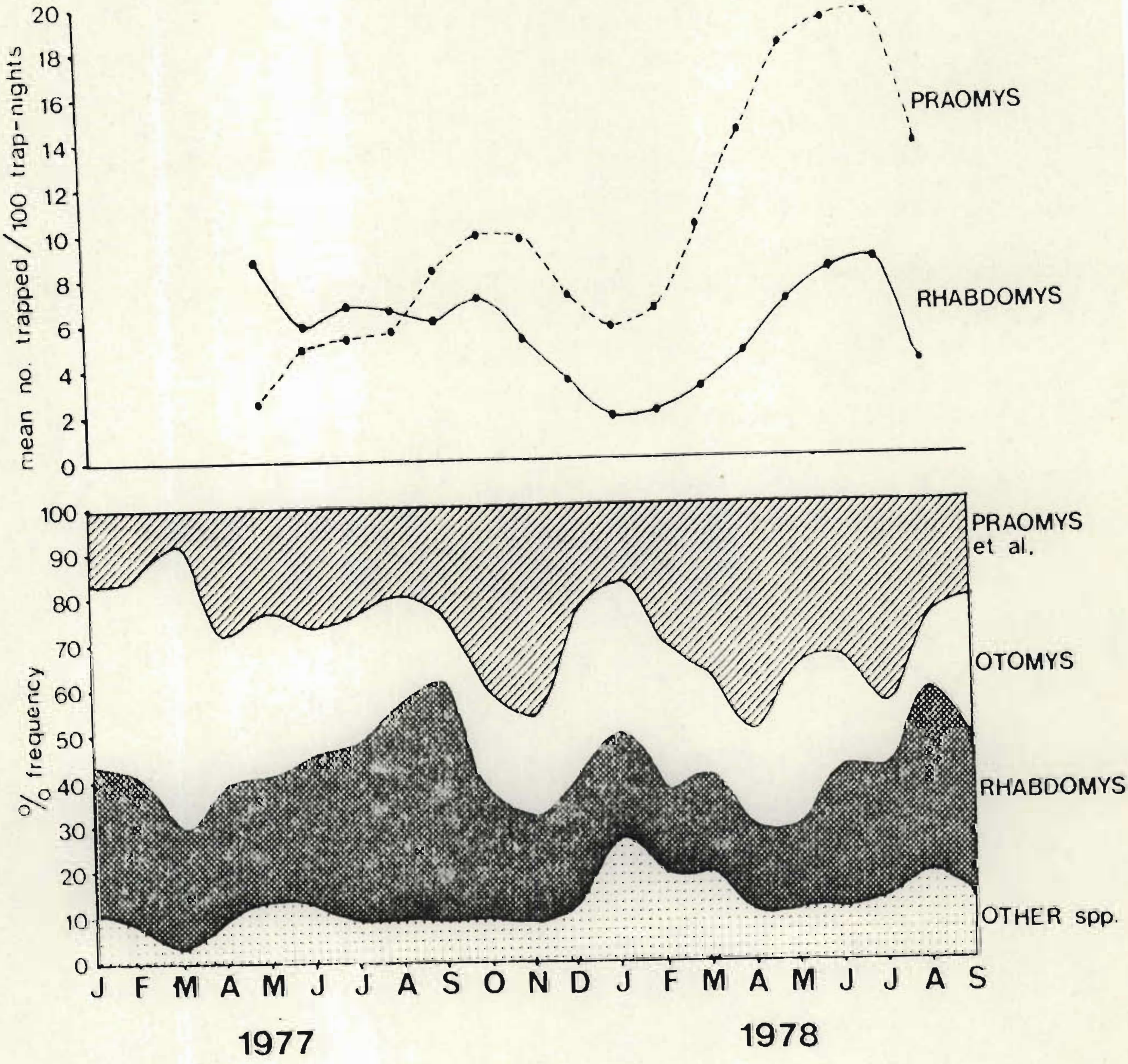


FIGURE 2.11 Seasonal changes in prey composition in pellets, and trapping success for Rhabdomys and Praomys. Trapping success rates were calculated in the same way as Figure 2.7b. "Praomys et al." includes Praomys and other nocturnal rodents: Saccostomus, Dendromus and Steatomys (see Table 2.6).

numbers (Fig. 2.11).

Hunting differences between mating classes

Some aspects of the feeding ecology of unpaired, paired and breeding kites (Chapter 3, p. 84) are compared in Table 2.13. Data for breeders were mainly those of breeding males over the whole breeding cycle; breeding females seldom hunted (Chapter 4). The proportions of hovering and perched-hunting suggest that breeders and unpaired kites hovered more than paired birds. Hunting success data indicate that unpaired kites had the lowest and breeders the highest success. However, this conclusion is supported by only two significant differences (Table 2.13). Breeding kites also made significantly more successful full-strikes from perches than unpaired birds.

The difference in pellet weight between breeding and non-breeding kites was highly significant (Table 2.13). Using Tarboton's (1977) regression equation (food weight = (pellet weight-0,056)/0,025), and a 20% wastage correction factor (estimated from Table 2.5), non-breeding and breeding kites consumed 36,6 g/day and 43,7 g/day respectively. Breeders thus had a daily food intake 19,4% higher than non-breeding kites. This difference may have actually been greater because some breeders' pellets were included in the sample from non-breeding kites. Most non-breeders' pellets came from communal roosts (Chapter 5, p.224),but some breeding males and dependent flying young joined these roosts. Pellets from different birds could not be distinguished below communal roosts.

The most significant difference between unpaired and paired kites lay in the composition of their prey (Table 2.13). Unpaired birds may have caught a greater proportion of Praomys because food shortages during the day forced them to hunt at dusk; their crepuscular hunting may be reflected in their higher frequency of hovering (Table 2.13). In spite of the dietary differences, the pellet weights of paired and unpaired birds were similar

TABLE 2.13 The hunting performance and prey of unpaired, paired and breeding kites.

Variable	Unpaired	Paired	Breeding
% hovering of all kites seen seen hunting (no. hunting)	11,2^{a} (294)	9,2 (502)	19,4^{a} (180)
% perch-hunting kites to start hovering (no. perch-hunting)	49,2^{bc}(120)	38,0^{c} (216)	41,1^{b} (107)
HOVERING			
% successful full-strikes (no. full strikes)	47,3^{d} (55)	41,8 (91)	39,3^{d} (56)
min/all-strike (no. all-strikes)	9,7^{e} (80)	8,3 (147)	7,9^{e} (83)
min/kill (no. kills)	40,9^{f} (19)	38,0 (32)	34,6^{f} (19)
Hovers/descent (no. descents)	8,0^{gh}(175)	6,9^{g} (281)	6,3^{h} (174)
min/hovering bout (no. bouts)	3,84^{i} (75)	4,32^{i}(131)	4,55^{i} (68)
sec/hover (no. hovers)	8,0^{j} (42)	11,3^{j} (179)	14,1^{j} (73)
PERCH-HUNTING			
% successful full-strikes (no. full-strikes)	38,5^{k} (39)	44,1^{l} (111)	56,7^{kl} (67)
min/all-strike (no. all-strikes)	26,5^{m} (84)	25,4 (158)	20,4^{m} (103)
min/kill (no. kills)	278,3^{no} (8)	133,9^{np}(30)	75,1^{po} (28)
min/perch change (no. changes)	7,2^{q} (310)	7,0 (572)	6,8^{q} (311)
Mean pellet weight ± S.D. (n)	1,20^{r} ± 0,58 (1231)		1,42^{r} ± 0,69 (759)
PREY COMPOSITION			
% *Praomys natalensis*	54,7^{s}	29,4^{s}	31,6
% *Otomys angoniensis*	16,8	28,0	27,8
% *Rhabdomys pumilio*	15,1	29,4	28,9
% other species	13,4	13,3	11,7
mean prey weight from prey composition	28,2	31,4	31,6
mean prey weight from prey seen caught (no. seen caught)	32,7^{t}(40)	22,7^{t}(86)	27,0 (60)
prey items/pellet (no. items)	1,31^{u} (2312)		1,37^{u} (1096)

aa_{++}; bb_{NS}; cc_{++}; dd_{NS}; ee_{NS}; ff_{NS}; gg_{NS}; hh_{++}; ii_{NS}; jj_{NS}; kk_{++}; ll_{NS};

mm_{+}; nn_{+}; oo_{+++}; pp_{++}; qq_{NS}; rr_{++++}; ss_{++++}; tt_{+++}; uu_{NS}

+ $p < 0,1$; ++ $p < 0,05$; +++ $p < 0,01$; ++++ $p < 0,001$

($\bar{x}$ paired = 1,39 g; S.D. = 0,68; n = 192 & $\bar{x}$ unpaired = 1,40 g; S.D. = 57; n = 127). The pellets on which these data are based were collected from solitary-roosting kites. Perhaps pellet weights would have differed if samples had also been collected from communal roosts, since communally-roosting birds produced pellets with lower weights than solitary kites (Chapter 5 — Table 5.2).

Conflicting results were obtained from three methods used to compare the prey sizes of the mating classes. Firstly, although the number of prey items/pellet was similar for non-breeding and breeding kites, breeders produced heavier pellets (Table 2.13), suggesting that they caught larger prey. Secondly, the sizes of prey seen caught suggest that unpaired kites caught larger prey than paired birds, while breeders obtained intermediate sized prey. Finally, prey sizes determined from the composition of pellets indicated that the three mating classes caught prey of similar size (Table 2.13).

Sexual differences in hunting success

Results in Chapter 3 (Tables 3.4; 3.5 & 3.6) indicate that kites usually deserted when food supply was lowest, and that females deserted more frequently than males. This difference in behaviour might have been due to separate feeding strategies, with females more sensitive to food shortages. However, comparisons in Table 2.14 suggest that there were no important differences in hunting behaviour and success between males and females. The relevance of the two significant differences is not clear.

Nothing is known of the composition of prey caught by paired males and females. However, most females were resident as paired birds (Chapter 3 — Table 3.1), and since paired kites caught more diurnal prey than unpaired birds (Table 2.13), females were probably only resident when diurnal prey was abundant. Most unpaired kites, in contrast, were males (Chapter 3 —

TABLE 2.14 The hunting performance of paired males and females.

Variable	Males	Females	Difference
% hovering of all kites seen hunting (no. seen hunting)	8,0 (238)	10,9 (256)	N.S.
% perched-hunting birds to start hovering (no. perched-hunting)	36,5 (96)	37,5 (112)	N.S.
Hovering			
% full-strikes of all strikes (no. all strikes)	63,6 (55)	44,4 (81)	p < 0,01
% successful full-strikes (no. full-strikes)	45,0 (40)	39,5 (43)	N.S.
Minutes/all strike (no. all strikes)	9,3 (55)	7,5 (81)	N.S.
Minutes/kill (no. kills)	34,0 (15)	40,6 (15)	N.S.
Duration (min) of hovering bouts (no. bouts)	4,7 (53)	4,0 (78)	N.S.
Duration (s) of hovers (no. hovers)	12,0 (90)	10,6 (89)	N.S.
No. hovers/descent (no. descents)	7,4 (103)	6,5 (172)	N.S.
Perched-hunting			
% full-strikes of all strikes (no. all strikes)	47,1 (68)	48,7 (78)	N.S.
% successful full-strikes (no. full-strikes)	43,2 (44)	44,1 (59)	N.S.
Minutes/all strike (no. all strikes)	24,8 (68)	26,0 (78)	N.S.
Minutes/kill (no. kills)	139,7 (12)	126,7 (16)	N.S.
Minutes/perch change (no. perch changes)	6,5 (259)	7,5 (271)	p < 0,1
Mean weight of prey seen caught (no. prey items)	23,8 (37)	21,9 (43)	N.S.

Table 3.1), suggesting that males remained resident irrespective of the relative abundance of diurnal and nocturnal prey.

Activity and energy budgets

Average activity and energy budgets are estimated here for non-breeding kites at Settlers; equivalent budgets for breeding males and females are given in Chapter 4 (Table 4.9). The daily food intake of 36,6 g (see p. 56) for non-breeders represented an energy intake of 67,3 kcal using the following conversion factors: 35% dry matter in rodents, 5,84 kcal/g dry matter, and an assimilation efficiency of 0,9 (Bird & Ho 1976; Cummins & Wuycheck 1971). A correction factor of 0,8 has already been introduced (see p. 56) for the weight of prey usually discarded.

Table 2.15 gives estimates of the time non-breeders spent in various activities. Periods spent in "low activity", feeding, soaring, and in directional flight were those measured for non-breeding kites by Tarboton (1978 a). "Low activity" was a general category which included preening and other miscellaneous perched behaviour. Times spent perched-hunting and hovering were the calculated periods needed to catch 36,6 g/day, given 70% perched-hunting and 30% hovering (see p. 21), and prey sizes and capture rates in Table 2.16. Inactive periods during the day were obtained by subtracting the total time spent in other activities from a 13,6-h daylength period. (Chapter 1, p. 9).

Three models (Koplin <u>et al</u>. 1980; Tarboton 1978 a; Wakeley 1978 a,c) were used to convert the activity budget into an energy budget for non-breeding kites (Table 2.15). The models are explained in Appendix 2.1. Tarboton's method, which gave a total daily energy budget (DEB) of 59,9 kcal, probably underestimated the costs of perched activity and exaggerated those of flight. While the agreement between the results produced by Wakeley's model (DEB = 67,9 kcal) and those produced by the

TABLE 2.15 Activity and energy budgets for non-breeding kites at Settlers (see p. 60). The three models used to estimate energy expenditure from the activity data are explained in Appendix 2.1

Activity	Activity h/24 h	Daily energy expenditure (kcal)					
		Tarboton (1978 a)		Wakeley (1978 a,c)		Koplin *et al.* (1980)	
Perched							
Inactive - night	10,40	22,8	$1,0BM_t$	19,2	$1,7BM_n$	13,6	$(1-p)(SM_{nt})$
Inactive - day	7,49			25,5	$1,7BM_d$	38,7	$NFA(EM_{dt}-(1-p)(SM_{nt}))$
Low activity	3,05	5,0	$1,3BM_t$				
Feeding	0,52	1,7	$2,5BM_t$				
Hunting	1,35	4,3	$2,5BM_t$	6,4	$3,5BM_d$		
SUBTOTAL	22,81	33,8		51,1		52,3	
Flying							
Soaring	0,35	7,7	$17,2BM_t$	3,6	$7,5BM_d$	17,8	$FA((BM_n)(p)(13,7))$
Directional	0,26	5,7	$17,2BM_t$	4,1	$11,5BM_d$		
Hovering	0,58	12,7	$17,2BM_t$	9,1	$11,5BM_d$		$\frac{1,19}{13,6}((26,1).13,6.13.7)$
SUBTOTAL	1,19	26,1		16,8		17,8	
Grand total	24,00	59,9		67,9		70,1	

model of Koplin et al. (DEB = 70,1 kcal) may be partly fortuitous, it is significant that their rather different approaches gave similar estimates of energy expenditure. The DEB estimates predicted by their methods were also close to the daily energy intake of 67,3 kcal estimated in this study. For the present I suggest that Wakeley's model is the most useful in that it provides an estimate of 67,9 kcal that agrees well with other estimates, and it furthermore predicts separate costs for perched-hunting and hovering (see below).

The estimates in Table 2.15 suggest that inactivity accounted for the greatest portion of daily activity, about 75% of a 24-h day. Hunting occupied only 8% (116 min) of 24 h or 14% of 13,6 h of daylight, but used about 23% of the DEB. Flight was similarly expensive, since about 25% of energy and only 5% of the time was spent in flying. However, as shown by the activities of five kites during dawn-to-dusk watches, all these periods varied greatly in response to changes in daylength and fluctuations in hunting success (see DISCUSSION p.64). Additional data on daily activities are given in Chapter 5.

Table 2.16 compares the foraging success (kcal of food/min spent hunting) and efficiency (kcal of food/kcal spent hunting) of breeding and non-breeding kites, and of the two hunting methods. Breeders had greater success and efficiency rates than non-breeding kites, by about 1,5 times for hovering, and by about 1,8 times for perched-hunting.

Foraging success by hovering was greater than by perched-hunting; non-breeding and breeding kites respectively obtained about 3,0 and 2,5 times more energy per unit time of hovering. However, perched-hunting was slightly more efficient energetically than hovering, by about 1,1 times in non-breeders and 1,3 times in breeders (Table 2.16).

TABLE 2.16 Food intake, energy intake and expenditure values for hovering and perched-hunting by non-breeding and breeding kites. Data for non-breeders from Table 2.13 and 2.15; data for breeding males from Table 2.13 and Chapter 4 - Table 4.9. Prey weights (g) estimated from prey seen caught. See p. 60 for methods used to estimate energy values of prey.

	Non-breeding males and females	Breeding males
Hovering		
Minutes/kill (no. kills)	39,1 (51)	34,6 (19)
Mean prey weight (no. prey items)	23,1 (52)	29,1 (22)
Grams caught/min	0,591	0,841
kcal caught/min	1,087	1,547
kcal spent hovering/min	0,261	0,253
kcal caught/kcal spent hovering	4,165	6,115
Perched-hunting		
Minutes/kill (no. kills)	164,3 (38)	75,1 (28)
Mean prey weight (no. prey items)	32,2 (64)	25,6 (38)
Grams caught/min	0,196	0,341
kcal caught/min	0,360	0,627
kcal spent perched-hunting/min	0,079	0,077
kcal caught/kcal spent perched-hunting	4,557	8,143

DISCUSSION

Daily hunting time

Using observed capture rates, prey sizes and proportions of 30% hovering and 70% perched-hunting (see p. 21), I estimated that non-breeding kites spent an average of 116 min or 14% of daylight activity hunting. The fact that this was lower than the average of 295 min spent hunting by five kites during dawn-to-dusk watches (Fig. 2.1), was probably due to the poor capture rates of the focal birds. The estimate is also lower than Tarboton's (1978 a) figure of 54% of daytime activity spent hunting by non-breeders. However, his results were probably biased in favour of hunting because he mainly observed kites encountered along the roads (W.R. Tarboton pers. comm.). Most of the birds encountered would have been hunting, while inactive kites perched in the shade of trees (Chapter 5, p. 207) would have been missed. Nevertheless, lower capture rates than those at Settlers (see p. 27) suggest that Tarboton's kites did have to hunt for a greater part of the day. From the capture rates recorded by Tarboton (1978 a), calculations suggest that his kites actually spent about 179 min (23%) of the day hunting. I assumed that they hovered for 30% and perch-hunted for 70% of their hunting time, and caught prey similar in size to those recorded at Settlers (Table 2.9). Tarboton's (1978 a) kites also mainly caught Otomys, Rhabdomys and Praomys.

Irrespective of the discrepancies between the above estimates, it is clear that daily hunting time varied greatly. This is shown by the activities of five kites in Figure 2.1. Presumably, variable intervals between successive prey captures (Fig. 2.2) meant that kites often hunted for variable periods each day. The ability to vary daily hunting periods probably explains why seasonal changes in food intake (pellet weights and numbers of kites seen with prey — Figure 2.8) were smaller than changes in prey availability (rodent trapping rates — Figure 2.7). The daily energy requirements of non-breeders probably remained relatively constant, and to meet these requirements kites adjusted the time they spent foraging to compensate for changes in prey availability.

Estimates of daily hunting periods also show that kites usually spent relatively short periods hunting, leaving long periods of inactivity or loafing (Fig. 2.1; Table 2.15). This was true also of breeding males (Chapter 4 — Table 4.9) which caught many more prey items to feed their mates and young. Many other raptors that catch a few prey items each day with long intervals between successive captures seem to have short hunting periods (Table 2.17). The non-breeding raptors in Table 2.17 all appear to hunt for an average of less than 30% of daylight time and, having little else to do, spend the remaining time loafing. Results for these species could only be obtained because they hunted actively, and hunting could therefore be separated from other activity. Other species in which hunting activity is not as obvious may either show similar patterns of short hunting periods, or they may hunt more passively. Passive hunting may be used by large eagles and buzzards that remain perched for most of the day. While they are probably on the look-out for prey during these long periods of inactivity, it is certain that they spend very little time in active pursuit of prey (Brown 1980).

Such inactivity contrasts with the activity and hunting behaviour of small insectivorous and granivorous passerines. These birds spend most of the day foraging for items that are consumed at intervals of a few seconds. For example, Pied Wagtails _Motacilla_ _alba_ have to catch an average of 7854 insects (one every 4 s) during an 8,5-h mid-winter day (Davies 1980). Four tits (_Parus_ spp. and _Aegithalos_ _caudatus_) studied by Gibb (1960) spend 75-95% of each day foraging. Breeding House Martins _Delichon_ _urbica_ need to forage in flight for about 81% of each day to obtain enough food to meet the requirements of their young and themselves (Bryant & Westerterp 1980). Similar results were obtained for several other passerines (Ettinger & King 1980; Pulliam 1980; Royama 1966).

TABLE 2.17 Foraging and loafing activity in non-breeding and breeding raptors. Data are given as means (single figures) or normal ranges (two figures). The two figures for Blackshouldered Kites refer to hovering and perched-hunting respectively.

Species	Breeding (B) or non-breeding (N)	No. prey items/day	% daytime hunting	Intervals (min) between captures	% daytime inactive	Source
Whitetailed Kite *Elanus leucurus*	N	-	5-9	-	-	Warner & Rudd 1975 Koplin *et al.* 1980
Blackshouldered Kite *E. caeruleus*	N	1-2	54	52 & 278	13	Tarboton (1978a)(see text)
" "	N	1-2	14	39 & 164	55	This study
Goshawk *Accipiter gentilis*	N	0,5	25	-	-	Hantge 1980
Sparrowhawk *A. nisus*	N	2	25	-	-	" "
Peregrine *Falco peregrinus*	N	0,5	15-25	-	-	" "
Rock Kestrel *F. tinnunculus*	N	-	15-25	-	-	" "
Osprey	B	1-7	25-35	85	-	Green 1976
Pandion haliaetus	B	2-7	8-26	10-117	43-75	Levenson 1979
" "	B	-	33	-	44	Stinson 1978
Ferruginous Hawk *Buteo regalis*	B	8-9	45-53	45-60	37	Wakeley 1978a
Whitetailed Kite	B	-	12-15	-	-	Warner & Rudd 1975
Blackshouldered Kite	B	3-10	30	35 & 75	37	This study

Some insectivorous kestrels appear similar to small passerines in spending long periods hunting and catching prey rapidly (Balgooyen 1976; Mendelsohn 1979; A.C. Kemp pers. comm.). This suggests that differences in foraging activity between most large raptors and small insectivores and granivores are due mainly to the effects of prey size. Small birds are unable to consume a few large food items to meet their daily energy requirements. They therefore take great numbers of relatively abundant and evenly spaced small prey. However, long periods and substantial energy costs are required to collect such food. These costs further extend their foraging time since additional prey must be obtained to replace the energy used in foraging (Norberg 1977). Small birds taking small prey items therefore have a high rate of energy intake and expenditure.

Large birds, in contrast, can meet their energy requirements by consuming a few large food items and by storing substantial energy reserves (Ceska 1980; Marcström & Kenward 1981). However, because large prey is usually sparse and irregularly distributed, prey capture tends to be unpredictable and predators may have to wait long periods between successive kills. Large birds therefore probably use little energy in foraging because they may be unable to predictably replace greater quantities of energy. They probably minimize their energy costs by either using inexpensive foraging methods or by hunting for as little time as possible. The former method may be most developed in the many large eagles that perch for long periods while searching passively for prey (Thiollay 1980). The active hunters shown in Table 2.17, in contrast, probably attempt mainly to minimize their daily hunting time (but see p. 68).

Hunting methods

In recent years biologists have attempted to predict those patterns of behaviour which enable animals to meet their requirements optimally. The predictions involve both identification of the required goals and those decision criteria that are used by animals in choosing one of several possible courses of action. Such optimality theory has been used in the study of foraging behaviour, since hunting animals have to choose where to hunt, how long to remain searching in one place, and what type and size of prey to take etc. (Krebs 1978; MacArthur & Pianka 1966; Pyke et al. 1977; Schoener 1971).

Few attempts have been made to consider how alternative hunting methods can be used optimally, but Norberg (1977) predicted that because the most efficient hunting methods are usually the most energy consuming, they would only be used when prey densities were high. Hovering and perched-hunting, the two methods used by kites, differed in the proportions with which they were used (Table 2.1), in the rate at which energy was obtained and spent, and in their energetic efficiencies (Table 2.16). Several predictions can be made as to why kites hovered and perch-hunted and why they used the methods in different proportions. Some of the predictions can be tested using available data but others require further study.

The testable predictions involve single factors. Firstly, kites may have attempted to minimise the time they spent hunting. This seems reasonable because kites usually spent a small proportion of the day hunting (see p. 62). However, if time was the only factor that determined hunting activity, kites would only have hovered since that was the quickest method of obtaining food (Table 2.4).

Secondly, assuming a limited hunting period, kites may have attempted to catch as much prey as possible. Again, this cannot apply because perched-hunting reduced the amount of food obtained per unit time.

Thirdly, kites may have tried to use as little energy as possible in hunting. However, if this was true they would only have perch-hunted because energetically expensive hovering added to their costs.

Fourthly, hunting might have been as energetically efficient as possible, but, on the basis of the costs estimated in Table 2.16, this was not feasible because perched-hunting was more efficient than hovering.

These results suggest that either hovering or perched-hunting (not both) was optimal. However, each method was in some way beneficial in terms of time or energy use and it is likely that hunting activity was determined by a combination of factors. For example, kites may have attempted to obtain as much prey, as quickly, and using as little energy as possible. This seems to be a likely goal because it takes into account the related requirements of conserving energy and obtaining prey as predictably as possible (see p. 67). While the concurrent use of hovering (as a relatively predictable method of catching prey) and perch-hunting (as an energy-saving strategy) would probably enable kites to meet this goal, the prediction remains to be tested.

Furthermore, the use of two hunting methods probably helped to increase the options open to kites. Hovering obviously enlarged the potential hunting area, since many cultivated areas were devoid of perches (Chapter 1 — Fig. 1.2 & 1.3). It was probably also useful for kites to be able to change hunting areas and therefore methods according to changes in profitability (see below).

While it may not be possible at this stage to identify which factors were most important in causing kites to hover and perch-hunt, it is worth considering why kites hovered for about 30% and perch-hunted for about 70% of their hunting time. Wakeley (1978 c) showed that Ferruginous Hawks hunt from perches and in flight at frequencies proportional to the efficiencies (prey obtained/energy spent) of the two methods. Using estimates in Table 2.16 similar comparisons can be made for kites. The ratios between hovering and perched-hunting efficiency for non-breeders (4,165/4,557 = 0,91) and breeders (6,115/8,143 = 0,75), however, differed from the ratio (30%/70% = 0,43) between the relative frequency of hovering and perched-hunting. There may be better agreement for breeding kites if the ratio, 30%/70%, is adjusted by an unkown amount to account for the slightly greater time they spent hovering (Table 2.13). Nevertheless, the comparisons indicate that non-breeders, at least, spent substantially more time perch-hunting and less time hovering than was energetically optimal. This may have been to reduce their total daily energy expenditure since although more hovering would have increased their energy intake, it would also have added to their total daily costs.

The frequency of hovering and perch-hunting can also be compared to the number of prey items obtained by each method. In 2864 min (25,2%) of hovering and 8520 min (74,8%) of perched-hunting (Table 2.1) I observed 72 kills by hovering and 67 kills by perch-hunting kites (Table 2.4). Although these percentages differ slightly from the estimated 30% and 70% for the two hunting methods, the ratio, 71/67 kills = 1,06, suggests that the two methods were not used in proportion to the number of prey caught.

In these comparisons I have again considered single factors and it is likely that several factors influenced the proportion of hovering and perched-hunting. One such factor was the relative success of each method. Hovering occurred less frequently during months in which it gave a poorer rate of prey capture (Table 2.12), and kites hovered more in the afternoon (Table 2.2) when a higher rate of descents (Table 2.4) suggested that it was most successful. Heat stress and food demands may also have influenced hunting methods. Heat during the middle of the day may have made hovering less stressful than perched-hunting because kites could then hover and soar alternatively at lower temperatures high above the ground. Greater demands for food may have caused unpaired and breeding kites to hover more than paired birds (Table 2.13). Unpaired kites faced greater food shortages than paired birds and breeding males had to catch many more prey items to feed their mates and young (Chapter 4). The demand for food may provide another explanation for the higher proportion of hovering in the afternoon: kites could have attempted to catch prey as quickly as possible before roosting to compensate for energy losses during the night.

Daily energy budget

The daily energy budgets (DEB) estimated in Table 2.15 are intended to show the average energy spent by non-breeders. While these are general estimates of how the kites spent their energy, they do not take into account seasonal and daily changes in temperature (Chapter 1 — Fig. 1.5), hunting methods (Table 2.12), and total time spent hunting (Fig. 2.1 & p. 64). These and other factors such as hunting success, energy reserves, and other climatic factors, probably caused substantial daily changes in the DEB of non-breeding kites. Other changes associated with breeding are discussed in Chapter 4.

Tarboton (1978 a) estimated the daily energy budget of non-breeding kites from pellet weights and activity budgets (as in Table 2.15). His results of 99,7 kcal/day energy intake and 98,3 kcal/day energy expenditure are about 50% higher than the 67 kcal/day estimated for energy intake and expenditure for non-breeders at Settlers (Table 2.15). His high figure for energy expenditure was due to the long hunting periods he observed (see p. 64) and the high cost values he attached to flight activities (see Table 2.15). The energy intake of 99,7 kcal is probably also too high because it was based on pellets collected mainly around nest areas, unlike the roosts where most pellets at Settlers were collected. (The kites studied by Tarboton (pers. comm.) roosted in a reed bed where pellets could not be collected.). Pellets from breeding kites found near nests were heavier than those obtained from non-breeding birds (Table 2.13).

The average proportion of the DEB spent in perched activity for non-breeders at Settlers was estimated to be about 51 kcal (Table 2.15). This agrees well with a DEB of 56 kcal measured on a resting captive kite by recording daily food intake and body water turnover with the hydrogen isotope, tritium (C.W. Sapsford pers. comm.). The agreement between these estimates and those for wild kites at Settlers is not changed substantially if the budgets are adjusted to take into account the fact that the captive kite did not hunt. It therefore seems quite probable that perched kites that are not hunting use about 50-60 kcal/day. The remaining daily energy costs concerning flight activities are more questionable. The flight costs given by the three models in Table 2.15 vary greatly, and although Koplin et al. (1980) and Wakeley (1978 a) base their estimates on several experimental studies, the cost of hovering in birds other than hummingbirds has never been measured.

Another estimate of daily energy expenditure can be made using equations given by Kendeigh et al. (1977). The equations,

$$\text{DEB} = 1{,}079\ W^{0,67} \quad \text{for } 30^{0}\text{C}$$

$$\text{and DEB} = 8{,}059\ W^{0,50} \quad \text{for } 0^{0}\text{C}$$

give an estimated DEB of 78,9 kcal for non-breeding kites, where body weight (W) is 244 g and mean daily temperature is 17°C (see Appendix 2.1 for examples of similar calculations). These equations are based on very few measured DEB values; the only species for which adequate data exist is the House Sparrow Passer domesticus (Kendeigh et al. 1977).

Prey

If prey densities and handling times and costs are similar, birds usually select large prey in preference to small items. This has been shown by several studies of birds that feed on small arthropods, and is supported by many studies of other predators feeding on generally small types of prey (Krebs 1978). Although I have no evidence for or against prey selection according to size in kites, observations of hunting birds suggested that they took the first items that became available, irrespective of size. This was apparent while trapping kites with Bal-chatri traps (Chapter 1, p. 9) when, on seeing the traps, kites often flew without hesitation towards them. Kites also regularly took very small and large prey items (Table 2.7 & 2.8) which obviously differed substantially in food value.

Only Marti & Hogue (1979) have studied prey size choice in raptors that feed on large prey items. They offered captive Screech Owls Otus asio several mice of various sizes simultaneously and found that the smallest ones were consistently preferred. Marti & Hogue give several explanations for this result, but I believe that their owls were offered an inappropriate choice. A hunting owl is unlikely to be confronted with a choice of several mice, and it also seems likely that an owl would take the first available item. Prey such as mice are usually widely spaced and their capture tends to be unpredictable (see Fig. 2.2). Insectivorous birds, in contrast, can expect to obtain prey more frequently, and they may therefore be more discriminating in their choice of prey. This may apply to usually insectivorous raptors such as kestrels that preferentially hunt vertebrate prey during the breeding season (Balgooyen 1976; Brown & Amadon 1968; Newton 1979). Being adapted to taking insects as a relatively abundant and predictable source of food, these raptors can possibly be more selective when greater quantities of food are demanded. However, raptors that specialise in taking large prey may not be as discriminating because they are unable to depend on such a regular source of prey.

Kites generally seem to be specialist small mammal predators, as shown in this study (Table 2.6) and elsewhere (Amat 1979; Siegfried 1965; Tarboton 1978 a). Other Elanus species show similar preferences (Hobbs 1971; Hollands 1977; Meserve 1977; Parker 1971; Schlatter et al. 1980; Warner & Rudd 1975; Waian 1973), suggesting that the genus evolved as specialist predators. This is in contrast to most raptors that take a wide variety of prey, and it is surprising that Elanus kites, while concentrating on rodents, apparently seldom widen their range of prey. I expected that kites would have sporadically taken insects, since great numbers of insectivorous Lesser Kestrels Falco naumanni, Greater Kestrels F. rupicoloides and Eastern Redfooted Falcons F. amurensis in the Settlers study area suggested that potential insect prey was abundant. That they did not do so, even during summer 1977-78 when rodents were in short supply (Fig. 2.7), is of interest because Marsh Owls Asio capensis showed a switch from rodents to insects during this period (pers. obs.). Even though kites may be morphologically best adapted to taking mammalian prey, they could probably easily catch insects on the ground.

The absence of caching is another unexplained feature of feeding in kites. Many owls and falcons store uneaten prey (Mueller 1974; Phelan 1977) and this would be to the advantage of a predator that has caught a very large item or that can catch several prey items quickly. The prey discarded by satiated kites can therefore only be seen as having been wasted.

Rodent populations

Rodent densities are usually considered to fluctuate greatly. In southern Africa evidence for such changes consists of reports of rodent plagues or population explosions and the results of trapping studies.

Rodent plagues have been reported several times (De Graaff 1981; Skead 1974; Smithers 1971; Van der Merwe & Keogh 1970; Wilson 1970,1975). Praomys natalensis and Tatera leucogaster are the species usually involved, but very high densities of Rhabdomys pumilio, Lemniscomys griselda and Mus minutoides are also known (Choate 1972; Smithers 1971; J. Collett in litt.) While predators may have access to very many rodents during plagues, they may in fact find prey even more readily than would be expected from the rodent numbers. This is because the rodents often forage in areas with little cover after having probably depleted food sources in areas where they are less exposed to predators.

The highest average number of rodents caught during this study was about four times greater than the lowest average, and even greater changes were shown by trapping rates on individual traplines (Fig. 2.7). Similar results are shown by several other studies (Table 2.18) in which trapping success rates changed 4-10 times. Although some changes occur regularly as a result of seasonal breeding, others are irregular with marked differences between years. The populations studied by Brooks (1974); David (1980) and Davis (1973) (see Table 2.18) showed peak densities in late summer and autumn, but the peaks varied 2-4 times in magnitude between years.

In addition to unpredicted increases in density, very sudden reductions in numbers may occur at any time. Densities during rodent plagues usually crash, probably as a result of disease (Smithers 1971). Similar sudden reductions may be caused by flooding (Brooks 1974; Davis 1973), grazing, harvesting of crops and other agricultural practices. At Settlers I observed large areas quickly rendered unsuitable for most rodents because of burning and the ploughing of wheat fields.

While some rodents in southern Africa breed sporadically throughout the year, most breed during summer (Brooks 1974; Chidumayo 1980; Coetzee 1965, 1967; David 1980; Davis 1973; Dean 1973 b; De Graaff 1981; De Wit 1972; Perrin 1980; Rautenbach 1978). Breeding usually starts in early summer, reaches a peak in mid and late summer, and may continue into autumn if the summer rainfall is high. Juveniles recruited to the population boost densities until they peak between late summer and early winter. Numbers then decline and reach a minimum in spring before breeding resumes.

These findings probably explain the peak densities observed during autumn and early winter at Settlers (Fig. 2.7). However, they do not

TABLE 2.18 Changes in rodent densities shown by trapping success rates. The various methods used in the studies were usually not comparable, but in each study the same method was used to obtain highest and lowest trapping rate. Data given by De Wit (1972) show the estimated number of animals/ha in a community of 12 small mammal species.

Species	Greatest no. caught/ trapping session	Lowest no. caught/ trapping session	Source
Rhabdomys pumilio	92	25	Brooks 1974
" "	160	15	David 1980
" "	58	6	Perrin 1980
Otomys irroratus	26	5	" "
" "	113	27	Davis 1973
Tatera brantsi	91	9	De Moor 1969
Rodent community	48	6	De Wit 1972

explain the other population peak in spring and the low numbers of juvenile Praomys and Rhabdomys produced during summer (Fig. 2.4). Most of the studies that demonstrated summer breeding activity did so by noting adults in reproductive condition. However, results using this method do not always agree with those obtained by recording the presence of juveniles in trapped samples. This is shown by the results of several studies that were similar to those obtained in my study. Davis (1973) and Perrin (1980) observed lower numbers of juvenile Otomys irroratus and Rhabdomys pumilio during mid summer than during early and late summer, and Brooks (1974) and Chidumayo (1980) found that populations of R. pumilio and Tatera leucogaster decreased during summer. Adult rodents sampled during these studies continued to show reproductive activity throughout the summer, suggesting that environmental conditions were not always suitable for the actual production, or survival, of young.

These observations therefore suggest that rodent populations may not always breed throughout the summer, and that densities may not always show single peaks during late summer and autumn. They also suggest that the peak numbers found in spring (Fig. 2.7) resulted from the production of juvenile Rhabdomys and Praomys (Fig. 2.4). Similarly, low densities recorded during mid summer may have been caused by the low rates at which juveniles were then recruited. However, an alternative explanation is that the apparent changes in rodent numbers were caused by changing feeding conditions and the availability of cover. These factors can also explain why the same changes in rodent numbers were indicated by trapping (Fig. 2.7) and by measuring the food supply of kites (Fig. 2.8 a,b). Rodents often start breeding before seasonal rains (Taylor & Green 1976) and this appeared to be the case at Settlers when breeding started during September-October 1977 and July-September 1978 (Fig. 2.4) before much rain had fallen (Chapter 1 — Fig. 1.4). Presumably feeding conditions were poor and there was little cover available during these dry months. Consequently, rodents may have foraged widely and become more accessible to predators in areas with sparse grass cover. The rodents may also have found baited traps very attractive. In contrast, dense grass cover and a good food supply during mid summer may have meant that rodents were less exposed to predators and were less attracted to bait in traps.

SUMMARY

The feeding ecology of kites was studied by observing hunting performance, trapping rodents, and by analysing pellets.

Kites hunted for average periods of about 116 min each day; about 30% of this was by hovering and 70% by perched-hunting. However, these periods and proportions varied greatly.

Hovering and perch-hunting behaviour is described and related to the time of day and weather conditions. Hovering occurred more frequently during the afternoon than at other times.

Prey was caught after average, but highly variable periods of 39,8 min of hovering or 127,2 min of perched-hunting. Rates of strikes at prey suggested that hunting was more successful in the morning and afternoon than at midday.

Most of the 205 prey items seen caught were eaten on perches such as fence posts, telephone poles and thick branches. Very heavy rodents were partially consumed on the ground where they were caught.

One pellet was usually produced daily and this reflected feeding conditions on the previous day. There was an average of 1,32 animals/pellet in the 2573 pellets analysed. Otomys angoniensis, Rhabdomys pumilio and Praomys natalensis formed 86,8% of prey numbers and 92,3% of prey weight. Most other prey consisted of other small mammals.

Average prey weight was estimated to be 31,6 g or 26,4 g. Perched-hunting kites caught larger prey than hovering birds.

Rodents were trapped on six trap-lines in different habitats. Rodent diversity was greatest where plant communities were most varied. Otomys and Rhabdomys were trapped more frequently on black turf than on red clay.

Otomys may have bred throughout the year, but Rhabdomys and Praomys produced young mainly during spring and autumn.

Hovering occurred mainly over areas with sparse grass cover, while perched-hunting was more frequent over dense cover. Hunting success on black turf did not differ consistently from that on red clay.

Seasonal changes in food supply were measured using rodent trapping rates, pellet weights, and the number of kites seen carrying prey. There were significant correlations between these measures which showed two peaks in food supply, one in early summer and one in early winter.

The proportion of hovering and perched-hunting also varied seasonally, with hovering less frequent during summer when it gave a lower rate of prey capture.

Marked seasonal changes in prey composition were recorded, which for Praomys significantly matched changes in numbers caught in rodent traps.

Unpaired and breeding kites probably hovered more than paired birds. The hunting success of unpaired birds was poorest, and that of breeders the best. Differences in pellet weights suggested that breeding kites consumed about 19% more food/day than non-breeders. Paired kites caught a greater proportion of diurnal prey than unpaired birds.

Consistent differences were not found between the hunting performance of paired males and females.

Three models were used to estimate the energy expenditure of non-breeders from activity budgets. Two of the models produced similar estimates (67,9 and 70,1 kcal) of total energy expenditure which agreed with the estimated daily energy intake of 67,3 kcal.

Hovering was found to provide a higher energy intake per unit time, but a lower energy intake per unit energy cost than perched-hunting.

The results are discussed with particular reference to energy and time spent hunting, hunting methods, prey selection, and rodent population dynamics.

It is suggested that kites spent short periods hunting to minimize their daily energy expenditure in hunting. If longer periods had been spent hunting the higher energy costs incurred may not have been readily replaced because prey capture was so unpredictable.

Several advantages to hovering and perched-hunting were identified, but it was not possible to state which factors were most important in determining the use of the two hunting methods.

Kites probably do not select prey according to size because their preferred rodent prey items are widely and unpredictably distributed.

Rodent densities fluctuate greatly and unpredictably as population explosions and 'crashes', as seasonal changes, and as year-to-year variations. While many studies have shown that adult rodents remain in breeding condition throughout summer, there is some evidence that juveniles may not be produced throughout the summer.

APPENDIX 2.1

Aschoff & Pohl (1970) give two equations for basal metabolic rate, one for diurnal (BM_d) and one for nocturnal activity (BM_n)

$$BM_d = 0{,}5928W^{0{,}729}$$ 32,61

$$BM_n = 0{,}4616W^{0{,}734}$$ 26,10

where W is the bird's weight (g); W = 244,2 g for non breeding kites of both sexes (Chapter 6 - Table 6.3).

Tarboton (1978a) used another basal metabolic rate (BM_t) intermediate between those given by Aschoff & Pohl (1970):

$$BM_t = 0{,}5410W^{0{,}734}$$

In addition to his flight cost of 17,2BM_t, Tarboton gave calculations using a cost of 12,0BM_t, which, if applied to the Settlers data in Table 2.15, gives a daily energy budget (DEB) of 52,0 kcal.

Wakeley (1978a, c) used the two Aschoff & Pohl equations for BM_d and BM_n. The costs given in Table 2.15 were drawn from his two papers which differ only in the costs for perched-hunting (2,5 or 3,5BM_d) and flapping flight (11,5 or 12,5BM_d). I chose the higher cost of perched-hunting because of the many short flights during perch changes and strikes. The lower cost of 11,5BM_d for flapping flight seems more reasonable for kites because hovering included brief periods of soaring. In studying Ferruginous Hawks, which do not hover, Wakeley considered only flapping flight and soaring. In Table 2.15, however, I have used his costs to estimate energy expenditures separately for hovering and directional flight.

The model of energy expenditure presented by Koplin *et al.* (1980) considers three activity categories only: perched diurnal activity, flying, and nocturnal rest. Their model can be expressed as:

$$DEB = NFA(EM_{dt}-(1-p)(SM_{nt})) + FA((BM_{n})(p)(FC)) + (1-p)(SM_{nt})$$

where:

NFA is the duration of perched activity as a proportion of daylength,

FA is the duration of flying as a proportion of daylength,

p is the daylength and 1-p the duration of the night; daylength at Settlers was 13,6 h (Chapter 1, p. 9),

FC is the flight cost, taken as 13,7 by Koplin *et al.*,

EM_{dt} is the existence metabolic rate as a function of average temperature (dt) during the day; at Settlers dt was about 20,4°C (data from nearest weather station with suitable data at Pretoria (25 45S; 28 14E), South African Weather Bureau, WB19),

$$EM_{dt} = 4{,}235W^{0{,}5316} + \left((dt)\left(\frac{1{,}455W^{0{,}6256} - 4{,}235W^{0{,}5316}}{30}\right)\right)$$

SM_{nt} is the standard metabolic rate as a function of average nocturnal temperature (nt); the Pretoria value used for Settlers data is 13,7°C

$$SM_{nt} = 1{,}810W^{0{,}5944} - (nt)(0{,}0457W^{0{,}5886})$$

BM_{n} is the Aschoff & Pohl equation (above) for basal metabolic rate at night. Koplin *et al.* used this rate as a measure of the lowest possible metabolic rate (see Kendeigh *et al.* 1977).

CHAPTER 3

SOCIAL BEHAVIOUR AND DISPERSION

INTRODUCTION

Many studies of raptor populations, particularly in Europe and North America, have compared the densities and dispersion of raptors in different areas and years. Some comparisons have also been made between numbers and feeding conditions and pesticide levels, the latter aspect becoming important in recent years. Generally, densities were low where food supply was poor and pesticide levels were high. Newton (1979) has reviewed the subject in depth and pointed to several gaps that await study. Among these are an understanding of the proximate effects of food on individual performance and how these relate to the behaviour of whole populations. The social organisation of raptors, too, has received little study; one result is that the same individuals are often assumed to remain paired and in the same areas for life (*e.g.* Brown & Davey 1978). Most raptor population studies have been done in the temperate Holarctic and little is therefore known of raptor populations outside this region.

Blackshouldered Kite populations are often described as unpredictable and eruptive with great numbers congregating in rich feeding areas (Brown & Amadon 1968; Morel & Poulet 1976; Skead 1974). However, these statements refer to whole populations in large areas and little is known of how, when and by whom these movements are made. The aims of this chapter are to present data on the performance of individuals as residents, their movements, and the associations and differences in behaviour between the sexes. An attempt is then made to relate these aspects to feeding conditions (Chapter 2), breeding (Chapter 4), and the dynamics of kite populations.

METHODS

The presence or absence of birds in the study area was determined by recording the identity and position of all kites sighted. Each kite was seen an average of nine times per month. Dates of arrival (when kites became resident) or desertion (when kites left the area) were taken to be the dates the individuals were first or last seen. The composition of the population was assessed each half-month (see below) and a bird not seen during a particular half-month was assumed to have deserted. An individual was considered resident only if it was seen repeatedly in an area over several days.

Occupancy periods were measured in days; occupancy periods pooled for a number of birds are expressed as bird-days. Occupancy periods started on 1 March 1977 or ended 579 days later on 30 September 1978 for individuals present when the study started or ended respectively. In measuring the performance of residents I have presented occupancy data for each kite on each territory separately. If a kite moved to a "new" territory, a separate set of data is shown for that bird on the "new" territory. Similarly, certain birds performed the roles of <u>territory-holders</u> and <u>mates</u> (defined below) at different times and their performances in each role have also been measured and presented separately.

Sex identification was based on observed sexual behaviour (Chapter 4) or a discriminant analysis of certain body measurements (Chapter 6). A bird that paired with one of known sex was assumed to be of the opposite sex. Residents were also classified into one of three mutually exclusive mating classes: <u>unpaired</u>, <u>paired</u> (but not breeding) or <u>breeding</u>. Not all breeding birds were paired because most females left males before their young became independent (Chapter 4, p. 167),(such deserted, unpaired breeding males were classed as breeders). Kites were considered to be breeding if they showed any of the behaviour described as such in Chapter 4.

A bird that first occupied a territory was termed a territory-holder, while a kite that joined a territory-holder to form a pair was a mate. Some birds were either territory-holders or mates at different times. Periods spent as territory-holders and mates, and in each mating class, were measured separately for each bird.

Thirty-five of the 102 kites resident during the study were not colour marked (Chapter 1, p.11) and, because each remained resident in one area for some time, several days or weeks, these were assumed to be 35 individuals. Five marked kites (7%) moved from one part of the study area to another and it is therefore possible that some unmarked birds did likewise. However, all the unmarked birds stayed for short periods and contributed little to the total time spent by kites in the population. Had they stayed longer, they would probably have been caught and marked.

A kite seen once only in the area was classed as a nomad. However, a resident seen intruding on a neighbouring territory was not classed as a nomad.

The size of the population was measured every half-month, each resident recorded in a half-month being listed as a population member. Small errors in these counts resulted from rapid population turnover — if a kite deserted and was replaced by another during the same half-month, both were counted.

All sightings and movements were plotted on maps. After August 1977, at the end of each month composite maps were drawn of all territories in the study area. Boundary positions were based on plotted sightings, territorial conflicts and a knowledge of boundaries in previous months. Spatial changes in the use of small areas of territories meant that kites were not always seen regularly throughout their territories. Unless observations showed that such apparently vacant areas had been expropriated by other birds, I assumed they still belonged to those kites that occupied them in previous months. Territory sizes were measured on the maps to the nearest 0,25 km^2.

Some data on long distance movements were obtained from the South African Bird Ringing Unit and H.P. Mendelsohn. References to individual kites in the text, e.g. ♂50, ♂27, ♀68 relate to Appendix 3.1 where brief summaries are given of their social and spatial behaviour.

RESULTS

Sexual comparisons

The social and spatial behaviour of males and females differed markedly (Table 3.1). Males were resident for average periods of 205,5 days (n = 38) and females for 97,3 days (n = 51) on each territory ($\chi^2_1 = 41{,}8$; $p < 0{,}001$). Males were unpaired residents for 3222 bird-days and females for 751 bird-days only. Females frequently moved territories but each male occupied one territory only during the study (see Appendix 3.1 — ♀♀ 68, 88, 98 and all males).

Most males and females performed the roles of territory-holders and mates respectively (Table 3.1). Thus males usually established territories and females then joined them as mates. From Table 3.1 males behaved as territory-holders certainly for 6298 bird-days, and probably for 7592 bird-days (I took males to be territory-holders in pairs that formed before the study and in those arriving together on new territories (see Pairing, p.88), hence the probable greater total of 7592 bird-days). Only five females were territory-holders for substantial periods (♀♀ 12, 28, 62, 80 & 86).

Unsexed kites (Table 3.1) were not marked. However, most appeared to behave as males when occupying territories alone. All were resident for short periods ($\bar{x} = 27{,}5$ days; n = 18).

Males spent more time breeding (2207 bird-days) than females (1821 bird-days) (Table 3.1) because most females deserted before their young became independent and males were therefore left to care for the flying young

TABLE 3.1 Total time (bird-days) spent by male, female and unsexed kites as territory-holders and mates, and as unpaired, paired or breeding birds.

Sex and status (no. of birds)[a]	Mating class			Total
	Unpaired	Paired	Breeding	
Males				
Territory-holders (36)	3222	2268	2102	7592
Mates (3)	0	125	105	230
Females				
Territory-holders (10)	751	125	105	981
Mates (49)	0	2268	1716	3984
Unsexed				
Territory-holders (14)	424	36	0	460
Mates (4)	0	36	0	36
Totals				
Terrritory-holders (60)	4397	2429	2207	9033
Mates (56)	0	2429	1821	4250
Grand totals (116)	4397	4858	4028	13283

[a] The time spent as territory-holders or mates for 14 kites was listed twice (13 birds) or three times (one bird) because at different times they were both territory-holders and mates or lived on separate territories (see METHODS).

(Chapter 4, p. 167).

There were more males than females during all 38 half-month counts of the kite population in the study area. The mean proportion of males was 60% (range 52-71%). This could have been because females spent more time as nomads, but of 20 sexed nomads only seven (35%) were females. In addition, more territory-holders than mates were observed as nomads (see *Movements*, p. 117).

Pairing

Twelve pairs were in the area at the start of the study. A further 63 pairs were formed during the following 19 months. In 45 cases the pairs were new, the pair members having never been seen together (Table 3.2.1). Most (37) were formed by new birds joining resident territory-holders (Table 3.2.1 a-e). Where the sexes were known, 32 were females and three were males new to the area. Three pairs were formed after the territory-holders had probably been absent temporarily (Table 3.2.1 b-c). Six territories may have been established by pairs (Table 3.2.1 f), but nomads were never seen in pairs, suggesting that the kites did not arrive paired. Slight differences in the arrival times of the pair members might not have been recorded. The four kites(♂34, ♀62, ♂51 and ♀80) that joined territories (Table 3.2.1 g) had been unpaired for long periods before pairing (75, 249, 113 and 91 days respectively).

Eighteen pairs were re-established after one of the birds had been absent from the territory (Table 3.2.2). More females (ten) than males (five) were absent temporarily. One pair (♂83; ♀64) were seen together immediately before and after their absence but may have separated as nomads during their absence (Table 3.2.2 d).

Several observations were made that suggest how males and females behave during the first stages of pair formation (possible advertisement by

TABLE 3.2 Movements of kites associated with pair formation at Settlers in 1977 and 1978.

Situation	Observed frequency
1 New pair	
a) ♀ arrives to pair with resident ♂	29
b) ♂ usually resident, but ♂ & ♀ arrive simultaneously after temporary absence of ♂	2
c) normal resident ♂ arrives back at territory after temporary absence and pairs with new ♀ that has independently settled on the territory	1
d) mate arrives to pair with unsexed resident	2
e) ♂ arrives to pair with resident ♀	3
f) both birds arrive together and establish new territory	6
g) unpaired ♂ & ♀ on adjacent territories pair and join territories	2
Total	45
2 Pair re-established	
a) ♂ resident, ♀ arrives back after temporary absence	10
b) ♀ resident, ♂ arrives back after temporary absence	5
c) ♂ resident, ♀ arrives back after temporary absence during the post-nestling dependence period	2
d) pair arrive back together after temporary absence of both birds	1
Total	18

unpaired males is considered in Chapter 5 (p. 208). On 15 March 1978 I saw ♂71 associating with an untagged intruder for 15 min. On six occasions ♂71 flew towards the intruder which then flew off with ♂71 in pursuit. The six pursuits ended with both birds landing on bushes 20-50 m apart. With the intruder perched, ♂71 several times flew to another bush, hovered and descended into the foliage (pairs starting to breed often did this, the behaviour probably representing nest-site inspection and/or advertisement (Chapter 4, p. 150). The pursuits finally ended about 750 m into a neighbouring territory with the intruder flying away and ♂71 stopping his pursuit. Normally, territorial conflicts ended near territory boundaries and displays to potential nest sites were never seen during conflicts (Chapter 5). The behaviour of ♂71 appeared to contain aggressive and sexual components. Similar behavioural combinations were seen in several recently established pairs. For example, on the day that ♂34 and ♀62 were first seen paired I saw the male fly at the female six times between 08s55 and 11s30. Each time she crouched horizontally in a posture normally adopted by copulating kites (Chapter 4, p. 148). Five of the male's flights ended with him dive-bombing her and on the sixth occasion he attempted to copulate. In other new pairs, dive-bombing was always the aggressive component, but sexual behaviour varied between copulations, displays to nest sites and prey being offered to the female (See Chapter 4 for descriptions of these behaviour patterns).

Sixty-seven pairs separated during the study; 48 separations were permanent and 19 were temporary (Table 3.3). Mates deserted more often than territory-holders and females more often than males. The members of eight pairs are listed as having deserted simultaneously (Table 3.3.2 & 3.3.5), but slight differences in their departure dates may have been missed.

Analyses of when pairs formed and separated, and for how long they were maintained, are given below (see <u>Arrivals and desertions</u>, p. 98 and <u>Occupancy</u>, p. 105).

TABLE 3.3 Causes and frequencies of pair separation in kites at Settlers in 1977 and 1978.

Cause of separation	Observed frequency
1. Permanent desertion by mate:	
a) female	32
b) female with fledged chicks	4
c) unsexed mate	3
d) male	1
Total	40
2. Permanent desertion by both birds	6
3. Permanent desertion by territory-holder	2
4. Temporary desertion by mate:	
a) female	9
b) male	1
c) female with fledged chicks	3
Total	13
5. Temporary desertion by both birds	2
6. Temporary desertion by territory-holder:	
a) female	1
b) male	3

Dispersion

Unpaired kites and pairs occupied exclusive areas which they defended vigorously (Chapter 5). Figure 3.1 a shows 14 areas in which the majority of territories were situated, and Figures 3.1 b-d show examples of month to month changes in boundary positions. Territory boundaries varied according to the presence of neighbours and the use of favoured hunting areas (see example in Fig. 3.2).

Sixty-four territories were formed during the study, 35 by new kites and 29 by birds returning after a temporary absence. Temporarily vacant territories were accessible to other kites, and eight territories were formed in these areas for short periods. Whether the new occupants were evicted, or delayed the return of the original occupants, is not known. However, the new occupants were usually last seen several days before the original birds returned. Single kites formed territories in 57 cases, and seven other territories were established by males and females apparently arriving together.

Twenty-five new territories were established in vacant areas and 10 in poorly frequented parts of existing territories (see Fig. 3.2). The 10 existing territories which became divided were particularly large, with the established occupants concentrating their activities in the remaining areas. Territories formed in vacant areas were occupied for longer ($\bar{x}$ = 146,5 days; S.D. = 153,1 days) than those established within existing territories ($\bar{x}$ = 38,0 days; S.D. = 68,3 days) (Mann Whitney U = 213,5; $p < 0,001$).

Two independent juveniles (♂41, Clev. chick) established territories within their parents' territories. Territorial conflicts between these parents and juveniles were often observed.

Several observations suggested that kites might select territories instead of merely arriving in an area and settling there immediately.

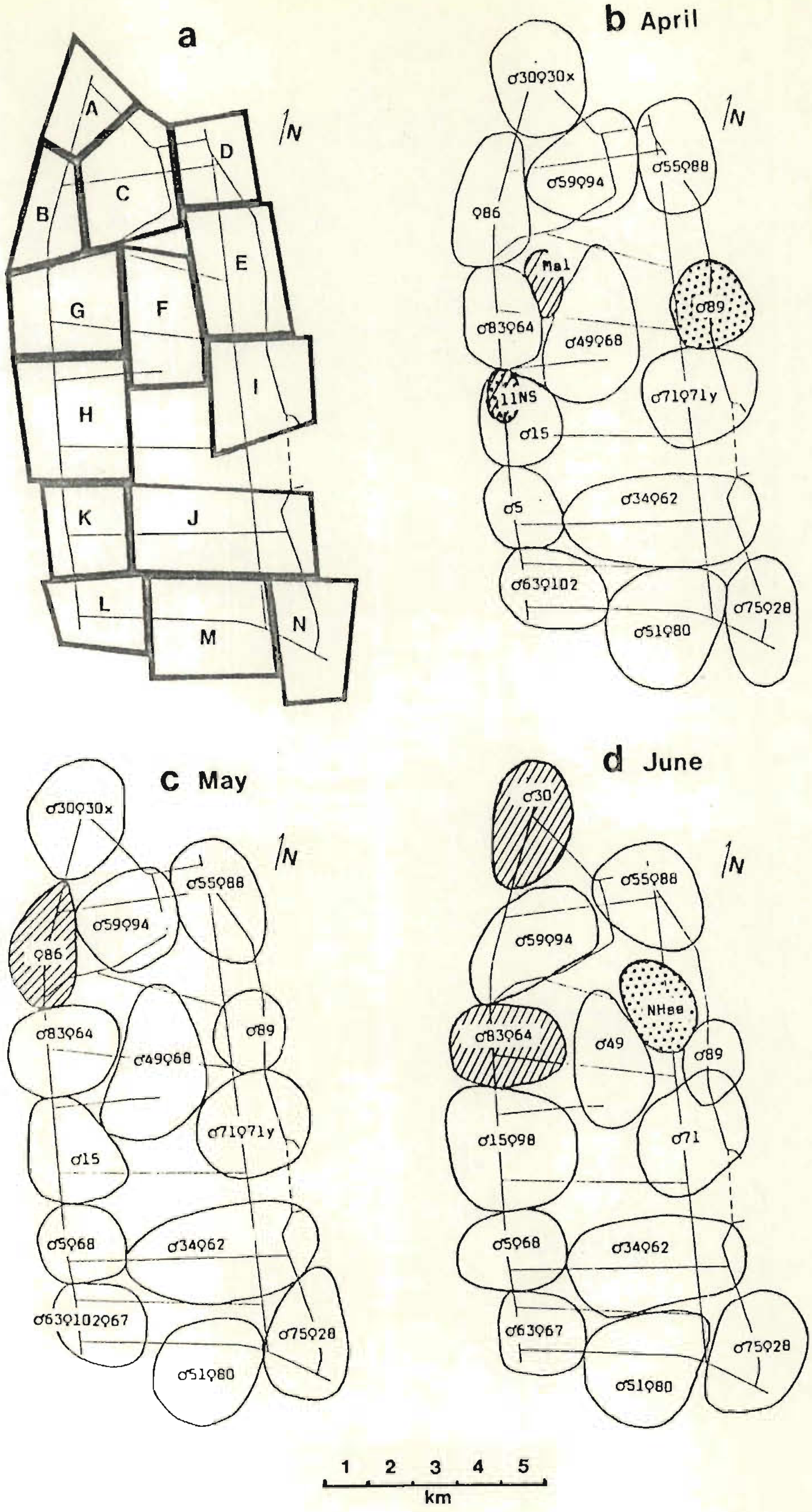
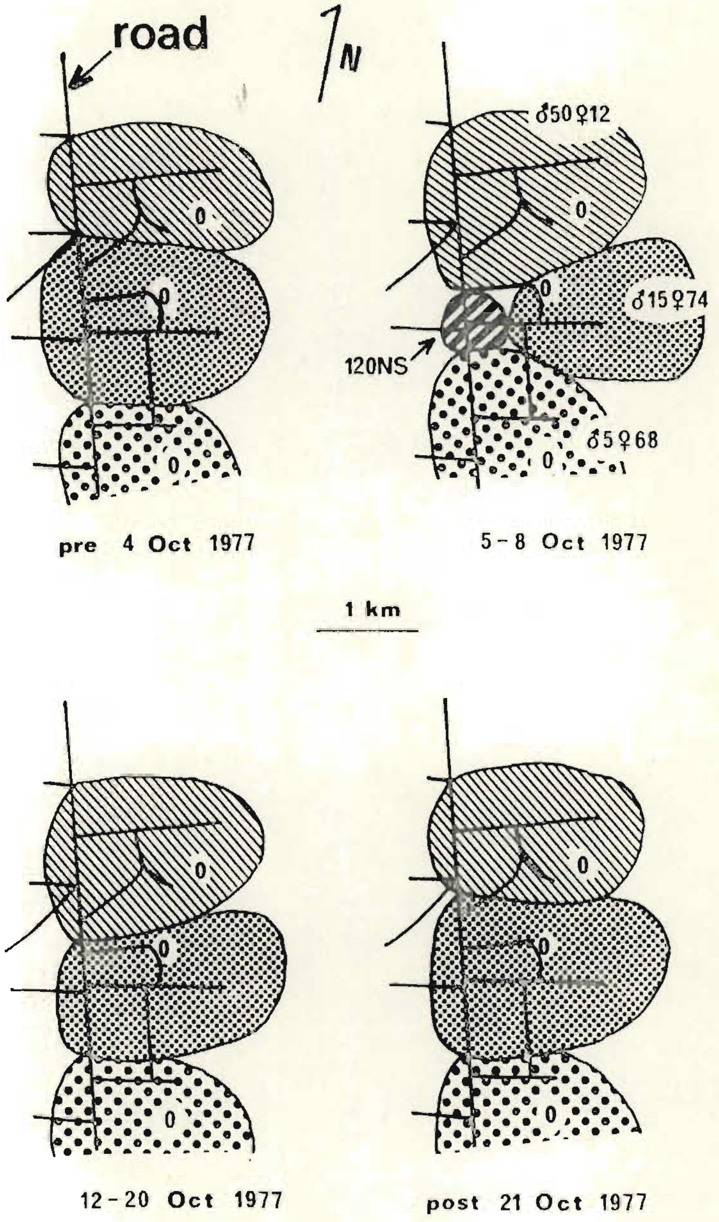


FIGURE 3.1 a) 14 areas in which most territories were situated. b-d) territories and their occupants during April-June 1978. Stippled and hatched territories were established and/or deserted during the month. See Appendix 3.1 for the occupancy and movements of all kites.



pre 4 Oct 1977

5 - 8 Oct 1977

12 - 20 Oct 1977

post 21 Oct 1977

FIGURE 3.2 Rapid territorial changes during October 1977. Focal areas are indicated by'0'. The unmarked kite, 120NS, occupied a territory for two days when ♂15,♀74 withdrew from part of their normal range. ♂50,♀12 and ♂5,♀68 also extended their territories to fill part of the vacant area. ♂15,♀74 then returned to this area and the other residents withdrew, 120NS leaving the area.

Five birds (♂♂1, 50, 55, 71 & 89) remained for 2, 1, 3, 1 and 1 days, where they were first found and caught, and only 3, 3, 4, 6 and 9 weeks later respectively did they become permanent residents in the same areas. Another kite (♂75) was initially present for five days, then absent for five weeks, present for four days, absent for six weeks, and finally resident for the next nine months. ♂34 showed similar behaviour; he was present for one day, absent for ten weeks (when seen as a nomad elsewhere), present for one day, absent for four weeks, and then resident for the next ten months. These seven kites represent 10% of all marked residents, suggesting that their behaviour was not irregular. Some of the 46 unmarked kites that were seen once and treated as nomads may have later returned as territorial birds.

The mean sizes of "stable" territories, i.e. those occupied continuousl during each month, are shown in Figure 3.3. The size of a territory usuall changed when new birds or neighbours annexed parts of it, or when some parts were vacated and other areas became occupied. Persistent fighting between neighbours also resulted in boundary changes. I observed boundaries moving 100-500 m in 1-4 weeks of repeated disputes. The two territories formed after unpaired neighbours paired with each other (♂34 & ♀62; ♂51 & ♀80) were unusually large (6-7 km^2).

From September 1977 to February 1978 territories were both smaller and more numerous than between March and September 1978 (Fig. 3.3). The inverse relationship between size and number of territories was highly significant (Spearman's Rank $r_{13} = -0,92$; $p < 0,001$). The total occupied area (sum of all territory sizes) also increased between September 1977 and 1978 (Fig. 3.3), indicating that areas vacant in 1977 became occupied in 1978.

Territories held by unpaired kites were smaller than those occupied by pairs. Sixteen territories were significantly smaller in the month

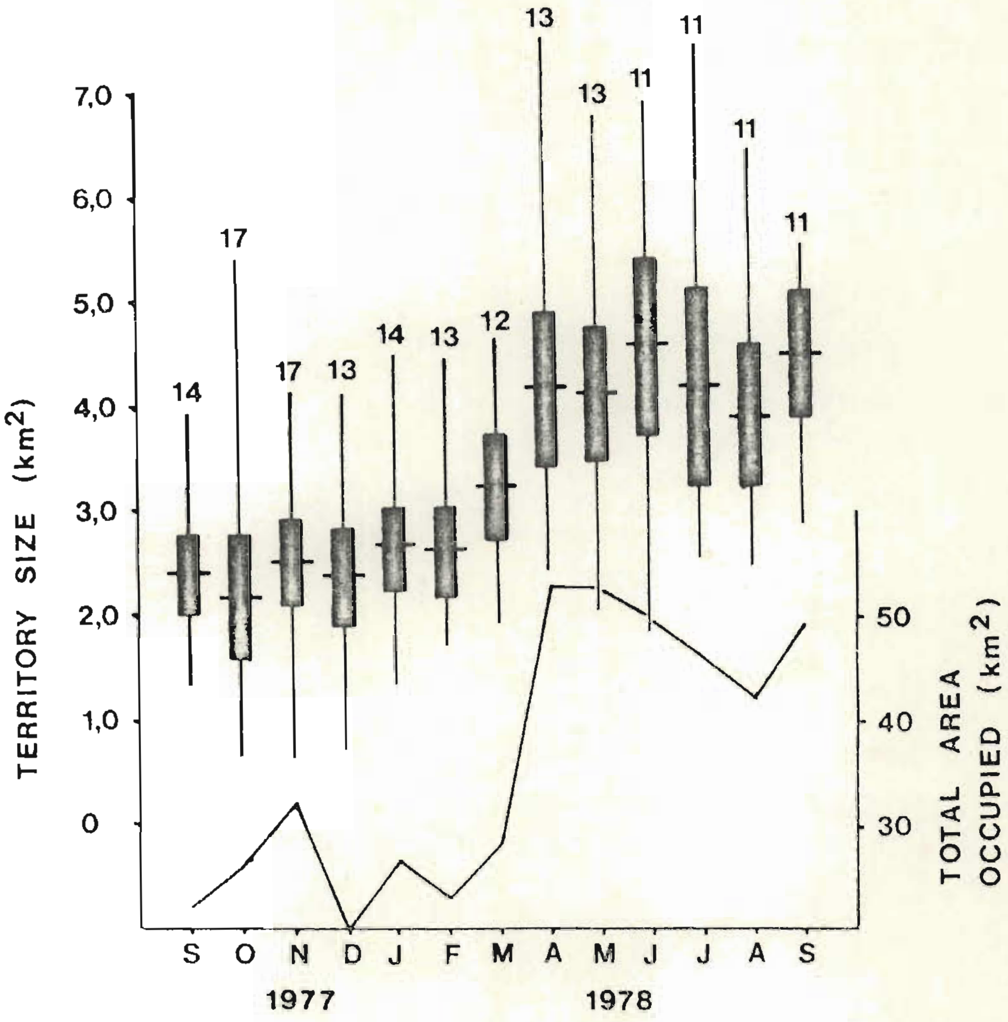


FIGURE 3.3 Changes in size of "stable" territories (see p. 95) and total area occupied by kites between September 1977 and September 1978. Horizontal lines are means, vertical bars are 2 x S.E. ($\bar{x}$) above and below means, vertical lines show the range, and sample sizes are given above the upper range.

before arrival of a mate ($\bar{x}$ = 2,49 km^2) than in the next month ($\bar{x}$ = 3,36 km^2; Matched Pairs t_{15} = 3,39; $p < 0,005$). In contrast, paired territories were similar to breeding territories in size; sizes in the month prior to breeding (when the pair was hunting) were close to sizes in the following month when the female was restricted to the nest area (Chapter 4) (Matched Pairs t_8 = 0,42; NS).

Although levels of significance were low, two tests suggested that territories became larger the longer they were occupied. Within the periods September 1977 - February 1978, and April - September 1978, territory size and duration of tenure were positively correlated (Spearman's Rank r_{22} = +0,35; $p < 0,1$, and r_{13} = +0,39; $p < 0,1$, respectively). The mean size of each territory was calculated from measurements made within each test period and the duration of tenure of a territory was the time it was under observation. Territory sizes did not vary significantly within each test period (Fig. 3.3).

The vertical extent of territories is unknown but kites rarely flew above 150 m. Intruders flying overhead were often chased (Chapter 5). Each territory had a focal area consisting of one or more trees used for nesting and roosting during the day or night.

Territory desertion was preceded by an apparent restlessness. I often saw kites hunting in areas they usually avoided, and I also failed to find them regularly in their preferred hunting areas. Two males (♂♂ 7 & 55) abandoned territories while tending flying young. The chicks followed their fathers when they left their territories. ♂7 nested outside the study area but moved with his single chick into the area for a short period.

Arrivals and desertions

This section considers arrivals and desertions by mates and territory-holders. Analyses of these movements also provide statements on when pairs formed and separated, and when territories were established and abandoned. This is because pairs and territories largely depended on the presence of mates and territory-holders respectively (see <u>METHODS</u> and data for mates in Table 3.3). For territory-holders, territories became vacant after 68 of the 74 desertions by these birds; mates remained resident in the other six cases (♀28 twice, ♀64, ♂75, ♀80, ♀94). Territories were established after 64 of the 68 arrivals by territory-holders; mates were already present in the remaining cases (♀28, ♀64, ♀94 & ♂75).

Analyses here exclude desertions by mates with flying chicks. These were considered to differ from other desertions by mates (see DISCUSSION, p. 129).

Numbers of new arrivals and returning birds varied each month (Fig. 3.4 An index of the number of new mates relative to the number of available unpaired territory-holders (Fig. 3.4 b) was positively related to the proportion of pairs copulating (Table 3.4). This suggested that most mates arrived when most pairs started breeding. The number of new mates each month was not related to other social or feeding conditions (Table 3.4).

An index of the number of new territory-holders (Fig. 3.4 d) was positively related to the frequency of territory desertion (Table 3.4). (The index was pooled into two-month periods because of small samples.) This indicates that new territory-holders normally arrived when occupied areas fell vacant. The mean interval between territory desertion and occupation by a new bird was 25,7 days (S.D. = 18,0 days; n = 12). Table 3.4 shows inverse correlations between the index of new territory-holders and measures of food supply and breeding activity. These inverse relationships simply indicate that few territories were established and deserted when most birds were breeding and food supply was good.

Mates and territory-holders deserted (Fig. 3.5) at directly proportional frequencies (Table 3.4). Most desertions occurred when few

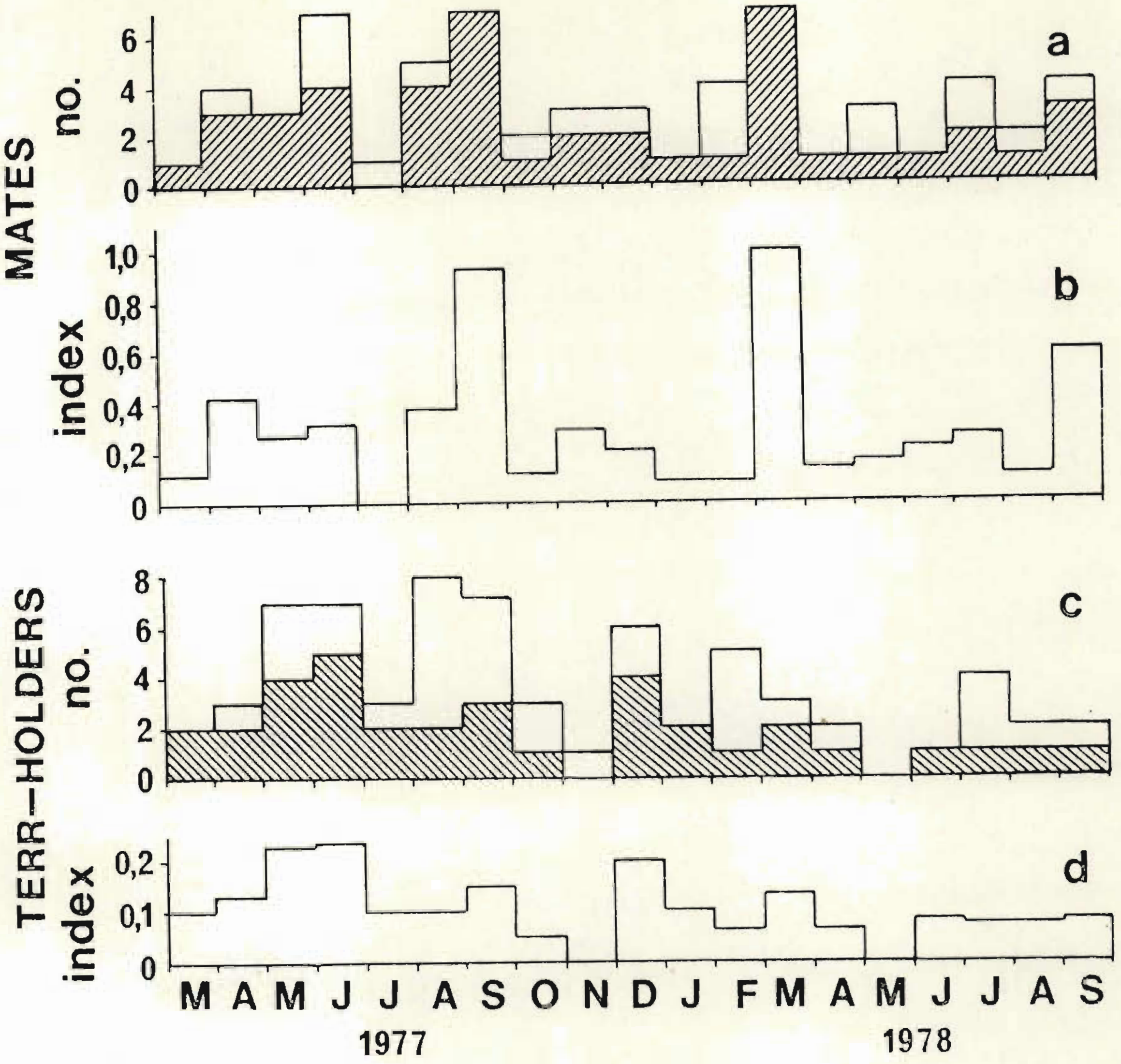


FIGURE 3.4 Arrivals each month by new and returning mates and territory-holders. a) number of new (hatched) and returning (unshaded) mates; b) number of new mates/number of unpaired territory-holders in the study area; c) number of new (hatched) and returning (unshaded) territory-holders; d) number of new territory-holders/number of territory-holders present in the study area.

TABLE 3.4 Tested relationships between monthly indices of arrivals, desertions, pairs starting to breed, pairs breeding and food supply. Tests are Spearman's rank correlations and show significance levels (+ $p < 0{,}1$; ++ $p < 0.05$; +++ $p < 0{,}025$; ++++ $p < 0{,}005$; N.S. - not significant) and degrees of freedom. Negative correlations in parentheses .

Category	New[a] mates	New[b] territory-holders	Mate[c] desertions	Territory-holder[d] desertions
New territory-holders	N.S. 9			
Mate desertions	N.S. 19	++++ 9		
Territory-holder desertions	N.S. 19	++++ 9	++++ 19	
% starting breeding[e]	++ 19	(+) 9	(+++) 19	(+++) 19
% breeding[f]	N.S. 19	(++) 9	(+) 19	(++++) 19
Food supply[g]	N.S. 17	(++++) 8	(+++) 17	(++++) 17

[a] no. new mates/mean no. unpaired territory-holders (Fig. 3.4b)

[b] no. new territory-holders/mean no. territory-holders - two-month samples (Fig. 3.4d)

[c] no. desertions by mates/mean no. mates (Fig. 3.5b)

[d] no. desertions by territory-holders/mean no. territory-holders (Fig. 3.5d)

[e] % of pairs starting to breed (Chapter 4 - Fig. 4.6c)

[f] % of pairs breeding (adapted from Fig. 3.7)

[g] index of food supply (Chapter 2 - Fig. 2.8c)

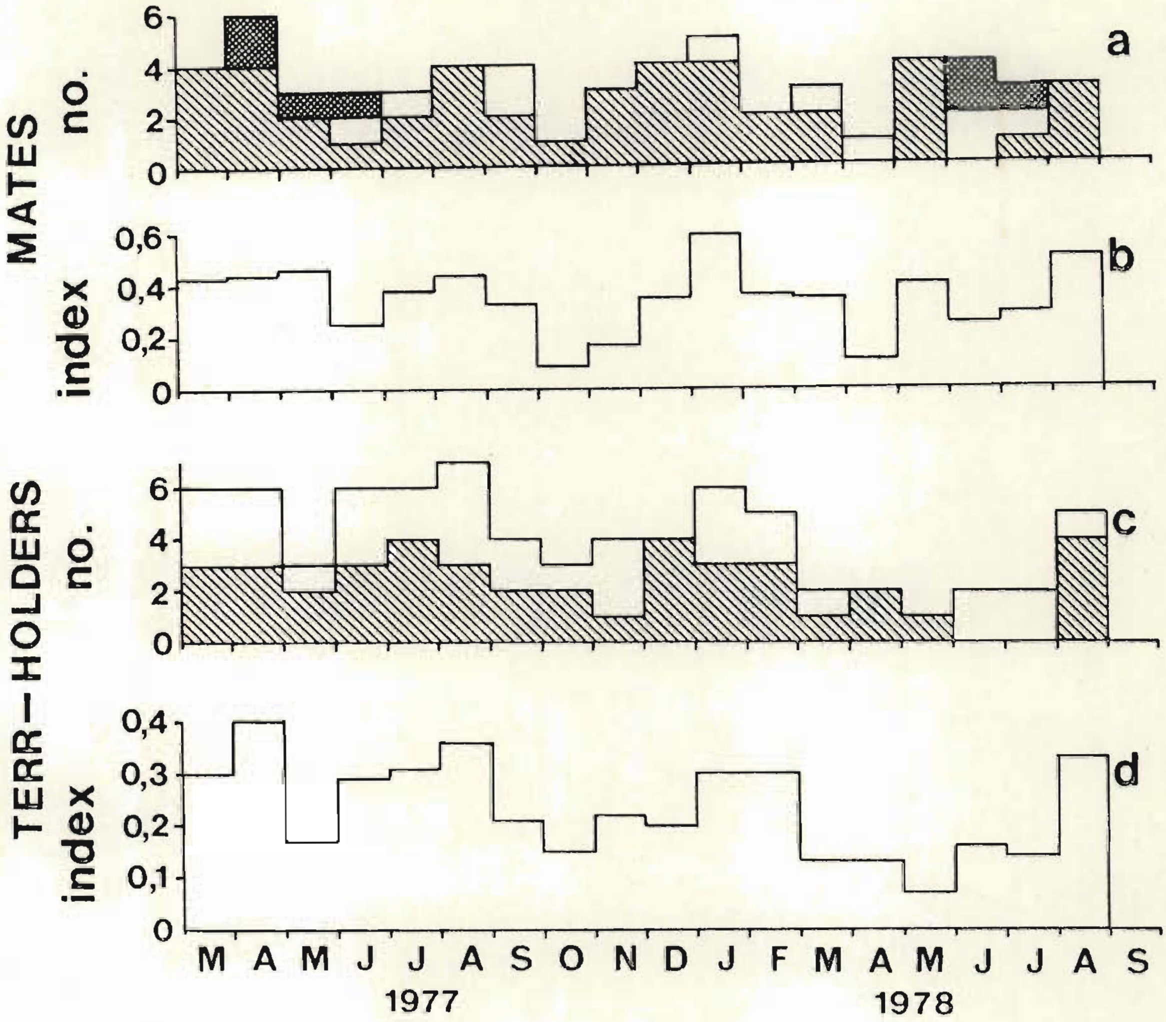


FIGURE 3.5 Permanent and temporary desertions each month by mates and territory-holders. a) number of permanent (hatched) and temporary (unshaded) desertions by mates. Other mates (heavy stippling) deserted after their young left the nest; b) total number of desertions by mates/number of mates present in the study area; c) number of permanent (hatched) and temporary (unshaded) desertions by territory-holders; d) total number of desertions by territory-holders/number of territory-holders in the study area.

pairs were breeding and feeding conditions were poor. Relationships between food supply and breeding are considered in Chapters 2 and 4.

Mates deserted independently of mating class (Table 3.5) since paired and breeding mates deserted at the same rate (χ^2_1 = 1,09; NS). In contrast, among territory-holders resident for longer than 100 days (Table 3.6) unpaired kites deserted more often than paired and breeding birds (χ^2_1 = 12,18; $p < 0,005$). Paired and breeding territory-holders resident longer than 100 days deserted equally often (χ^2_1 = 1,97; NS). Desertion by territory-holders resident for less than 100 days was independent of mating class (χ^2_2 = 0,77; NS).

Overall, territory-holders returned to their territories more often than mates (Tables 3.5 & 3.6; χ^2_1 = 4,83; $p < 0,05$). However, among kites resident for less than 100 days, territory-holders returned less frequently than mates (χ^2_1 = 4,23; $p < 0,05$ — corrected for continuity).

Although some short temporary desertions were probably not detected, many others evidently lasted for substantial periods. Those by mates lasted an average period of 35,7 days (S.D. = 16,1 days) and those by territory-holders 35,2 days (S.D. = 22,9 days). Unpaired territory-holders deserted for longer periods ($\bar{x}$ = 39,6 days; n = 23) than paired and breeding territory-holders ($\bar{x}$ = 25,2 days; n = 10; Mann Whitney U = 149; $p < 0,05$).

The longer a territory-holder was resident, the less often it deserted temporarily. There was a significant positive correlation between "occupancy" and "occupancy/number of temporary desertions" for nine territory-holders that deserted temporarily and were resident for longer than 200 days (Spearman's Rank r_9 = +0,77; $p < 0,025$).

Occupancy

The occupancy of mates and territory-holders directly affected the duration of pair bonds and territories respectively (see above). Analyses

TABLE 3.5 Frequencies of permanent (perm.) and temporary (temp.) desertion of territory by mates according to mating class and duration of occupation.

Period of occupation (days)	No. of birds	Mating class						Total		
		Paired			Breeding					
		Bird-days	No. desertions		Bird-days	No. desertions		Bird-days	No. desertions	
			Perm.	Temp.		Perm.	Temp.		Perm.	Temp.
1 - 100	43	806	25	6	600	13	3	1406	38	9
101 - 200	8	558	2	1	656	3	3	1214	5	4
201 - 300	2	222	2	0	282	0	0	504	2	0
301 - 400	2	529	0	2	192	0	0	721	0	2
401 - 500	1	314	1	0	91	0	0	405	1	0
Total	56	2429	30	9	1821	16	6	4250	46	15

TABLE 3.6 Frequency of permanent (perm.) and temporary (temp.) desertion by territory-holders according to mating class and duration of occupation.

Period of occupation (days)	No. of birds	Mating class									Total		
		Unpaired			Paired			Breeding					
		Bird-days	No. desertions		Bird-days	No. desertions		Bird-days	No. desertions		Bird-days	No. desertions	
			Perm.	Temp.		Perm.	Temp.		Perm.	Temp.		Perm.	Temp.
1 - 100	33	842	21	0	72	3	0	95	3	0	1009	27	0
101 - 200	11	1171	7	9	210	2	3	167	1	0	1548	10	12
201 - 300	5	554	2	4	260	0	1	417	1	0	1231	3	5
301 - 400	3	356	1	5	382	0	3	290	0	1	1028	1	9
401 - 500	3	859	0	4	332	0	0	218	0	0	1409	0	4
501 - 600	5	615	0	1	1173	0	1	1020	0	1	2808	0	3
Total	60	4397	31	23	2429	5	8	2207	5	2	9033	41	33

of mate and territory-holder occupancy in this section therefore also provide examinations of pair and territory durations.

Most mates were resident for short periods (Table 3.5); 33 (59%) stayed less than 50 days and only five (9%) more than 200 days. Unlike territory-holders (see below), mate occupancy was not directly related to the proportion of time spent breeding (Fig. 3.6 a). Instead, mates seemed to show two trends, one of intense breeding activity among short-term birds, and the other of little breeding activity by long residents. The second trend was shown by nine mates resident for longer than 150 days; there was a significant inverse correlation between "occupancy" and "percentage time breeding" (Spearman's Rank $r_9 = -0,75$; $p < 0,025$). However, the first trend was not confirmed by comparing the same variables for 47 mates resident for less than 150 days (Spearman's Rank $r_{47} = +0,20$; NS). In spite of these inconclusive tests, further data in Table 3.7 suggest that at least two groups of mates could be identified:

1) short to medium-term mates resident only while breeding or while prospects for breeding were probably favourable, and

2) long-term mates that spent little time breeding.

The contrast between these groups was emphasised by the performance of several mates. From November 1977 to February 1978 little breeding occurred (Chapter 4 — Fig. 4.6), yet several mates remained during this period (e.g. ♀♀ 28, 64, 68, 80 & 102) and then started breeding in March 1978. ♀68, in particular, showed how a mate changed groups. In $7\frac{1}{2}$ months before March 1978 she copulated only occasionally with ♂5. Then, on 21 March 1978 she deserted and paired with ♂49. They immediately started breeding and four days later started a nest which they abandoned after 10 days of building. They then copulated and displayed to nest sites sporadically, and after 16 days started a new nest. This nest, too, was later abandoned. On 5 May 1978 she was back with ♂5 and remained with him until at least 30

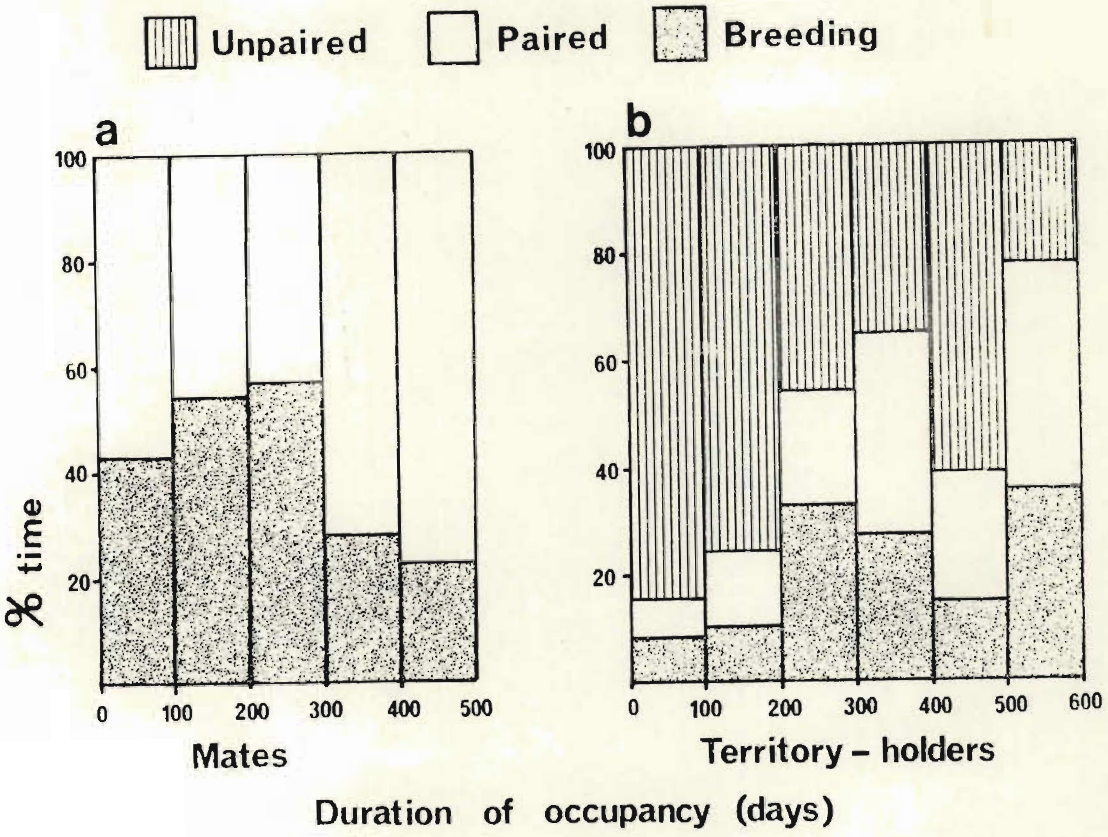


FIGURE 3.6 The percentage time spent by mates (a) and territory-holders (b) as unpaired, paired or breeding residents; calculated from data in Tables 3.5 & 3.6.

TABLE 3.7 Number of mates and percentage time of total occupancy spent breeding. Only mates resident for 30 days or longer are included.

% time breeding	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
No. of mates	6	2	3	3	3	2	3	1	3	6

September 1978. She spent 85% of her 54 days with ♂49 breeding, but only 9% of 367 days breeding with ♂5.

Like mates, most territory-holders were resident for short periods (Table 3.6). Forty-four territory-holders (73%) were resident for less than 200 days, but their residence comprised only 28% (2557 bird-days) of the total time spent by territory-holders. The remaining 16 birds (27%) spent 6476 bird-days (72%). Two territory-holders even occupied and vigorously defended territories for less than five days (see Fig. 3.2 & ♂46). Other territory-holders (♂♂ 5, 15 & 63) were resident for longer than the 579-day census period. There were many intermediates between these extremes and breeding was observed in all groups (Table 3.6; Fig. 3.6 b).

The longer a territory-holder was resident the greater the proportion of time it spent paired (Fig. 3.6 b). For data in Table 3.6, "occupancy" and "paired bird-days/unpaired bird-days" were positively correlated (Spearman's Rank $r_6 = +0{,}83$; $p < 0{,}025$). The same variables were positively related for 30 territory-holders resident for longer than 50 days and unpaired at some time (Spearman's Rank $r_{30} = +0{,}39$; $p < 0{,}025$). This sample excludes short-term residents where a few days either way would affect proportions markedly.

Long-term territory-holders also had a greater number of mates than short-term territory-holders (Table 3.8 a). Ten of the 12 territory-holders with more than one mate were resident for longer than 300 days. Table 3.8 b compares the occupancy of mates paired with territory-holders resident for different periods. These data show that mate occupancy varied greatly in relation to that of the territory-holders they paired with. Specifically, percentages in "X/Y(100)" indicate a) that mate occupancy was not proportionately related to the occupancy of their territory-holders, and b) that the greater proportion of time spent paired by long-term territory-holders was largely due to their greater number of mates, and not because

TABLE 3.8 a) Territory-holders grouped according to how long they were resident and the number of mates they paired with. b) Comparison of how long mates were resident while paired with territory-holders resident for different periods.

a) Occupancy and number of mates of territory-holders									b) Occupancy of mates and their territory-holders		
Period of occupation (days)	Number of mates						Total no. territory holders	Total no. mates	(X) mean occupancy of each territory holder (days)	(Y) mean occupancy of each mate (days)	X/Y (100)
	0	1	2	3	4	5					
1 - 100	21	8	0	1	0	0	30	11	31,8	15,2	48 %
101 - 200	2	8	1	0	0	0	11	10	140,9	37,9	27 %
201 - 300	1	4	0	0	0	0	5	4	246,2	136,2	55 %
301 - 400	0	1	0	2	0	0	3	7	342,7	45,0	13 %
401 - 500	0	0	0	1	1	1	3	12	469,7	45,8	10 %
501 - 600	0	0	2	2	1	0	5	14	561,8	145,1	26 %
Total no. kites	24	21	3	6	2	1	57	58			

their mates remained for longer periods.

The longer a territory-holder was resident the greater the proportion of time it spent breeding (Fig. 3.6 b). "Occupancy" and "breeding bird-days/non-breeding bird-days" from Table 3.6 were positively related (Spearman's Rank $r_6 = +0,77$; $p < 0,05$). This relationship was verified for 22 territory-holders that either arrived and were resident for more than 50 days before deserting, or were resident for longer than 200 days (Spearman's Rank $r_{22} = +0,495$; $p < 0,025$). This test excludes kites resident for shorter periods and those already breeding when the study started.

Since kites abandoned territories when food supply was poor (Table 3.4), I expected hunting success to be directly related to occupancy. Tables 3.8 and 3.9 compare the hunting success of mates and territory-holders resident for different periods, while Table 3.10 compares the success of territory-holders that deserted at various frequencies. The few significant differences in these Tables do not support the expected trends, suggesting instead that short-term residents had better hunting success than other birds.

Population dynamics

In 38 half-month counts population size varied between 19 and 35 individuals with a mean of 26,0 kites (S.D. = 4,2 kites) (Fig. 3.7). The numbers of paired ($\bar{x} = 17,6$; S.D. = 4.2; range 10-28 kites) and breeding ($\bar{x} = 9,4$; S.D. = 5.2; range 0-20 kites) kites present each half-month also varied substantially. There was an average of 17,1 territory-holders in the study area (S.D. = 2,8; range 12-22). There were 124 arrivals and 135 desertions during the study, or an average 3,3 new birds and 3,6 desertions each half-month. In a mean population of 26 kites, therefore, about 13% of residents were new and 14% deserted

TABLE 3.9 Hunting success of mates resident for less than, or more than 100 days. See Chapter 2, p. 16 for explanation of hunting terms.

Occupancy (days)	Perched-hunting			Hovering			
	Time observed hunting (min)	Minutes/ all strikes	Minutes/ kill	Time observed hunting (min)	Minutes/ all strikes	Minutes/ kill	No. hovers/ descent (no. descents)
1 - 100	395	32,9	131,7	182	13,0	22,7	5,8 (71)
101 - 500	1978	21,5	94,2	541	21,6	60,1	6,8 (130)
Difference		N.S.	N.S.		N.S.	$p < 0,05$	N.S.

TABLE 3.10 Hunting success of territory-holders resident for different periods. See Chapter 2, p. 16 for explanation of hunting terms.

Occupancy group (days)	Perched-hunting			Hovering			
	Minutes Observed	Min./ all strikes	Min./ kill	Minutes observed	Min./ all strikes	Min./ kill	Hovers/ descent (no. descents)
1 - 150	606	12,6[c]	60,6[a]	332	9,2	30,2	6,94 (77)
151 - 300	1262	21,8[c]	157,7	297	10,6[d]	59,4[b]	7,88 (26)
301 - 500	1309	30,4	145,4[a]	565	9,6	29,7[b]	7,95[e] (155)
501 - 600	2325	28,3	178,8	625	7,8[d]	36,8	6,40[e] (165)

[aa] $p < 0,05$; [bb] N.S.; [cc] $p < 0,005$; [dd] N.S.; [ee] N.S.

TABLE 3.11 Hunting success of 16 territory-holders resident for more than 200 days that either never deserted or deserted up to four times. See Chapter 2, p.16 for explanation of hunting terms.

Number of deserions	Number kites	Perched-hunting		Hovering	
		Minutes observed	Minutes/ kill	Minutes observed	Minutes/ kill
0	7	2692	168,2[ab]	788	35,8[e]
1-2	5	1068	89,0[ac]	360	25,7[de]
3-4	4	853	284,3[bc]	239	47,8[d]

[aa] $p < 0,1$; [bb] N.S.; [cc] $p < 0,1$; [dd] N.S.; [ee] N.S.

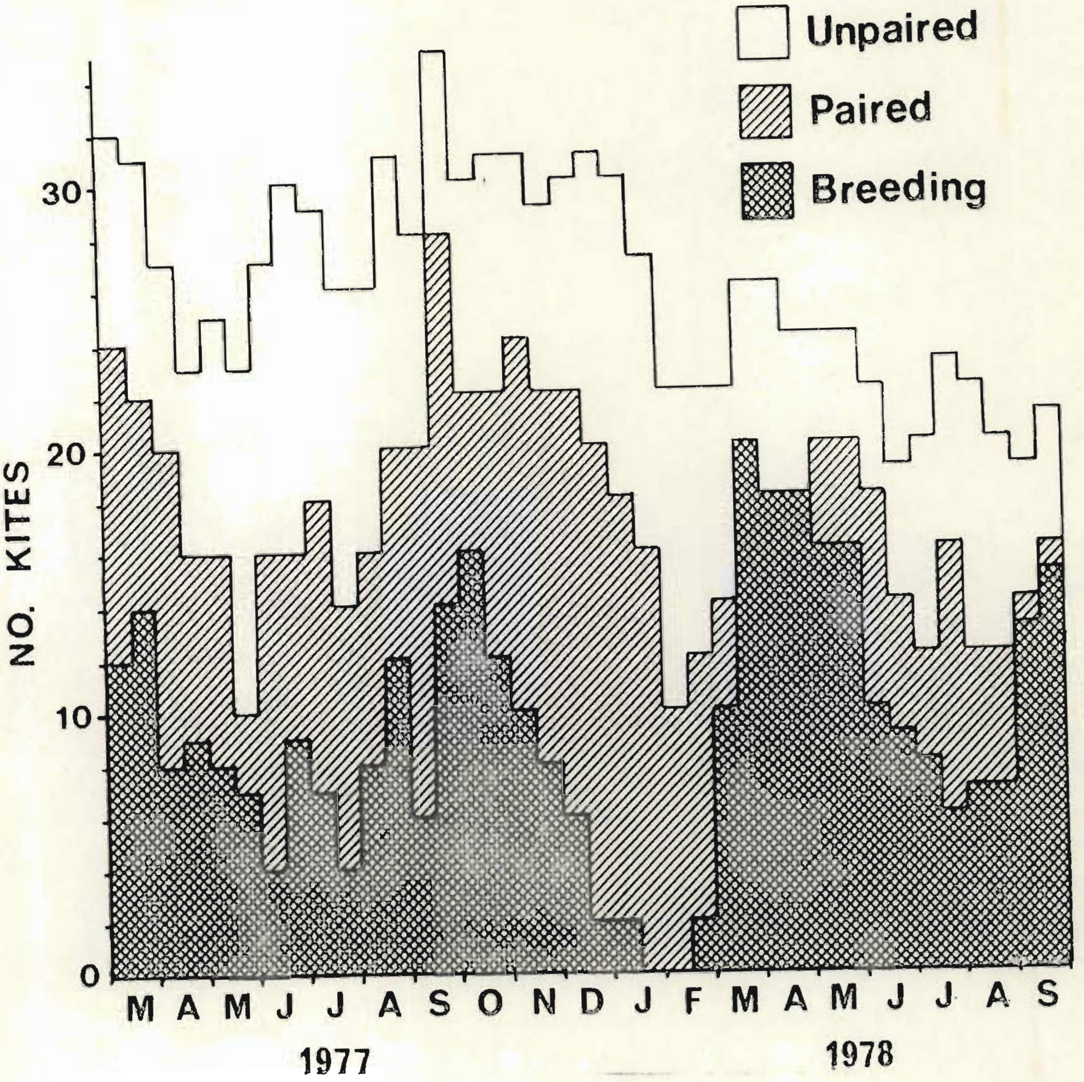


FIGURE 3.7 Half-monthly counts showing the total number of kites resident and the number of kites in each mating class.

each half-month. These rates varied with more arrivals and desertions in 1977 than in 1978 (Figs. 3.4 & 3.5). In 1977 up to 60% of kites resident during a particular half-month had disappeared three months later (Fig. 3.8).

In 1978 the population was generally smaller and the proportion of paired and breeding kites greater than in 1977 (Fig. 3.7). Factors affecting increases and decreases in population size have been considered previously (Table 3.4). However, neither the percentage of the population paired (Spearman's Rank $r_{19} = +0{,}15$; NS) nor the percentage breeding (Spearman's Rank $r_{19} = -0{,}29$; NS) was significantly related to population size. Significant correlations between these variables were found for certain periods only during the study. For example, "population size" and "percentage of kites paired" were positively related between March 1977 and February 1978 (Spearman's Rank $r_{12} = +0{,}80$; $p < 0{,}005$).

Population size and food supply were not positively correlated. Instead, they may have varied inversely (Spearman's Rank $r_{17} = -0{,}38$; $p < 0{,}1$) with the population lowest when food was most abundant.

Movements

Ninety nomads were seen in the study area between May 1977 and March 1978 (17 months). Those that intruded on occupied territories were rapidly repulsed (Chapter 5). I observed one nomad cross three territories while flying a distance of 6 km.

Sixteen of the nomads were marked and three of these were seen in the same place more than once. One nomad was caught in area J (Fig. 3.1 a) on 22 February, resighted after 19 days and again 30 days later in area H, recaptured eight days later in area J, and finally resighted four days later in area H. These records suggest that movements by nomads were not random.

An index of the number of sightings of nomads each month (Fig. 3.9)

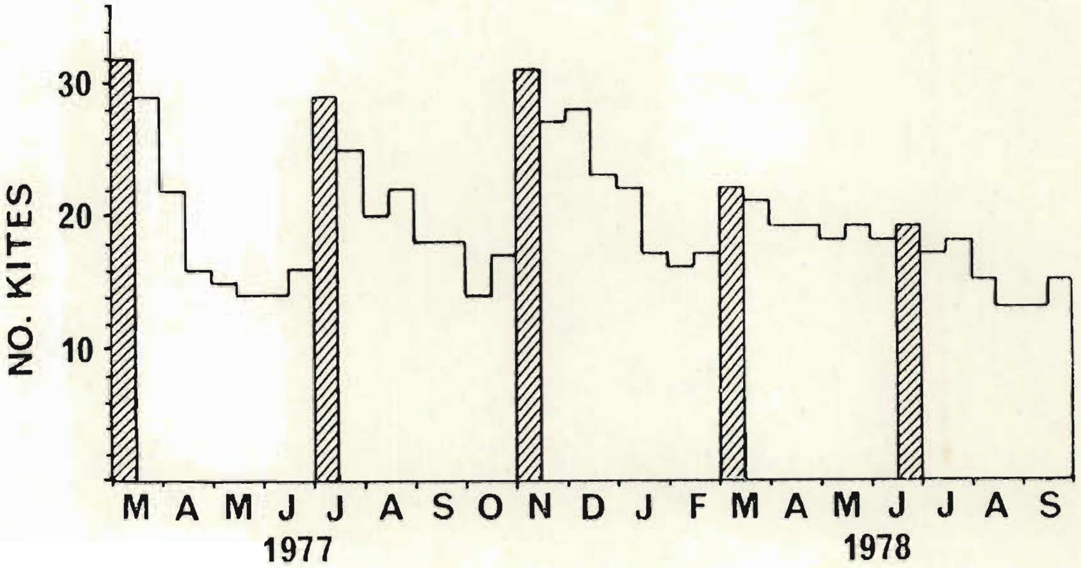


FIGURE 3.8 The number of residents present in the study area during certain half-months (hatched) and the numbers of these residents still present during subsequent half-months (unshaded).

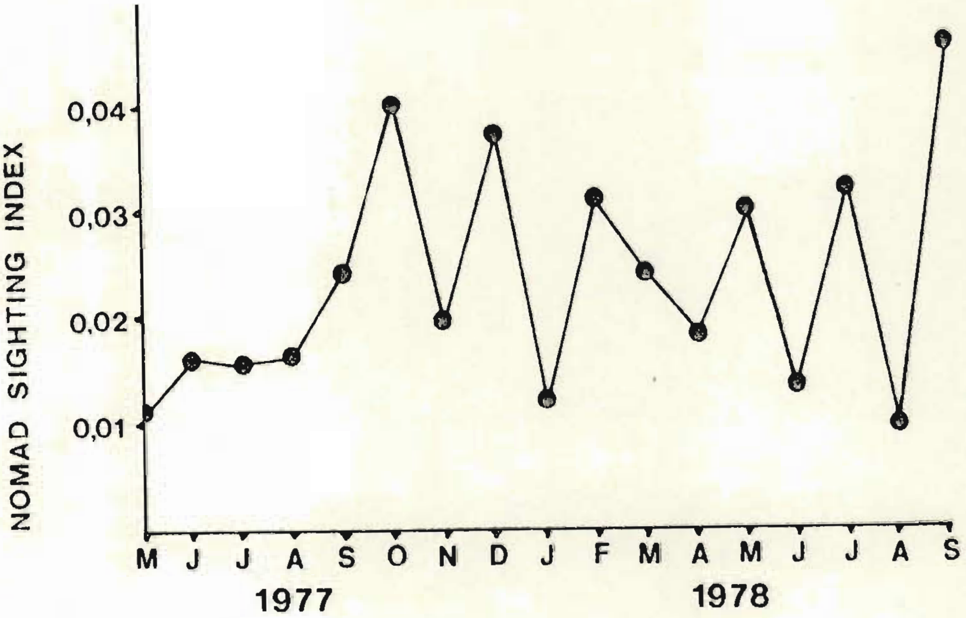


FIGURE 3.9 An index of the number of nomads sighted each month in the study area; index = number of sightings of nomads/number of sightings of residents.

was inversely correlated with frequencies of mate and territory-holder desertions (Fig. 3.5 b & d) (Spearman's Rank $r_{17} = -0{,}57$; $p < 0{,}01$; and $-0{,}55$; $p < 0{,}025$ respectively). Most nomads were therefore seen in months when few residents were deserting. The nomad index was not related to indices (as in Table 3.4) of new mates, new territory-holders, pairs copulating, pairs breeding, food supply or population size (Fig. 3.7) (Spearman's Rank $r_{17} = +0{,}24$; $-0{,}29$; $+0{,}30$; $+0{,}22$; $+0{,}26$; and $+0{,}11$ respectively). In most cases, however, significance levels were close to $p < 0{,}1$, suggesting that the presence of most nomads was positively related to good feeding and breeding conditions.

The weights of nomads were significantly lower than those of all other kites (Chapter 6 — Table 6.3). Three kites were weighed both as residents and nomads. ♂78 weighed 255 and 271 g as a resident and 212 g as a nomad. ♂89 weighed 246 g as a resident and 185 g as a nomad. The third kite was ♀6 (see Mortality, p. 119).

Deserting territory-holders usually became nomads. Ten territory-holders were seen as nomads before or after being residents, and none of the territory-holders occupied more than one territory during the study. This suggests that deserting territory-holders were unable to establish new territories rapidly and therefore spent a considerable time as nomads. In contrast, many deserting mates may not have become nomads. Only two mates were seen as nomads and, after deserting, seven mates moved immediately to other territories (♀♀ 98 twice, 68 twice, 12, 36 & 88). These seven desertions form 11,5% of all desertions by mates, and other mates probably paired immediately on territories outside the study area. The mates that made these seven movements may have known the positions of unpaired territory-holders since the territories they moved between were very close to each other (see Appendix 3.1).

Table 3.12 shows distances between ringing and recapture or recovery

TABLE 3.12 The number of movements by kites according to the distance between capture and recapture or resighting. Colour marked kites resighted in the Settlers study area are not included in these data.

Distance (km)	< 2	2 - 10	11 - 30	31 - 100	> 100	Total
No. of records	22	21	13	9	8	73

for 73 kites. Distances of less than 2 km probably indicate that the kites were recorded again on the same territories. Long distance movements are shown in Figure 3.10. Most movements were by kites ringed as adults or sub-adults; only three of the kites in Table 3.12 were ringed as nestlings and two as possible flying young not yet independent.

Mortality

Three adults (♂44, ♀12 & ♀30xx) were found dead and a fourth (♂4) probably died (see below). These four birds represent about 4% of the 102 residents observed over 19 months. Since some dead kites were probably not found, a 5-10% mortality rate per year among adult residents may be a reasonable estimate. Nomads probably suffered a higher mortality rate because of their poor condition. Seven (26%) of 27 young birds died between leaving the nest and becoming independent (Chapter 4, p. 170).

Several causes of mortality were identified. During and before the Settlers study, six kites were found dead after being hooked or spiked by *Acacia* thorns. ♀30xx, found dead on her nest, had several punctures through her dorsal thoracic wall into her lungs. Kites were seen struggling to free themselves from thorny thickets about 25 times. "Branching" chicks often clambered into the thicket of the nest tree and became entangled.

One observation suggested how poor body condition could result in death. When first caught as a resident, ♀6 weighed 273 g. Three days later it was recaptured and then weighed 231 g. Twelve days after this it was seen as a nomad in areas J and K (see Fig. 3.1 a) at 07s00 and 10s35 respectively. The bird was hunting intensively and at 10s55 made a strike into a road verge. There, it became trapped in the clinging inflorescence of the grass *Setaria verticillata*. After several minutes I freed the bird, which then weighed 209 g. Its flight was weak and laboured, and its prospects for further survival seemed poor. There was a 23% decrease in weight between initial and final capture.

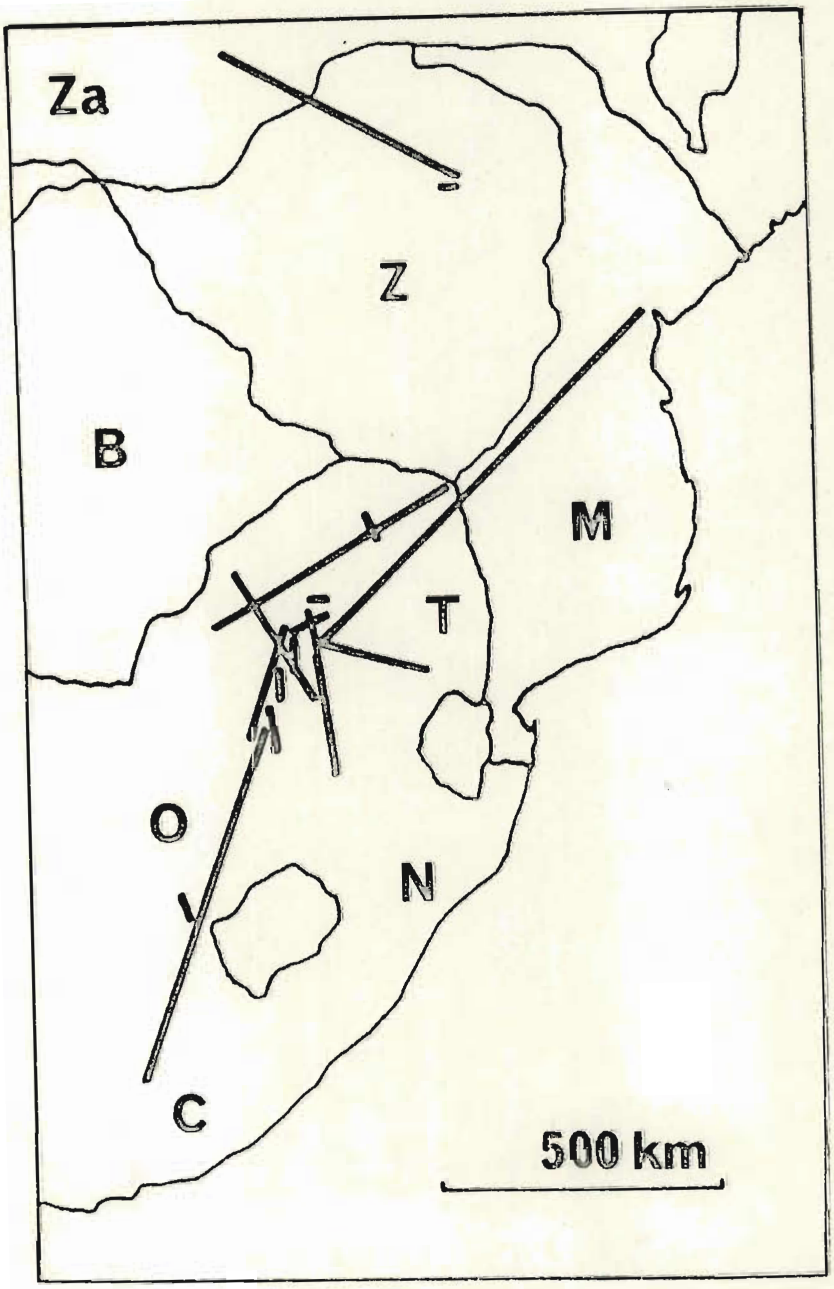


FIGURE 3.10 Movements of >30 km of kites in southern Africa, as shown by ringing recoveries; B - Botswana, C - Cape, M - Moçambique, N - Natal, O - Orange Free State, T - Transvaal, Za - Zambia, Z - Zimbabwe.

Cases are known of predation of kites by Tawny Eagles Aquila rapax (A.C. Kemp pers. comm.) and Spotted Eagle Owls Bubo africanus (P. Stidolph in litt.). The remains of ♂44 were found eaten below its roost tree, but whether the kite had been caught or scavenged by a small carnivore was unknown. A.C. Kemp (pers. comm.) recorded a similar death of a roosting male. Lanners Falco biarmicus often attacked flying chicks, but adult kites usually chased Lanners passing through their territories (Chapter 5, p. 218).

The following injuries were recorded on kites caught for ringing and those found dead: a deformed lower mandible, a 10-mm hole in the patagium, five adjacent secondaries missing, a fractured but healed radius, and a fractured tarsometatarsus. The last injury was found on a flying chick of ♂44. This chick was found dead below the same roost two days after I had found ♂44 dead. The chick had a very full crop the day before it died, suggesting that it did not starve.

Three kites were caught with growths on their gapes. A similar growth found on a dead bird (caught in a thorn tree) was malignant (Onderstepoort Veterinary Research Station report). ♂4 probably died from some other disease. During the last week before disappearing it often perched with drooped wings and closed eyes. It was also abnormally tame compared with its previous reactions.

Other causes of mortality were man-induced. Many specimens now in museums were found killed by motor vehicles on roads. Kites are probably most susceptible to collision during strong winds and while carrying heavy prey items, since their flight is laboured and low over the ground. Some farmers in the Settlers area claimed that kites took poultry. Many kites are presumably killed for this reason, especially in heavily populated areas. At Settlers, however, all farmers were aware of the project on kites and I doubt whether any were shot during this study. Although pesticides were used intensively on crops in the Springbok Flats, I found no evidence of mortality or reduced fecundity. Most of the pesticides were organophosphorus compounds that do not persist as active poisons (Newton (1979). It is possible that kites living along busy roads accumulate substantial amounts of lead. High levels of lead from exhaust fumes are known to occur in rodents and these may well build up in kites.

DISCUSSION

Results in this chapter showed that kites used several predominant and other subsidiary strategies in their social and spatial organization. The discussion below will focus on the significance of these tactics and suggest why certain were more important than others. The array of patterns observed at Settlers, however, did not include all the behavioural strategies; several others have been reported in the literature. These will be considered in an attempt to identify the range of responses to the variety of feeding conditions kites may encounter.

Male strategies

Males normally established and maintained occupancy of territories (Table 3.1 & 3.2). Similar behaviour has been recorded for other raptors, with males establishing territories before females arrived, being more attached to territories while not breeding and returning more frequently to the same territories each breeding season. These features have been recorded in the following species: Red Kite Milvus milvus, Ayres' Eagle Hieraaetus ayresii, Hen Harrier Circus cyaneus, Montagu's Harrier C. pygargus, Marsh Harrier C. aeruginosus, Swainson's Hawk Buteo swainsonii, Osprey Pandion haliaetus, Peregrine Falco peregrinus, Gyrfalcon F. rusticolus, Prairie Falcon F. mexicanus, American Kestrel F. sparverius, Greater Kestrel F. rupicoloides, European Kestrel F. tinnunculus and Merlin F. columbarius (Brown & Davey 1978; Enderson 1960; Green 1976;

A.C. Kemp pers. comm.; Newton 1979; Webster 1944). Males of these species and Blackshouldered Kites feed their females while breeding (Chapter 4). By establishing territories early, males probably gain more experience of the best hunting areas and such experience probably enhances their ability t provide sufficient food for the females and young. A good food supply may also allow the pair to start breeding immediately after pair formation; pair starting to breed earliest usually have the best success (Drent & Daan 1980; Murton & Westwood 1977; Chapter 4 — Table 4.6). It may therefore be significant that in the two pairs formed by males joining resident females (♀♀ 12 & 28), breeding started only after delays of 12 and 15 weeks (Appendix 3.1).

The idea that males establish territories to gain hunting experience of food sources cannot apply to European Sparrowhawks *Accipiter nisus*, in which the females usually establish territories, but their mates supply them with prey (Moritz & Vauk 1976; Newton 1973). However, the choice of nest tree seems especially important for Sparrowhawks (Newton *et al*. 1979); the femal being restricted to the nest area while breeding, may therefore select the area best suited to her role in tending and protecting the nest.

Some male kites apparently arrived with females and established territories (Table 3.2). Similar behaviour has been noted in Pallid Harrier *C. macrourus*, Black Kites *Milvus migrans*, Peregrines and American Kestrels (Balgooyen 1976; Cade 1960; Desai & Malhotra 1979; Lundevall & Rosenberg 1955). Some of these records, and those for kites, may be inaccurate in failing to recognise small differences in the arrival times of males and females. Nevertheless, the observations do show that males could occasionally pair without long periods of previous residence. It would seem more efficient for males and females to search for territories independently, and for either to pair with any appropriate unpaired residents they might find. It might also be important for lone males or females to pair with residents that have already tested the feeding quality of their territories.

Several observations indicated that males occupied territories for as long as feeding conditions permitted. Firstly, males usually deserted when their food supply was poorest (Table 3.4). Secondly, deserting males became nomads and, since nomads were in poorer condition than residents, i is probable that food shortages forced males into this condition. Thirdly, sustained occupancy was associated with increasing social success in pairing and breeding (Fig. 3.6 b), these in turn being related to good food supply (Chapters 2 & 4). Finally, deserted territories were normally occupied quickly (see Dispersion p. 92) in contrast to several smaller areas that never held kites (Fig. 3.1 a). These vacant areas consisted largely of cultivated fields which supported few small mammals (Chapter 2).

However, in contrast to these observations, data on hunting success (Table 3.10 & 3.11) suggested that short-term males had at least equal, if not better feeding conditions than longer-term residents. One explanation may involve the positive correlation between occupancy and territory size (see Dispersion, p. 97). Long-term males might have been able to counter local food shortages by hunting elsewhere on their larger territories. Thei territories would thus have provided more stable feeding conditions than those of short-term residents. Short-lived territories may only have been occupied during periods of high prey availability. A further explanation is that short-term males formed part of a nomadic group of kites that sought mainly rich, eruptive food sources (see Overall strategies, p. 133).

The rapid re-occupation of deserted territories and the frequent sightings of nomadic males suggested that territories with good feeding conditions were at a premium. In spite of this, males evidently also selected territories since some areas remained vacant, the movements of nomads were not random, and males visited areas they later occupied (see Dispersion, p. 95 and Movements, p. 114). These observations suggest that nomadic males may have assessed the feeding conditions of several territorie before settling. The indiscriminate occupation of vacant areas would have been inefficient since there were probably more unsuitable than suitable vacant areas.

Temporary absences may have been "exploratory" trips for males searchin for better territories. Similar trips with probably the same function have been noted for Prairie Warblers *Dendroica discolor* (Nolan 1978). Males migh have searched for territories more attractive to females and/or with better feeding conditions. Both factors would be consistent with the observation that unpaired males deserted more often than paired or breeding males (Table 3.6). Alternatively, unpaired males (with poorer food supply than others - Chapter 2 — Table 2.13) may have simply deserted as a result of food shortag and then returned after failing to find other suitable territories.

Female strategies

The behaviour of males and females probably differed mainly because females were less restricted spatially than males. An excess of males in the population meant that females had greater opportunities for settling than males. Thus, they spent shorter periods on each territory, deserte more often, returned to territories less frequently (Table 3.5 & 3.6), and spent less time as nomads than males.

Females seldom established territories and probably did so only when foo supply was poor. In such conditions breeding was not possible and females could avoid competing with males on the same territories. If prey later became abundant, lone female residents could attract males and attempt breeding. The five females (♀♀12, 28, 62, 80 and 86) that maintained territories alone for long periods all paired when other pairs were starting to breed and feeding conditions were improving.

The presence of paired females appeared to be related to breeding and females probably moved between males in search of the best breeding prospect These conclusions are based on several observations. Firstly, most female arrived and paired when the greatest proportion of pairs were starting to breed (Table 3.4). The link between pair formation and breeding was, howev not invariable; some long-established pairs started breeding (e.g. ♂63, ♀102; ♂83, ♀64) and some recently-established pairs did not attempt breeding (e.g. ♂34, ♀76; ♂30, ♀30x). Secondly, rapid movements by females between males in the study area seemed to be associated with breeding (♀♀ 68; 88; 9 In each case the female had had poor success with one male and immediately attempted breeding with a new mate. Thirdly, females were paired only when diurnal prey was abundant (Chapter 2, p.58), this being a probable prerequisite for breeding (Chapter 4). Fourthly, females probably deserted when feeding conditions became too poor for breeding although adequate for their own energy requirements and survival. Deserted males remaining resident showed there was still sufficient food to support non-breeding birds. Finally, females usually deserted once their chicks had left the nest, and then probably paired and attempted breeding with new males (Chapter 4. p. 167).

The correlation between pair formation and the start of breeding suggests that they were initiated by similar factors. Breeding usually started when rodent populations were breeding (Chapter 4. p. 178). This, with the greater proportion of diurnal prey taken by paired and breeding kites, suggests that females may have paired with males when their diurnal rodent prey was breeding. Table 3.4 shows that the arrival of females was not related to food abundance.

Presumably females did not pair indiscriminately but selected the territories of certain males above others. Most mates remained resident for some time, suggesting that their initial assessment of feeding conditio was reasonable; only six (11%) mates paired for less than one week but some shorter term mates may have been missed. One way in which females could have tested feeding quality was on the basis of time and energy expended by males in display (see p. 90 and Chapter 5, p. 208). Well-fed males could have spent much time and energy in advertisement and display, while hungry males on poor territories could not have performed as well. Such criteria would have reflected both the hunting ability of males and the abundance of prey.

I have suggested that there were two groups of mates (see p. 105), one that spent most of their time breeding, while the other spent long periods as non-breeding residents. There were many intermediates (Table 3.5 & 3.7) and the groups may be better considered as extremes. However, the behaviour of long term mates appeared distinctive in that, against expectations, they did not go off in search of males on other territories. To this group may be added females that spent long periods as unpaired residents, since they too could have searched elsewhere for breeding prospects. Possibly, long term female residents were caught in a "bind", with feeding conditions good but not suitable to attempt breeding. Evidence for this comes from the better hunting success and greater proportion of diurnal prey of paired versus unpaired kites (Chapter 2). (The feeding data for paired kites were obtained largely from those long-term males and females that were observed often.)

Short-term mates probably had better hunting success than longer residents (Table 3.9). This unexpected result is hard to explain, but, as with males, may suggest that short-term residents remained paired only under conditions of above-average food supply (see Overall strategies, p. 134).

Sex ratio and mating system

The ratio of males to females during the study was about 3 : 2. This ratio may not have been representative of kites in general, since weight data for 816 kites in Chapter 6 (Table 6.3) indicate roughly equal numbers or only slightly more males than females. If the ratio were skewed substantially either way, one would expect the population mean to be closer to the mean weight of either sex. Sex ratios probably also varied according to food supply. During lean periods the majority of residents would probably have been males as unpaired residents. With abundant prey, and most of the residents paired, the ratio would have approached parity.

Successively polyandrous females deserting dependent young and pairing wi new males, could have bred three times each year (Chapter 4, p. 171). The parental investment (<u>sensu</u> Trivers 1972) of males was greater than that of females because they spent longer feeding chicks (Chapter 4, p. 171). Evidently, one parent could care for the flying young as effectively as two without greatly jeopardizing the chances of success. Furthermore, any reduction in success caused by one parent deserting was presumably balanced by the advantages (for the female) of another breeding attempt. With this background, it is of interest to examine the relationships between female desertion, the site tenacity of males, and the greater number of males than females. Three hypotheses are suggested.

Traditionally, sex ratios were thought to determine mating systems (Lack 1968) and this could explain why females deserted. With a surplus of males, females could pair with those males that had remained unpaired. If females deserted, males were obliged to remain and complete the breeding effort, since, had both birds deserted, the attempt would have been a comple failure. In this view, then, the sex ratio determined that females could desert and that males in turn had to remain resident.

Alternatively, selection could primarily have favoured the continued occupation of males (Lundberg 1979). Since territories with good feeding conditions were in short supply (see <u>Male strategies</u>, p. 124), breeding males good territories may seldom have found better alternatives. Males may also have remained resident because they hunted most efficiently on the territories where they had most experience. Sex ratios and repeated breeding by females may therefore have been largely incidental; females deserted because only one bird could leave, so selection favoured continued male occupation. Interestingly, high levels of paternal care in most animals are associated with male territoriality (Ridley 1978).

A third explanation involves Trivers' (1972) model of adaptive differential mortality of males and females. He argues that increasing paternal care leads to decreasing male, and increasing female mortality. Each male has a limited amount of reproductive effort (measured in time and energy), and this may be portioned in various ways, *e.g.* in male-male competition, female attraction, or paternal care of the young. Since the male's energy is limited, an increase in one form of reproductive effort will lead to a reduction in another form. Thus an increase in paternal care will be linked with a decrease in male-male competition, and, therefore, male mortality. An increase in male care for the young will also lead to increased female-female competition and female mortality, since females will compete for caring males. Successful females that pair with males showing a high degree of paternal care, may then be free to desert and breed with surplus males. Alternatively, such females could simply stop their involvement in breeding and save their energy.

None of the data assembled in this study is adequate to test the three hypotheses. However, Trivers' (1972) model may not be stable. Low male mortality rates would eventually lead to high male densities, reduced female-female competition, and lower female mortality. Increasing male densities would also lead to severe competition and higher mortality rates. This was probably the case at Settlers where males were apparently often unable to secure suitable territories.

The suggestion that either the skewed sex ratio or continued male occupat could provide females with the opportunity to desert may be equally probable.

However, deserting females could attempt breeding again only if a) there were surplus males, and b) feeding conditions were suitable for breeding again. This latter aspect may be the one most relevant to kites since unpredictable changes in rodent densities may often have provided suitable conditions for second or third broods (Chapter 4). Temporal changes in food supply that allow females to breed again may predispose birds to polyandry (Graul *et al.* 1977), but relatively few raptors exploit prey populations that show the necessary unpredictable increases or sustained high densities.

Territoriality

The poorer feeding conditions of nomads and desertion by residents durin lean periods suggested that territorial kites benefited by defending food resources. The defence of large prey populations may also have helped attract mates, ensure against local food shortages, and prevent other kites from breeding. Local rodent populations may have decreased rapidly as a result of fire, floods, grazing or harvesting (Chapter 2, p. 75). Verner (1977) has suggested that large territories may prevent other kites from becoming residents and breeding. This would give territorial birds the advantage of making relatively greater genetic contributions to future generations (but see Tullock 1979).

In most animals territory size and food supply vary inversely (Ebersole 1980; Hixon 1980). However, kite territories became larger while prey density increased during this study (Fig. 3.3 & Chapter 2 — Fig. 2.7). Similar trends are reported for other birds of prey and carnivores defending large territories (Brown & Watson 1964; Lockie 1966; Southern & Lowe 1968). This suggests that large predators maximise the area they defend and ensure greater reserves for periods of food scarcity (Hixon 1980). The upper limit to territory size are probably largely determined by energy constraints involved in defence against competitors.

However, very high densities of kites have been reported at rich food sources (see Overall Strategies, p. 133), suggesting that at some threshold of prey density, territoriality, as observed at Settlers, breaks down. During a period of escalating food supply resident kites would presumably attempt to prevent new birds from establishing territories. Newton et al. (1977) suggest that aggression may be reduced during periods of high prey density. Alternatively, a great number of invading birds attracted to a rich food source may make it energetically impossible for residents to defend large territories. Residents may then either cease defending territories or reduce the size of the defended area. Unfortunately, no information is available on the spatial behaviour of kites during rodent plagues.

Overall strategies

Most studies of birds have considered the social and spatial organisatio of species, or at least populations, as characteristic and fixed. Even genera and families are often said to have set mating systems and patterns of dispersion (Lack 1968). While such generalisations may sometimes be valid, many studies of marked birds now show a high degree of individual variability in these patterns of behaviour (Birkhead 1981; Emlen 1978; Hamerstrom 1969; Newton & Marquiss 1976; Nolan 1978). This is true even of Holarctic birds that migrate, establish territories and breed at set times of the year. This study has shown a similar high degree of individual variation in the behaviour of kites. For example, kites varied in their occupancy as residents and in the number of times they left and established territories (Table 3.5 & 3.6), males and females sometimes swopped roles (Table 3.1), not all females deserted fledged young to pair with other males (Chapter 4, p. 167), and kites roosted either communally or alone (Chapter 5, p. 223).

My impression of social and spatial behaviour at Settlers was one of relative, or at least attempted, stability. Kites, especially those males

TABLE 3.13 Two sets of behavioural strategies adopted by kites and the environmental conditions to which they are probably related. See text for further explanation.

"Stable" behaviour	"Unstable" behaviour
1. Males and females resident for long periods	1. Males and females resident for short periods
2. Little movement by kites	2. Extensive and frequent movements
3. Kites occupy large territories	3. If any areas are defended, territories are small
4. Residents roost alone on their territories	4. Kites form large communal roosts
5. Population density low and relatively constant	5. Numbers of kites fluctuate widely
1. Kites feed on several rodent species	1. Only one or two rodent species available
2. Prey availability fluctuates little	2. Erratic and marked changes in prey availability
3. High and seasonally predictable rainfall	3. Low and unpredictable rainfall

that spent a high proportion of their time paired and breeding, were dispersed on large territories and showed considerable site-tenacity. Many females, too, probably remained as long as feeding and breeding conditions were favourable. However, the majority of residents were short-term territory-holders and mates and their performance did not seem to depend on prey availability only. Their transience rather seemed to indicate a general nomadic pattern of behaviour. Several observations (see below) suggest that itinerancy may be regular and associated with eruptiveness and sociability. Indeed, it seems that kites show two main sets of life history tactics, one described as "stable" and the other as "unstable" (Table 3.13). The "stable" strategies were typical of the behaviour of many kites at Settlers, while "unstable" behaviour is shown vividly by the records of several observers.

In August 1975 J. Collett (in litt.) counted 200-300 kites hunting over 80 ha of cultivated land in the Eastern Cape (an equivalent density in the Settlers study area would have involved 16 000-25 000 birds). The kites arrived together, stayed for a week, and suddenly departed. This area normally held two pairs of kites. A high density of Rhabdomys pumilio and another rodent (probably Praomys natalensis) was noted at the time. Similar eruptions of kites during rodent plagues have been observed in the Transvaal (Malherbe 1963; A.C. Kemp pers. comm.; Skead 1974), Zimbabwe (J. Cooper in litt.), and Senegal (Morel & Poulet 1976). Eruptiveness has also been described in India (Brown & Amadon 1968).

While many other raptors also mass at sporadic food sources (Brooke et al. 1972; Galushin 1974; Newton 1979), most occupy large exclusive territories when breeding. Kites differ from these species in also breeding at high densities. Malherbe (1963, pers. comm.) found at least eight pairs of kites breeding in an area of about 6 km^2 that usually held one pair. Vernon (SAOS nest record cards) and Madden (1977) found occupied nests 140 and 200 m apart respectively. A.C. Kemp (pers. comm.) found three active nests in an area with a 200 m radius. These nest densities were far greater than any observed at Settlers, where the nearest active nests were about 900 m apart.

Communal roosting may be another aspect of nomadic and eruptive behaviour since these roosts probably serve as "information centres" (Ward & Zahavi 1973). Kites usually formed communal roosts when food supply was poor at Settlers (Chapter 5 — Table 5.2) and information from these roosts may have helped kites in moving to more profitable feeding areas (see Chapter 5, p. 228).

The behaviour patterns described as "stable" and "unstable" probably depend on different feeding conditions (Table 3.13) similar to those described for other nomadic and site-tenacious birds (Andersson 1980; Galushin 1974; Maclean 1973; Newton 1972, 1979; Serventy 1971). Populations of several rodents (mainly Praomys natalensis, Tatera leucogaster and Lemniscomys griselda) fluctuate markedly and unpredictably in southern Africa (Choate 1972; Coetzee 1965, 1967; van der Merwe & Keogh 1970; Wilson 1970; Chapter 2, p. 74). Nomadic kites probably gather at plagues of these species, while stable residents depend on rodent populations that remain relatively even. Long-term residents on large territories may also be able to survive on lower rodent densities than nomadic kites, since longer residents would have the opportunity to gain experience of the best feeding areas. Nomadic birds may have to depend on more readily available prey. The number of available prey species may also influence the feeding conditions of kites. Those feeding on one or two prey species may experience greater changes in food supply than those that can depend on several different sources of prey. Unpaired kites at Settlers demonstrated this by preying largely on Praomys natalensis (Chapter 2 — Table 2.13) and being more erratic residents than other kites (Table 3.6). Paired and breeding kites caught roughly equal numbers of three rodent species and were stable residents for long periods.

The other three *Elanus* kites show close parallels to the behaviour of Blackshouldered Kites. All three species also feed mainly on rodents (Hobbs 1971; Hollands 1977; Klapste 1979; Meserve 1977; Parker 1971; Schlatter *et al*. 1980; Waian 1973). Whitetailed and Blackwinged Kites may roost communally and mass and breed at rich food sources, while at other times they defend large territories (Brown & Amadon 1968; Dixon *et al*. 1957; Hayward & MacFarlane 1971; Hobbs 1971; D.G.W. Hollands *in litt*.; Waian 1973). The Letterwinged Kite is an arid-zone species that has specialised on the kind of nomadism, eruptiveness and sociability sometimes shown by the other species. They appear always to move in flocks, roost communally, and breed in loose colonies (Beruldsen 1971; Hollands 1977; Parker 1971). The species breeds only during rodent plagues and great numbers apparently starve to death in the absence of high prey densities (Hollands 1979; Klapste 1979).

The variable behaviour patterns shown by *Elanus* kites appear to be unique among raptors. Newton's (1979) review of social and spatial behaviour indicates that most species are either stable residents or nomadic and communal. The only exceptions are those that may flock while not breeding; but most raptor species remain to be studied and other combinations of strategies probably await discovery. Interestingly, other small-mammal specialists such as the Buzzard *Buteo buteo* and European Kestrel *Falco tinnunculus* appear to be territorial and widely spaced residents (Cave 1968; Mebs 1964; Weir & Picozzi 1975).

The two sets of strategies in Table 3.13 show several features characteristic of *r*- and *K*-selection (Pianka 1970) and have been presented as contrasting with each other. However, they may only be opposite ends of a spectrum with many intermediate conditions. Certainly, prey populations are unlikely always to be either "erratic" or "stable" and kites probably show a range of responses to varying situations. Several other factors (for example mate, space and communal roost availability) may also affect behaviour, but no attempt can be made at this stage to assess their importance and interrelationships.

While factors in Table 3.13 may be at opposite ends of a spectrum, they are useful points of reference and show that kites use different patterns of behaviour to survive and breed under a variety of feeding conditions. Real (1980) has shown that animals facing uncertain conditions evolve diverse strategies. This would appear to be true of kites where the nature of rodent population dynamics is often unpredictable; densities may vary erratically or remain reasonably stable. Nomadic and sociable behaviour, as responses to erratic prey densities, probably evolved in fairly dry conditions where rainfall is unpredictable. Similar behaviour is shown by many arid-zone birds (Maclean 1973; Serventy 1971). Rodent breeding is strongly affected by rainfall and plant growth. (Perrin 1980; Taylor & Green 1976) and rodent densities are therefore likely to be erratic in dry areas. "Stable" strategies, in contrast, probably evolved in wetter areas where rainfall is more predictable and rodent densities show more regular and less drastic changes. The wet and dry conditions suggested here are probably both experienced by kites. The species occupies a wide range of habitats with varying rainfall regimes and, in southern Africa, wet and dry periods alternate about every ten years (Tyson & Dyer 1978). Thus the variety of rainfall regimes, both geographically and temporally, could be the ultimate factor favouring the evolution of diverse strategies in kites. If kites lived under dry conditions alone, they would probably show only the kind of behaviour seen in the highly nomadic and sociable Letterwinged Kite.

SUMMARY

Males usually established territories where females joined them as mates. Males occupied territories for longer periods than females who tended to move around between territorial males. There were always more males (average

60%) than females (average 40%) in the study area.

Territories were exclusive areas containing the nesting and hunting areas of residents. The number of territories decreased and mean territory size increased during the study from about 2,3 to 4,5 km^2. The size of a territory tended to increase in direct proportion to occupancy. Unpaired residents held smaller territories than other residents.

Males usually established territories when occupied areas fell vacant, and most females arrived to pair with males when most pairs started breeding. Both sexes abandoned territories when food supply was poor and few pairs were breeding.

Paired and breeding females deserted equally often, but unpaired males deserted more frequently than paired or breeding males. Males tended to abandon territories temporarily more often than females. Both males and females deserted temporarily for average periods of 35 days but unpaired males were away from their territories for longer than other males.

Most kites (86%) were resident for short periods of less than 100 days. Females tended to spend either most or very little of their time breeding, while the longer males were resident, the greater was the proportion of their time spent paired and breeding. Long-term male residents also had more mates during the study than short-term males. Kites that spent short periods on territories may have had better hunting success than longer-term residents.

Population size varied between 19 and 35 kites (average 26 kites). About 13% of the population was replaced each half-month.

Nomads tended to visit the study area when feeding and breeding conditions were good. After deserting, males probably became nomads while females probably moved immediately to new territories.

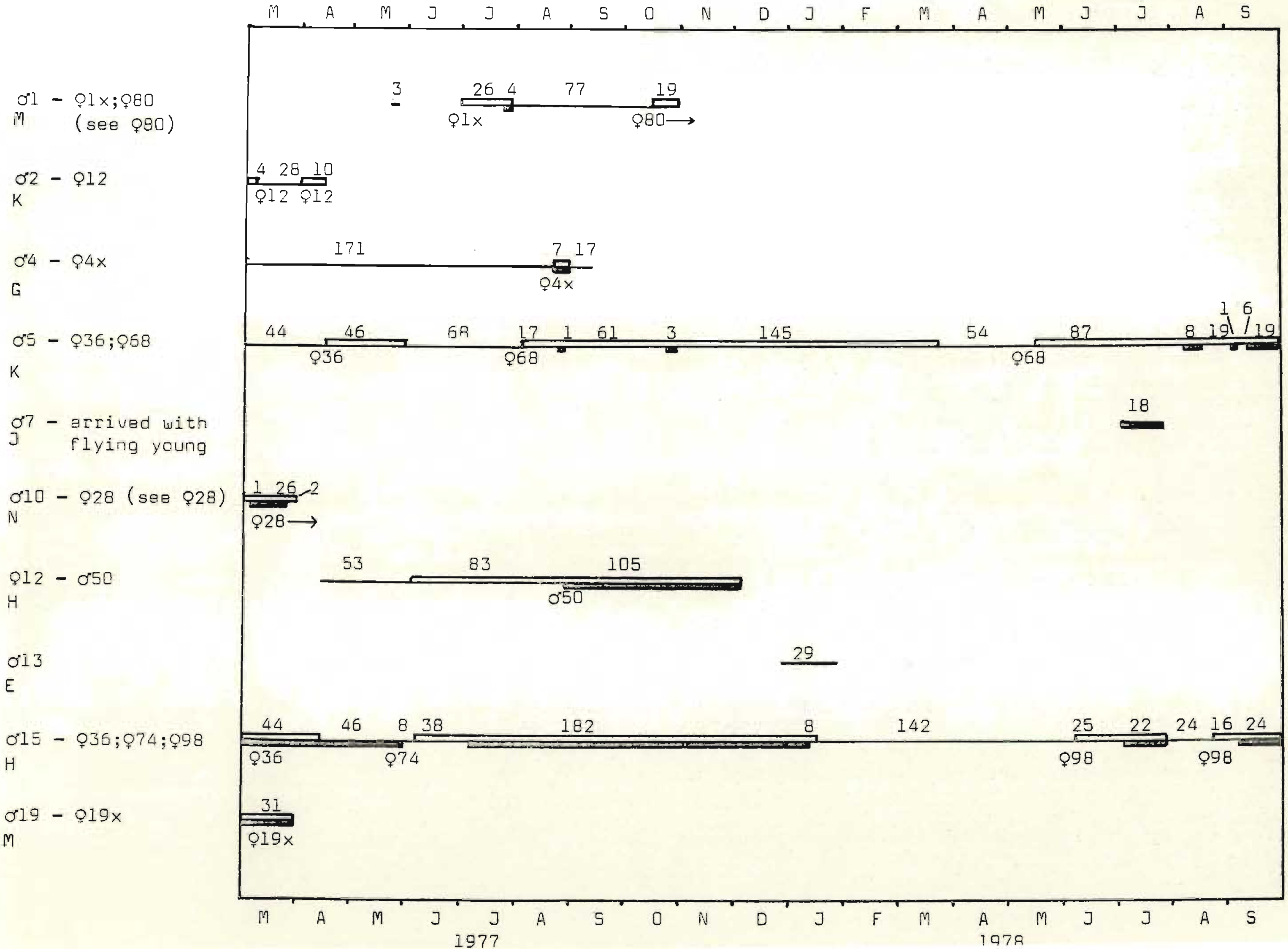
Poor condition as a result of food shortage, predation, and hooking and spiking by Acacia thorns are probably important causes of natural mortality.

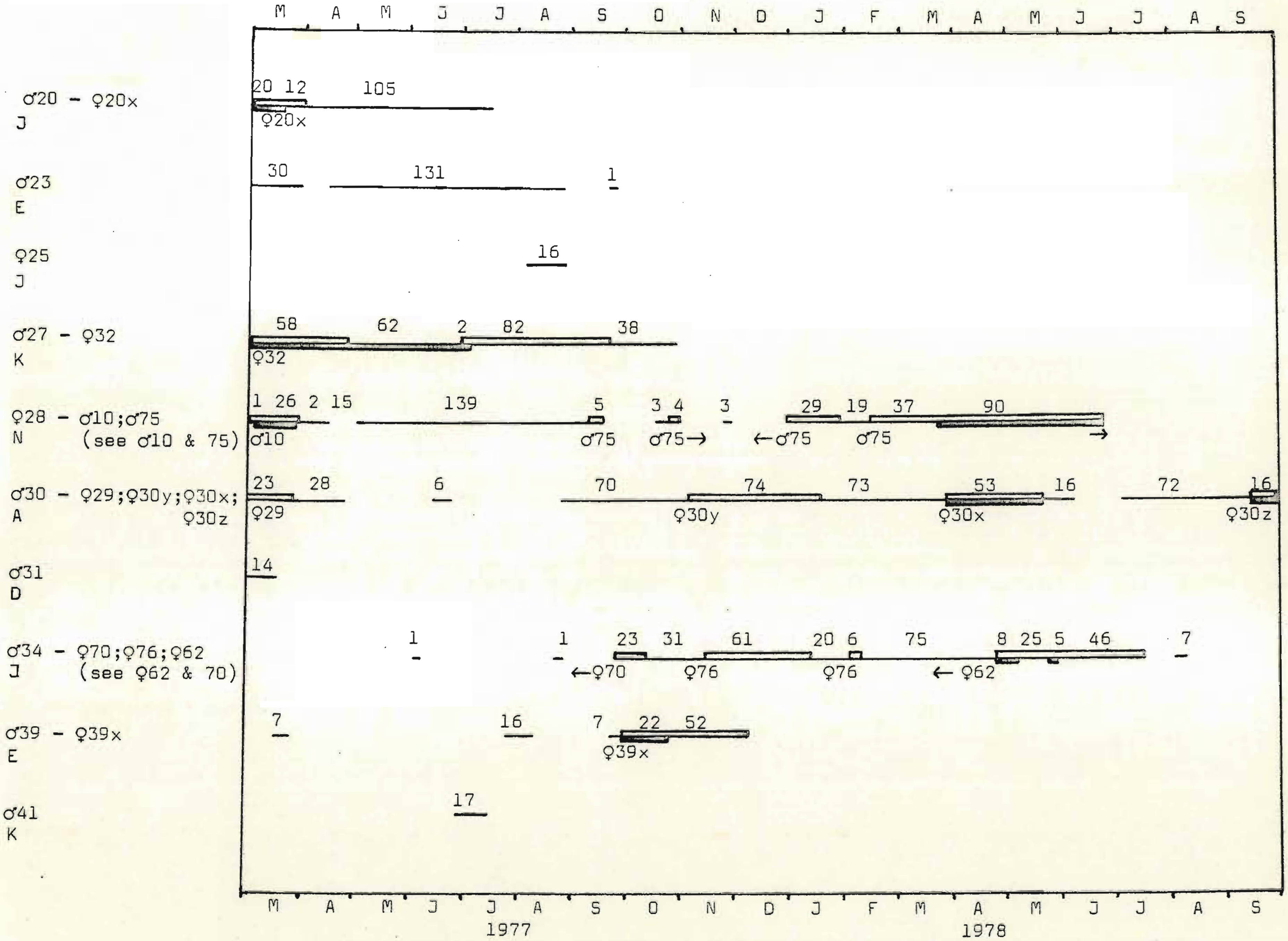
The results are discussed and compared with studies of other raptors. Males probably establish and occupy territories for as long as feeding conditions allow. This would help them maintain familiarity with the most profitable hunting areas. Females probably spend much of their time in search of the best territories with the best breeding prospects.

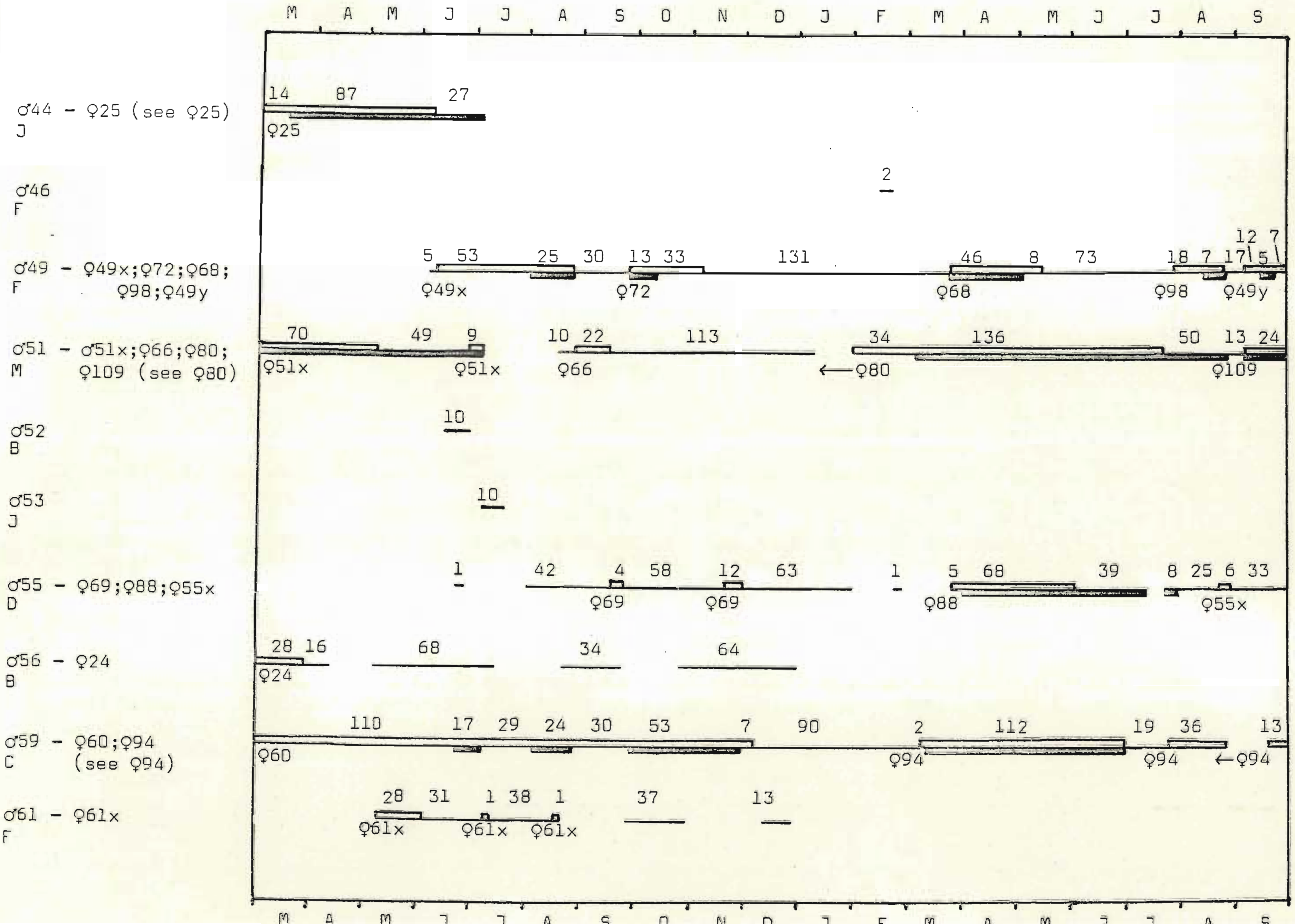
Successive polyandry (Chapter 4) is discussed with reference to continued occupation by males and the skewed sex ratio. Selection probably favours the sustained occupation of territories by males, while the availability of surplus males and the opportunity to breed again allows females to attempt breeding with new males.

Kites probably show two contrasting sets of behavioural strategies, one characterised by stability and the other by eruptiveness and sociability. Breeding kites at Settlers probably represented relatively stable behaviour while eruptiveness was suggested by the records of several other observers. These behaviour patterns are probably related to different feeding conditions, stability being associated with small, regular changes in rodent density and eruptive and sociable behaviour being a response to erratic fluctuations in prey availability.

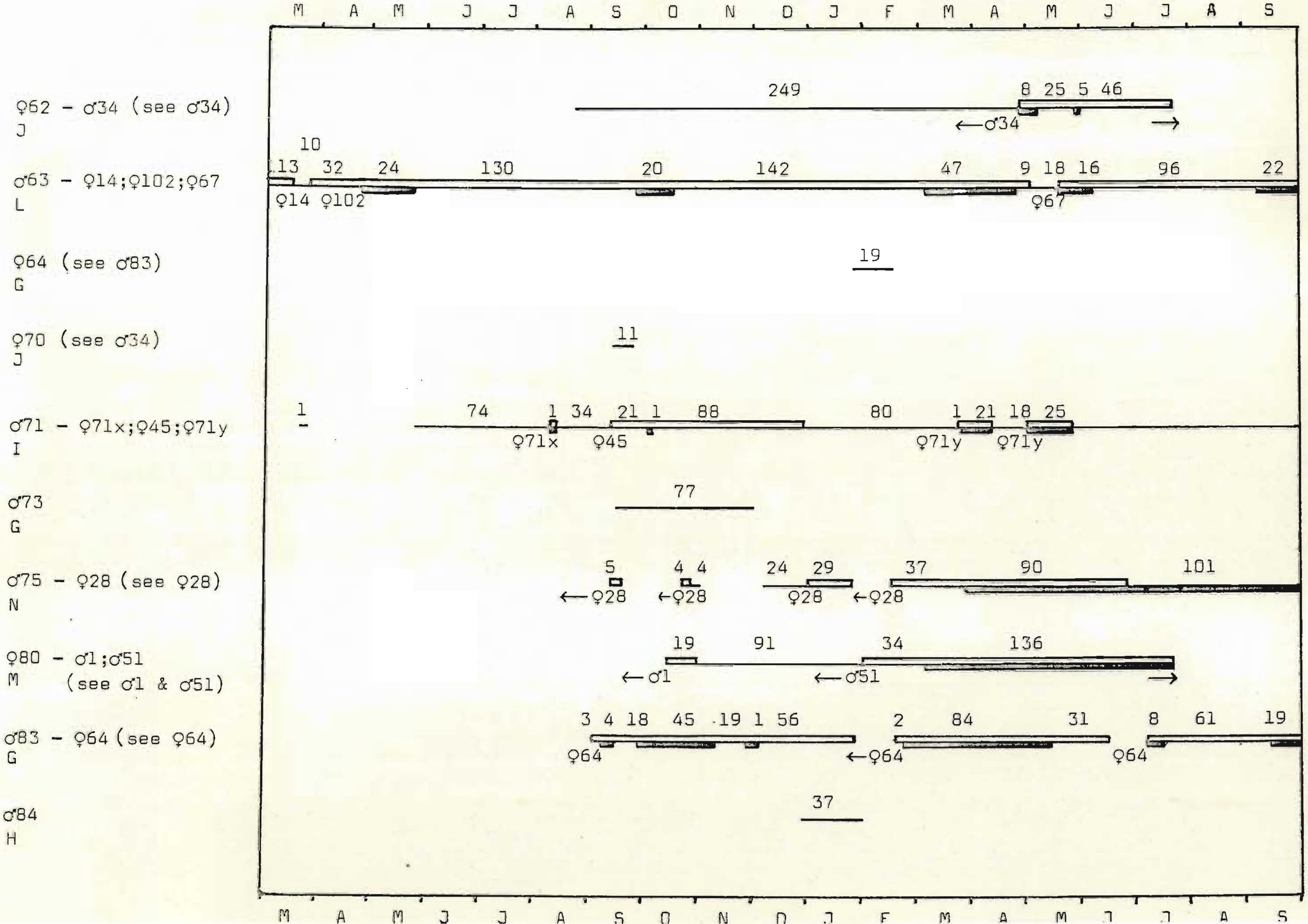
APPENDIX 3.1 The positions of territories, occupancies and mates of territory-holders during the study. The identity of the territory-holder (*e.g.* ♂1), the area it occupied (*e.g.* M - refers to Figure 3.1a), and its mates (*e.g.* ♀1x; ♀80) are listed on the left. Lines and bars indicate the territory-holder's mating class - unpaired (⟶), paired (⟹), breeding (━). Figures above the lines give the period (in days) spent in each class. The bird's mates are listed below the bars during the months in which they arrived. Arrows (*e.g.* ♀80 ⟶) indicate that mates were present before or after territory-holders arrived or deserted. The occupancy of these mates is shown separately, since they were classed as territory-holders while they were unpaired residents.


M A M J J A S O N D J F M A M J J A S
♂1 – ♀1x;♀80
M (see ♀80)
3
26 4
77
19
♀1x
♀80⟶
♂2 – ♀12
K
4 28 10
♀12 ♀12
♂4 – ♀4x
G
171
7 17
♀4x
♂5 – ♀36;♀68
K
44
46
68
17
1
61
3
145
54
87
8
19
1 6
19
♀36
♀68
♀68
♂7 – arrived with flying young
J
18
♂10 – ♀28 (see ♀28)
N
1 26 2
♀28⟶
♀12 – ♂50
H
53
83
105
♂50
♂13
E
29
♂15 – ♀36;♀74;♀98
H
44
46
8 38
182
8
142
25
22
24 16 24
♀36
♀74
♀98
♀98
♂19 – ♀19x
M
31
♀19x
M A M J J A S O N D J F M A M J J A S
1977
1978

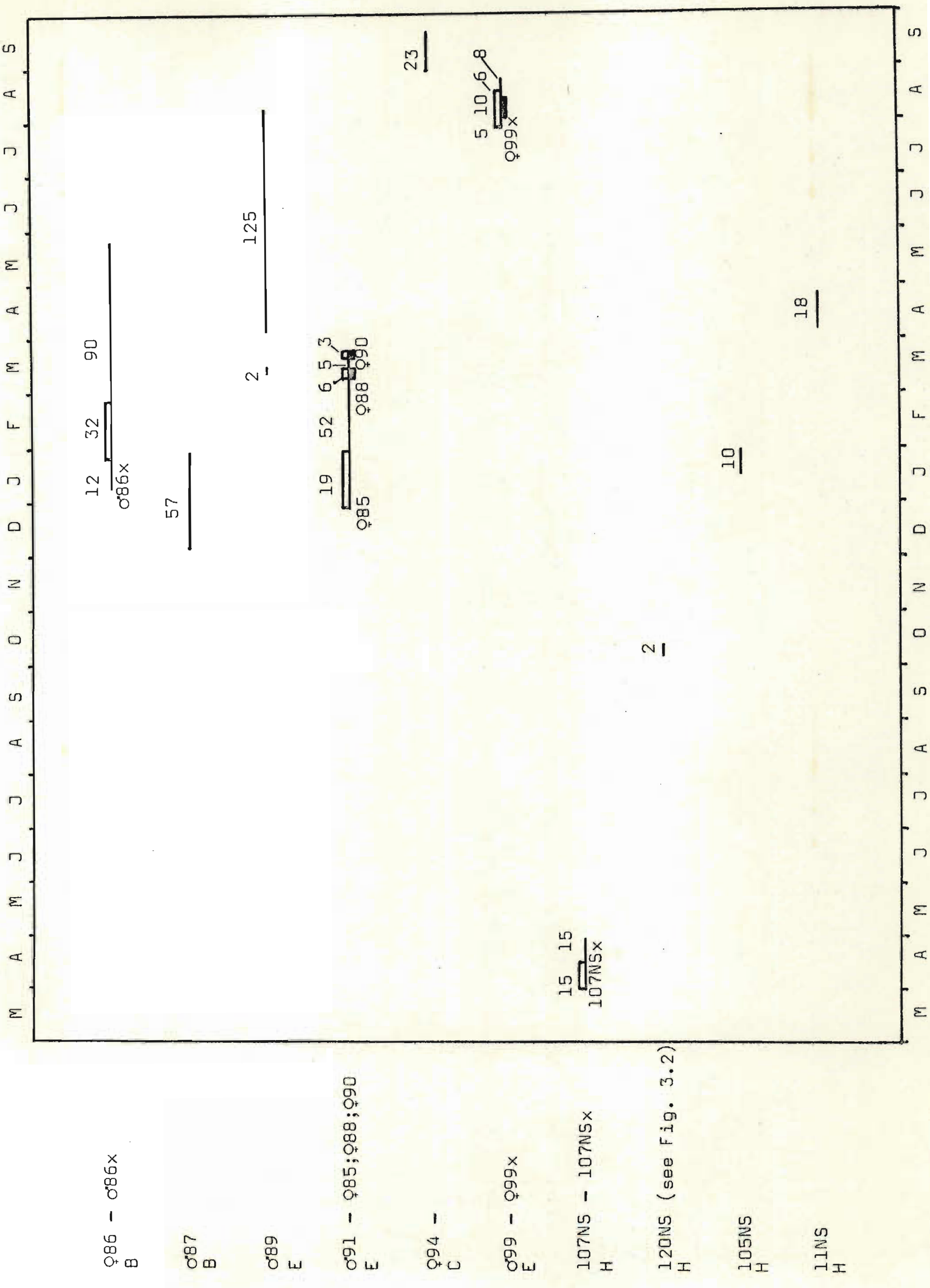

M A M J J A S O N D J F M A M J J A S
♂20 – ♀20x
J
20 12 105
♀20x
♂23
E
30 131 1
♀25
J
16
♂27 – ♀32
K
58 62 2 82 38
♀32
♀28 – ♂10;♂75
N (see ♂10 & 75)
1 26 2 15 139 5 3 4 3 29 19 37 90
♂10 ♂75 ♂75→ ←♂75 ♂75 →
♂30 – ♀29;♀30y;♀30x;
A ♀30z
23 28 6 70 74 73 53 16 72 16
♀29 ♀30y ♀30x ♀30z
♂31
D
14
♂34 – ♀70;♀76;♀62
J (see ♀62 & 70)
1 1 23 31 61 20 6 75 8 25 5 46 7
←♀70 ♀76 ♀76 ← ♀62
♂39 – ♀39x
E
7 16 7 22 52
♀39x
♂41
K
17
M A M J J A S O N D J F M A M J J A S
1977
1978

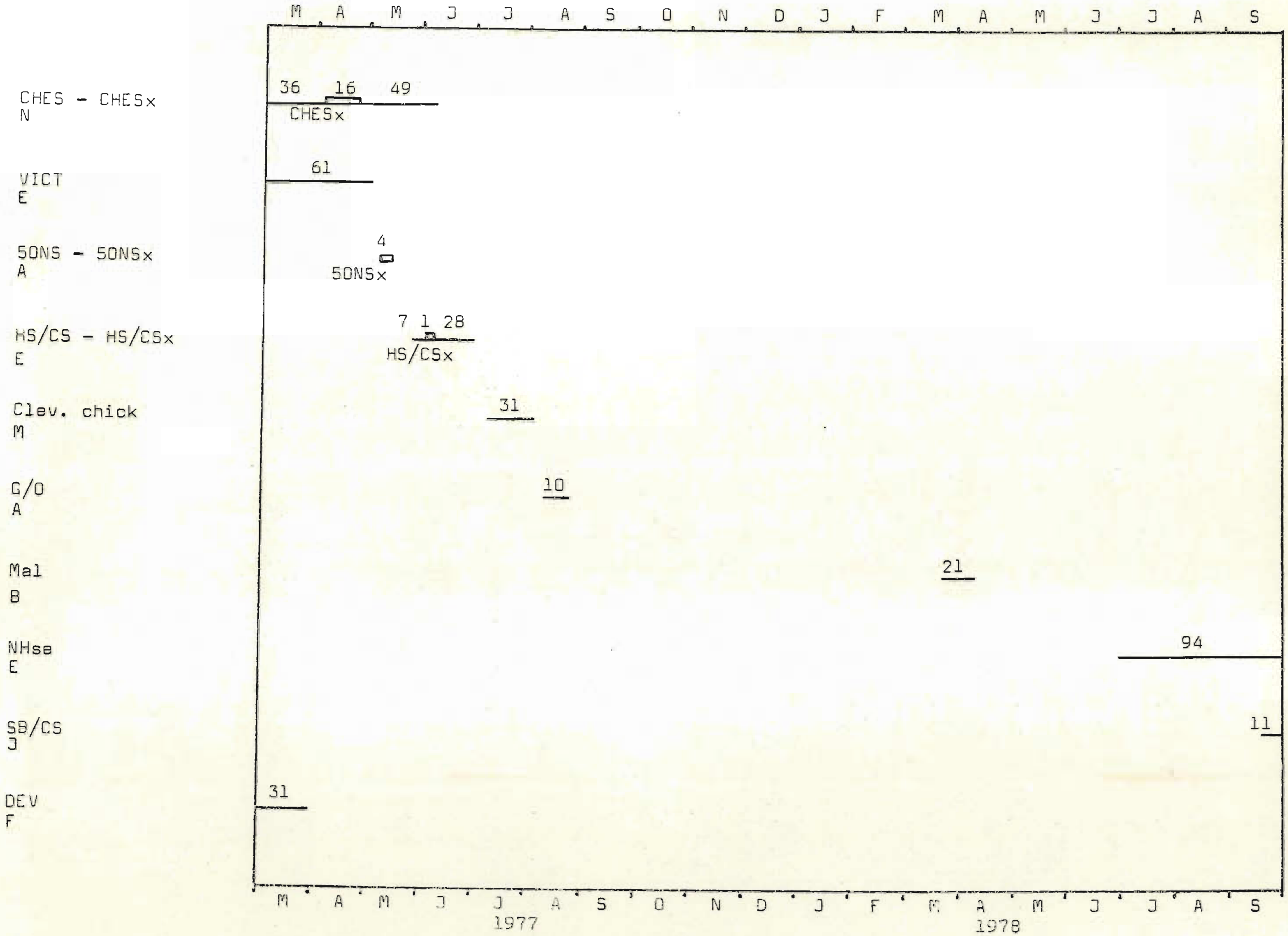


M A M J J A S O N D J F M A M J J A S
♂44 – ♀25 (see ♀25)
J
14 87 27
♀25
♂46
F
2
♂49 – ♀49x;♀72;♀68;
F ♀98;♀49y
5 53 25 30 13 33 131 46 8 73 18 7 17 12 5 7
♀49x ♀72 ♀68 ♀98 ♀49y
♂51 – ♂51x;♀66;♀80;
M ♀109 (see ♀80)
70 49 9 10 22 113 34 136 50 13 24
♀51x ♀51x ♀66 ←♀80 ♀109
♂52
B
10
♂53
J
10
♂55 – ♀69;♀88;♀55x
D
1 42 4 58 12 63 1 5 68 39 8 25 6 33
♀69 ♀69 ♀88 ♀55x
♂56 – ♀24
B
28 16 68 34 64
♀24
♂59 – ♀60;♀94
C (see ♀94)
110 17 29 24 30 53 7 90 2 112 19 36 13
♀60 ♀94 ♀94 ←♀94
♂61 – ♀61x
F
28 31 1 38 1 37 13
♀61x ♀61x ♀61x
M A M J J A S O N D J F M A M J J A S



M A M J J A S O N D J F M A M J J A S
♀62 – ♂34 (see ♂34)
J
249
8 25 5 46
←♂34
→
♂63 – ♀14;♀102;♀67
L
10
13 32 24 130 20 142 47 9 18 16 96 22
♀14 ♀102
♀67
♀64 (see ♂83)
G
19
♀70 (see ♂34)
J
11
♂71 – ♀71x;♀45;♀71y
I
1
74 1 34 21 1 88 80 1 21 18 25
♀71x ♀45 ♀71y ♀71y
♂73
G
77
♂75 – ♀28 (see ♀28)
N
5 4 4 24 29 37 90 101
←♀28 ←♀28 ♀28 ←♀28
♀80 – ♂1;♂51
M (see ♂1 & ♂51)
19 91 34 136
←♂1 ←♂51
→
♂83 – ♀64 (see ♀64)
G
3 4 18 45 19 1 56 2 84 31 8 61 19
♀64 ←♀64 ♀64
♂84
H
37
M A M J J A S O N D J F M A M J J A S


M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
♀86 - ♂86x
B
12
32
90
♂86x
♂87
B
57
♂89
E
2
125
♂91 - ♀85;♀88;♀90
E
19
52
6
5
3
♀85
♀88
♀90
♀94 -
C
23
♂99 - ♀99x
E
5
10
6
8
♀99x
107NS - 107NSx
H
15
15
107NSx
120NS (see Fig. 3.2)
H
2
105NS
H
10
11NS
H
18


M A M J J A S O N D J F M A M J J A S
CHES - CHESx
N
36
16
49
CHESx
VICT
E
61
SONS - SONSx
A
4
SONSx
HS/CS - HS/CSx
E
7 1 28
HS/CSx
Clev. chick
M
31
G/O
A
10
Mal
B
21
NHse
E
94
SB/CS
J
11
DEV
F
31
M A M J J A S O N D J F M A M J J A S
1977
1978

Chapter 4

BREEDING BIOLOGY

INTRODUCTION

Breeding is the best known aspect of raptor biology. Newton (1979) summarizes the main features of raptor breeding and provides a background against which new studies can be compared. However, relatively few quantitative data exist on the breeding of Elanus kites. Descriptive accounts for Blackshouldered Kites have been given by Collar (1978), Suetens & Groenendal (1977), Tarboton (unpubl. MS), Van der Merwe (1975), Van der Merwe & Heunis (1980) and Van Someren (1956). The breeding of Whitetailed Kites has been described by Dixon et al. (1957), Hawbecker (1940) Moore & Barr (1941), Pickwell (1930), Stendell (1972), Waian (1973) and Watson (1940). Letterwinged Kites have been studied superficially by Beruldsen (1971) and Hollands (1977). To my knowledge the breeding of Blackwinged Kites has not been studied, the account in Brown & Amadon (1968) being the best available.

Newton (1979) concludes his review by saying that many aspects of breeding in raptors can be related to food supply. There is abundant evidence for this idea, but relatively little is known of the proximate and ultimate roles of food supply (Drent & Daan 1980). In this chapter I have aimed to describe the basic details of kite breeding and to explore the effects of food supply on breeding. Particular attention has been paid to changes in food requirements and prey availability, and to the effects of food shortages. Finally, an effort is made to understand the separate roles of males and females and how these relate to feeding.

METHODS

Details of all breeding activity observed in the study area were recorded. Data from nests found in surrounding areas, and from Dean (1971), Tarboton (MS) and the Southern African Ornithological Society's (SAOS) nest records were incorporated into parts of the study. About 50 h were spent in hides placed near nests. Calls were recorded from hides using a Uher 4000C and later displayed on wideband sonagrams produced by a Kay Electric Sona-graph.

Two nestlings were hand-reared from an early age. The birds were weighed before feeding on most mornings and the weights of all meals were recorded. They were fed two or three meals daily of wild-caught Otomys angoniensis, Rhabdomys pumilio and Praomys natalensis. Skin and large bones were excluded from their diet during the first seven days (see p. 165). Two other chicks were reared for several days but later returned to their nests. All wild chicks were ringed at about three weeks and some were later retrapped and fitted with coloured patagial tags (Chapter 1).

Data relating to food have been analysed and presented using the calculations and units described in Chapter 2. Estimated food weights, therefore, reflect the actual quantiy of food ingested.

Nests were usually checked at least every second day. Dates on which breeding started were normally taken as the dates on which breeding was first observed. Similarly, independence of the young was taken as the date on which the fledged young were last seen. In a few cases average incubation and nestling periods were used to estimate dates.

RESULTS

Pre-laying period

The first signs of breeding included copulation, dive-bombing, FLUTTER displays by males, nest site inspection, following of one bird by the other, and a variety of vocalizations. Although some pairs did not proceed beyond this stage (see Success and Productivity, p. 169), successful pairs later started nest building and females became inactive as they were fed by males. Except while hunting, breeding kites were usually seen in the nest or focal area (Chapter 3, p. 97), an area of about 1-2 ha around the nest site.

Although the frequency of copulation was greatest in the morning (Table 4.1), it varied considerably. One pair with a well built nest copulated only three times during 774 min of observation on the ninth day before their first egg was laid. Another pair copulated five times in 155 min three days before even starting a nest. Many copulation attempts were aborted; the males either landed briefly on the females or merely hovered just above the unresponsive females. Nineteen copulations were timed, most of which were probably unsuccessful (seven lasted less than 3,0 s), or successful (seven lasted 7,0-11,0 s; $\bar{x}$ = 8,3 s). Accepting females crouched as their mates flew towards them, and sometimes females evidently could not discern their mates' intentions. Females would often crouch as males flew nearby either to dive-bomb them or perch elsewhere.

Males frequently dive-bombed females during the early stages of breeding. Usually the male left a perch and, flying strongly, dived to just above the female. Females were also dive-bombed if they left their nest areas to follow hunting males. However, hunting males behaved similarly towards flying young.

FLUTTER display flights by males were usually made 50-100 m above their nest areas. The pattern of flight was butterfly-like, the wings being held above the body and flapped rapidly through an arc of about 45°. Most flights lasted 30-60 s and were preceded and followed by periods of soaring. Similar FLUTTER displays were occasionally made by males flying low (5-20 m) above the ground towards their nest areas. The displays occurred infrequently, perhaps one to three times a day.

TABLE 4.1 Rates of copulation, nest building and delivery of prey items to females during the pre-laying phase. Periods of the day are defined in Chapter 1, (p.13).

Rates	Morning	Midday	Afternoon
Minutes observed	1311	1240	289
Minutes/ copulation (no. copulations)	48,6 (27)	112,7 (11)	72,25 (4)
Minutes/nest building trip (no. trips)	69,0 (19)	95,4 (13)	144,5 (2)
Minutes/prey delivery (no. prey items)	163,9 (8)	413,3 (3)	144,5 (2)

Members of a pair often followed each other, but females followed males more often than vice versa. Following occurred most frequently during periods of nest site inspection, with one bird flying to join the other at each site investigated. Kites also followed one another over greater distances between prospective nest areas and from hunting areas to nest areas.

Kites inspected many potential nest sites before starting to build. One pair visited at least 12 trees in 75 min. Behaviour during nest site inspection was characteristic. A kite would fly towards a tree with a rapid shallow wing beat, the wings held roughly horizontally, and the legs extended ventrally (this flight was very similar to the SHALLOW FLAPPING display seen during territorial conflicts (Chapter 5, p. 214.)). It would then hover briefly and slowly descend to a position well within the foliage, the normal site for a nest (see below), where it would remain perched for 10-30 s before flying to another site or a perch. While males and females often inspected different sites, nest sites were investigated only when both birds were present in the nest area.

One probable instance of kites choosing a site was observed. Both birds had been visiting sites for 50 min when the female flew to join the male at one site. He later flew off to another site, but the female remained perched there for about 5 min. She too then flew off, but over the next 90 min she returned six times to the same site. In the same period the male returned twice to the site. During the following three days the female was repeatedly seen perched on this site, although building started only four days after they had apparently chosen the site.

Kites usually inspected sites facing between west and south, the sector in which most nests were then built (Table 4.2). Mean nest height was 3,3 m (S.D. = 1,3 m; range 1,75-7,75 m), mean nest tree height was

TABLE 4.2 Tree species used for nesting (a), the heights of nests and and trees (b), and the orientation of nests in the Settlers study area.

(a) Tree species	No.	(b) Nest and tree height			(c) Orientation	
		Height (m)	No. nests	No. trees	Direction	No. nests
Acacia tortilis	18	< 2,0	1	0	central	7
A. flecki	15	2,0 -2,49	7	1	N	2
A. nilotica	8	2,5 - 2,99	10	7	NE	2
A. gerrardi	1	3,0 - 3,49	4	8	E	0
		3,5 - 3,99	2	5	SE	1
		4,0 - 4,49	4	2	S	7
		4,5 - 4,99	3	3	SW	5
		5,0 - 5,49	1	5	W	2
		5,5 >	2	3	NW	2

3,9 m (S.D. = 1,4 m; range 2,25-8,50 m), and the mean depth of the nest below the crown was 0,6 m (S.D. = 0,3 m; range 0,25-1,5 m). These data are based on measurements made at 34 nests. In some areas only small Acacia shrubs were available and kites nested at less than 2,5 m above the ground. In tall climax Acacia woodland nests were higher and, in general, kites nested in one of the tallest trees in the nest area. Figure 4.1 shows a range of trees and nest positions. At Settlers, nests were built only in trees with leaves, although in some cases the trees were leafless by the end of the breeding cycle.

Nesting material was usually collected within 100 m of the nest. All 62 items seen collected were taken from the ground, although kites were three times seen unsuccessfully trying to break twigs from trees. Tarboton (MS) and Van der Merwe & Heunis (1980) often observed kites collecting twigs from trees. However, Acacia twigs were difficult to break and kites in the Settlers area probably learnt to collect nesting material from the ground. Nesting material was always carried in the bill and usually directly from the ground to the nest. Most nest building took place in the morning (Table 4.1). Females collected 19 items (31%) and males 43 items (69%). Tarboton (MS) and Van der Merwe & Heunis (1980) recorded females collecting 59% and 43% of nesting material respectively. The proportion of material brought by each sex was not related to whether the nest was successful or not; at successful nests males brought 29 items and females 10 items, at unsuccessful nests males brought 14 and females nine items (χ^2_1 = 1,24; NS).

Herb stems and branches, grass stems and some twigs comprised the bases of nests. Fine grass, carried in the bill in small tufts to the nest, was added as lining several days before and after laying. All nesting material was dry when collected. On the nest, kites wove material by pushing loose ends into the framework and then shaking the

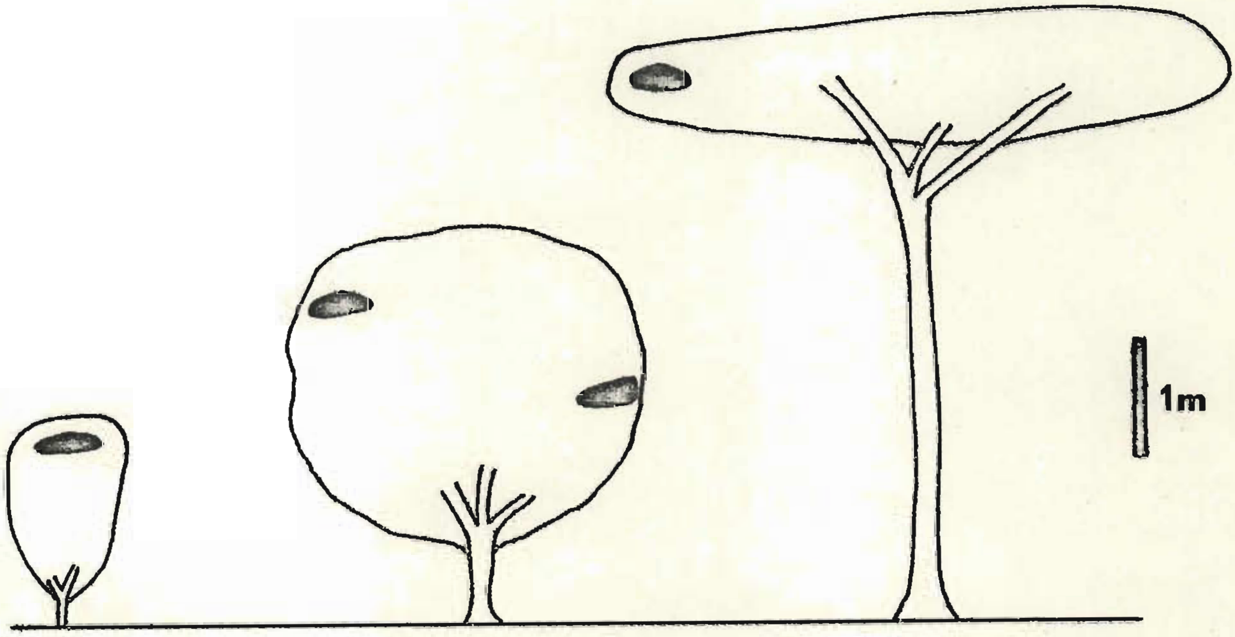


FIGURE 4.1 Typical nest sites observed in the Settlers area.

bill from side to side very rapidly. Kites also often visited nests without bringing new material, and arranged stems and twigs already in the nest. During 546 min of observation at one nest, the female visited the nest four times and on three visits did not bring new material. The male made 12 visits over the same period, on six of which he was without new material.

Of 34 nests observed during building, 30 were built on fresh sites and four on previously used sites. None of the four old nests had previously been laid in. One nest was built on top of a disused Wattled Starling _Creatophora_ _cinerea_ nest.

Males usually started feeding females one to three days after first copulating and investigating nest sites. However, two males were seen offering prey to their mates, while another female tried to snatch prey from her mate when no other signs of breeding were observed. Males offered prey by flying around their mates and calling (see below). Most feedings were in the morning and afternoon (Table 4.1) when kites did most of their hunting (Chapter 5, p. 207). Prey was exchanged in flight or on a perch. In flight, a female would fly towards a male returning to the nest area with prey, fly below and then up to the male, turn on her side and take the prey in her feet. On a perch, the female would land next to, or hop up to the male and take the prey in a foot. Males sometimes later snatched prey back or, in the case of large prey, both birds alternately fed on the same item.

Kites called a great deal during the pre-laying period. INTENTION WHISTLES (Fig. 4.2 a) were frequently heard from kites before they left a perch to copulate, visit a nest or go hunting. The three or four short whistles in this call appeared to increase in loudness. Bouts of RAPID WHISTLES (Fig. 4.2 b) lasting up to several minutes were also

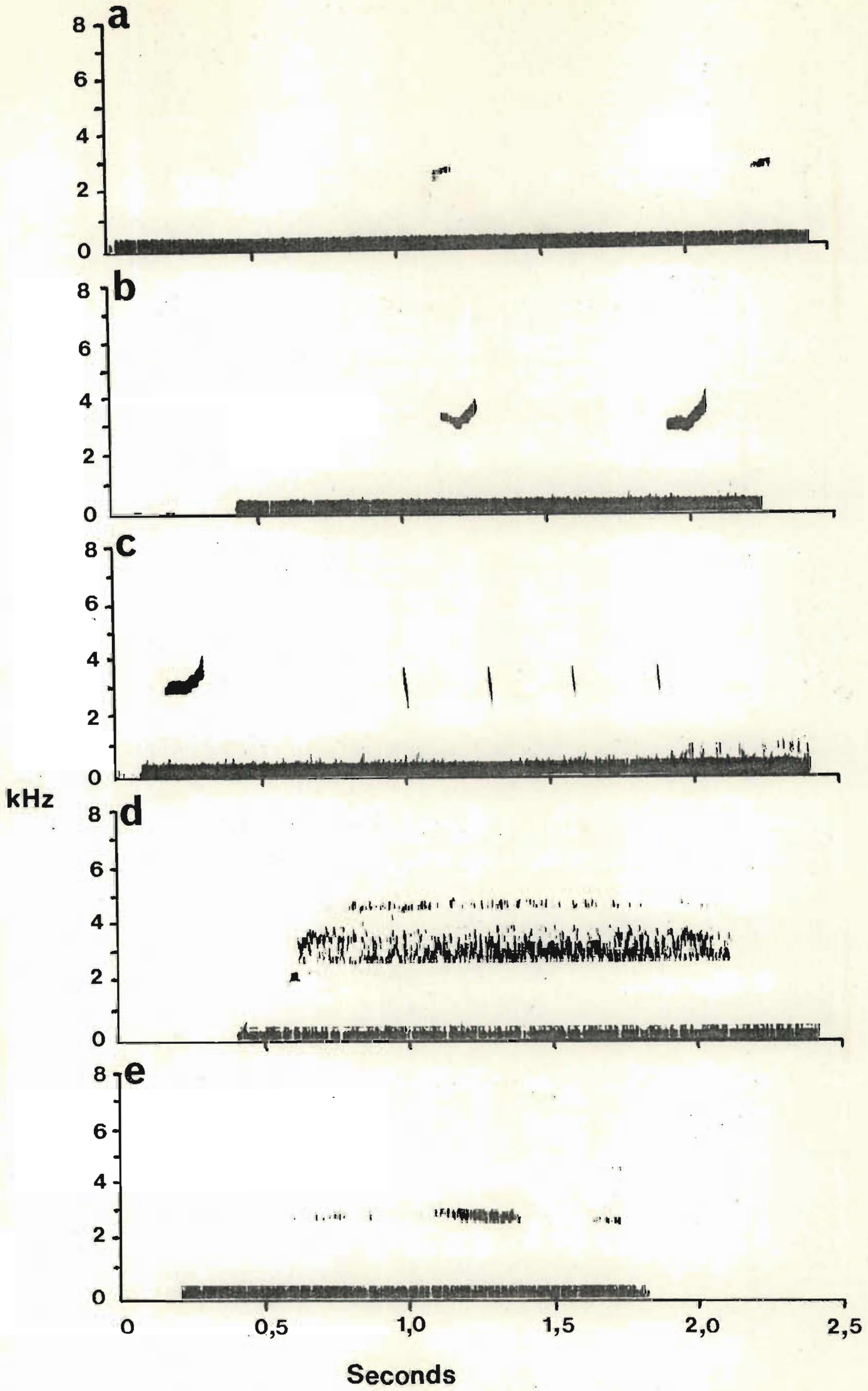


FIGURE 4.2 Wideband sonagrams showing calls heard during breeding. (a) LONG WHISTLE (two notes of the usual three or four), (b) RAPID WHISTLES, (c) TIP...TIP calls preceded by one RAPID WHISTLE, (d) BEGGING SCREAM, and (e) LONG SCREAM. The recording level for (a) and (e) was rather low.

commonly heard. These whistles were longer and louder than INTENTION WHISTLES and their intensity appeared to remain constant. TIP...TIP calls (Fig. 4.2 c) were often interspersed with RAPID WHISTLES and both calls were heard only from males. RAPID WHISTLES were given by males while they were feeding and perched near nests, on nests or on potential nest sites. TIP...TIP calls were noted while males were on nests and just before females flew towards males to take prey. CONTACT WHISTLES (not recorded on tape) were given by males flying towards their nest areas with prey. These whistles sounded similar to INTENTION WHISTLES but were uttered at about 2-s intervals. RAPID WHISTLES, TIP...TIP calls and CONTACT WHISTLES were all apparently given in situations in which males may have tried to attract females or their attention, but the precise functions of the calls were not evident.

Hungry females screamed repeatedly, particularly when their mates were feeding nearby. These BEGGING SCREAMS (Fig. 4.2 d) were the same as screams given by young kites begging food from adults (see p.167). The BEGGING SCREAMS also sounded similar to LONG SCREAMS (Fig. 4.2 e) which were often given by kites when their mates approached closely (< 5 m). LONG SCREAMS, however, indicated threat because they were given by feeding kites that mantled over their prey and TAIL WAGGED and TAIL FANNED (see Chapter 5, p.210). Females sometimes also gave LONG SCREAMS when males approached and attempted to copulate. Occasionally, kites uttered SHORT SCREAMS or WHISTLE-SCREAMS (Chapter 5 — Fig. 5.4 b,c) when their mates approached, but these threat signals were usually directed at territorial intruders (Chapter 5).

Apart from the few situations in which particular calls were noted, calling during the pre-laying period seemed to be very variable. Both kites were silent during some prey exchanges, while others were preceded by RAPID WHISTLES and TIP...TIP calls by males and followed by the LONG

SCREAMS of females. Kites also called variously before copulations; sometimes they were silent while at other times males gave INTENTION WHISTLES and females uttered LONG SCREAMS. Calls were occasionally heard during copulations, but it was not possible to identify which of the birds gave the various screams and whistles. The calls described here and in Chapter 5 (p. 214) are discussed and compared with those of other Elanus kites in Chapter 5, (p. 225).

On average, nest building started seven days after breeding activity commenced, and the first eggs were laid after 14 days of nest building (Table 4.3). Unsuccessful breeding attempts in which pairs failed to lay, were abandoned after an average of 20 days. However, all these periods varied greatly, as shown by high variance figures in Table 4.3. Food supply apparently played an important role in both the duration of the pre-laying period and its success or failure (Table 4.4). Pellet weights were indicative of food intake (Tarboton 1977; Chapter 2), and pairs that failed to lay produced smaller pellets than successful pairs (Table 4.4). Similarly, pairs that laid after short pre-laying periods produced larger pellets than those that laid after a long delay. Differences in behaviour between females also suggested that the success and duration of the pre-laying phase depended on food supply. Females that failed and those that laid after a long delay often gave BEGGING SCREAMS, followed their mates on hunting forays and hunted themselves. In contrast, more successful females were consistently seen perched inactive in their nest areas.

Egg laying and incubation

The following records suggest that eggs were laid during the day and at intervals of one to two days: Nest A — 5 May 00s45 no eggs, 6 May 11s00 one egg, 7 May 09s40 two eggs, 8 May 02s20 two eggs, 9 May

TABLE 4.3 Intervals (days) between events during the pre-laying period for 'successful' and 'unsuccessful' pairs.

Events	Successful - eggs laid				Unsuccessful - no eggs			
	mean	S.D.	range	n	mean	S.D.	range	n
Start of breeding to start of nest	7,0	8,0	1-25	9	6,3	4,3	3-16	10
Start of nest to first egg	14,7	4,2	8-21	10	-	-	-	-
Start of breeding to first egg	24,1	11,0	10-46	13	-	-	-	-
Start of breeding to end of attempt	-	-	-	-	20,4	12,5	4-46	13

TABLE 4.4 Pellet weights (g) produced by kites during the pre-laying period.

	Pairs failing to lay	All pairs that laid	Pairs that laid after pre-laying period of:	
			less than 24 days	more than 24 days
Mean	$1,34^a$	$1,53^a$	$1,64^b$	$1,27^b$
S.D.	0,48	0,79	0,76	0,59
n	55	78	27	26

$^{aa}p < 0,05$; $^{bb}p < 0,05$

10s20 three eggs, 11 May 04s15 three eggs and 10s30 four eggs (clutch complete). Nest B — 15 August 04s00 one egg and 10s00 two eggs, 16 August 03s45 and 10s42 two eggs, 20 August three eggs (clutch complete). Incubation probably increased substantially once the second egg was laid since females were frequently found incubating two eggs, but once only was a female seen covering a single egg. In addition, the first two chicks apparently hatched simultaneously (see p. 161).

In the 51 cases in which the incubating bird was individually identifiable, it was found to be female. Furthermore only one male was seen incubating during watches at nests, and incubation by this male was associated with his mate displaying an apparent lack of interest in the nest. On two days (10 and 16 November) when he was seen incubating for about 20 and 45 min respectively, the female perched nearby for most of the time. She occasionally visited the nest and supplanted the male. On 18 November the eggs were intact but the nest area was deserted. This observation of sustained incubation by a male closely matches a record by Tarboton (MS) of a male incubating for 70 min two days before desertion. He too noted that the female was disinterested in the nest and that she simply perched nearby, making no effort to incubate or hunt. Tarboton's observations of hunting by this pair suggested that their food supply was poor at the time of desertion.

Female inattentiveness associated with desertion was observed at one other Settlers nest. This female was seen flying about 500 m from her nest. The flight was without obvious purpose, e.g. pursuit of a predator or taking prey from her mate. On this day the eggs were intact, but four days later the nest was abandoned.

Most failures were probably due to desertion. Potential predators, such as Pied Crows Corvus albus, were vigorously attacked by incubating kites and their mates (Chapter 5, p.217). Broken eggs and/or disrupted nests were found at most deserted sites, but these were probably caused by subsequent scavenging rather than predation.

The role of food supply in causing desertions was suggested by deserting pairs producing smaller pellets ($\bar{x}$ = 1,16 g; S.D. = 0,48 g; n = 69) than pairs that successfully hatched their eggs ($\bar{x}$ = 1,33 g; S.D. = 0,67 g; n = 127) (z = 2,09; $p < 0,025$).

Females, even at unsuccessful nests, were never seen hunting during the incubation period. They were fed throughout the period by their mates. At the approach of a male carrying food, the female normally flew from the nest, took the prey, and flew to a nearby feeding perch. Males did not incubate while their mates were feeding.

Incubation periods determined for individual eggs were 31,5 ± 0,5; 32 ± 1; 30,5 ± 0,5; and 30 ± 0,5 days, giving an average of 31 days. This agrees with 29 ± 0,5 days (Tarboton MS) and 30 days (Rauch & Landman 1974). The sizes of 19 clutches at Settlers were: 3 x c/2, 6 x c/3, 9 x c/4 and 1 x c/5 - mean = 3,4 eggs. This was similar to a larger sample (n = 51) drawn from the SAOS nest records and Tarboton (MS) of 4 x c/2, 18 x c/3, 25 x c/4, 4 x c/5 and 1 x c/6 - mean = 3,6 eggs.

Nestling period

The first two eggs probably usually hatched simultaneously since I found no marked discrepancy in size between the two largest chicks in a brood. In addition, few nests were found to contain only one hatched chick. The spread of hatching dates was probably less than for laying; two broods of three hatched over four to six days and two to three days respectively, and a brood of two hatched over 2,5 to 3,5 days. Eggshells were removed from the nests by females and dropped some distance away.

Figures 4.3, 4.4 & 4.5 show aspects of physical growth for two captive females and several wild nestlings. The captives' weight changes paralleled

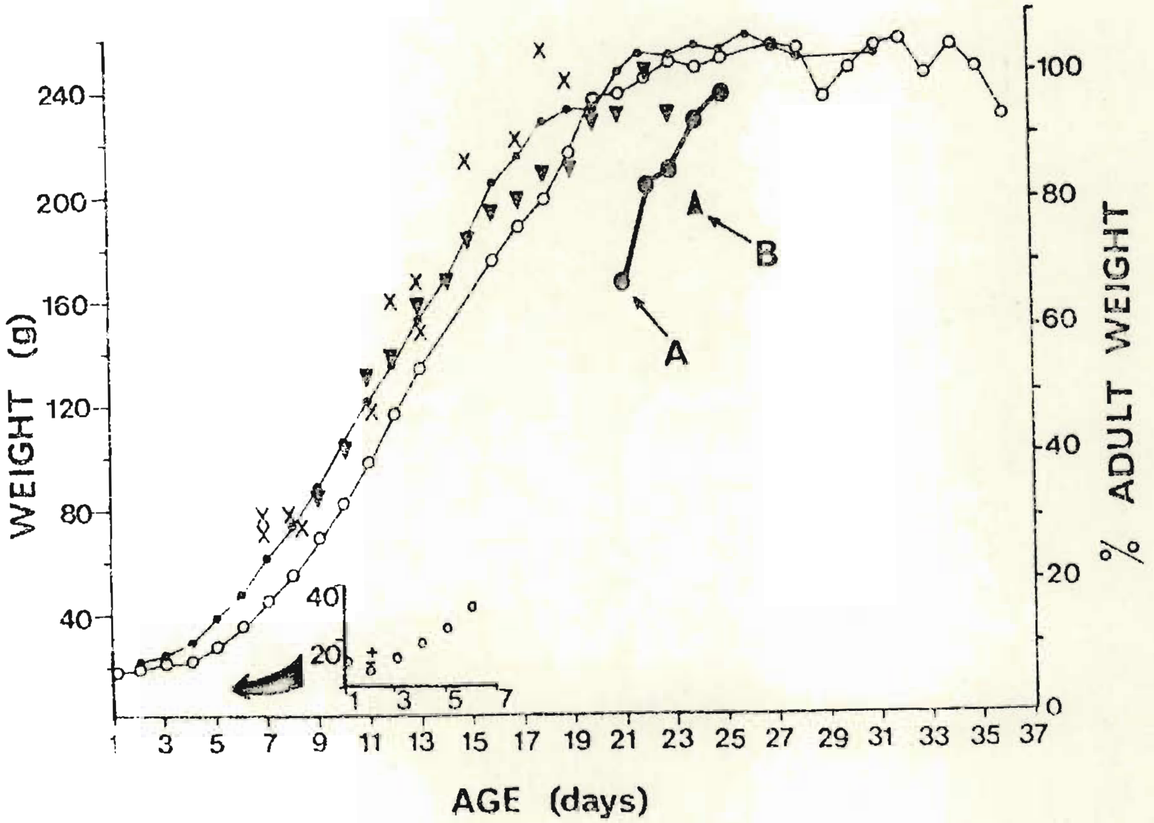


FIGURE 4.3 Weight changes of two captive female nestlings (●——●, ○——○) and wild nestlings (represented by various symbols). (A) and (B) are two wild nestlings (see p. 166).

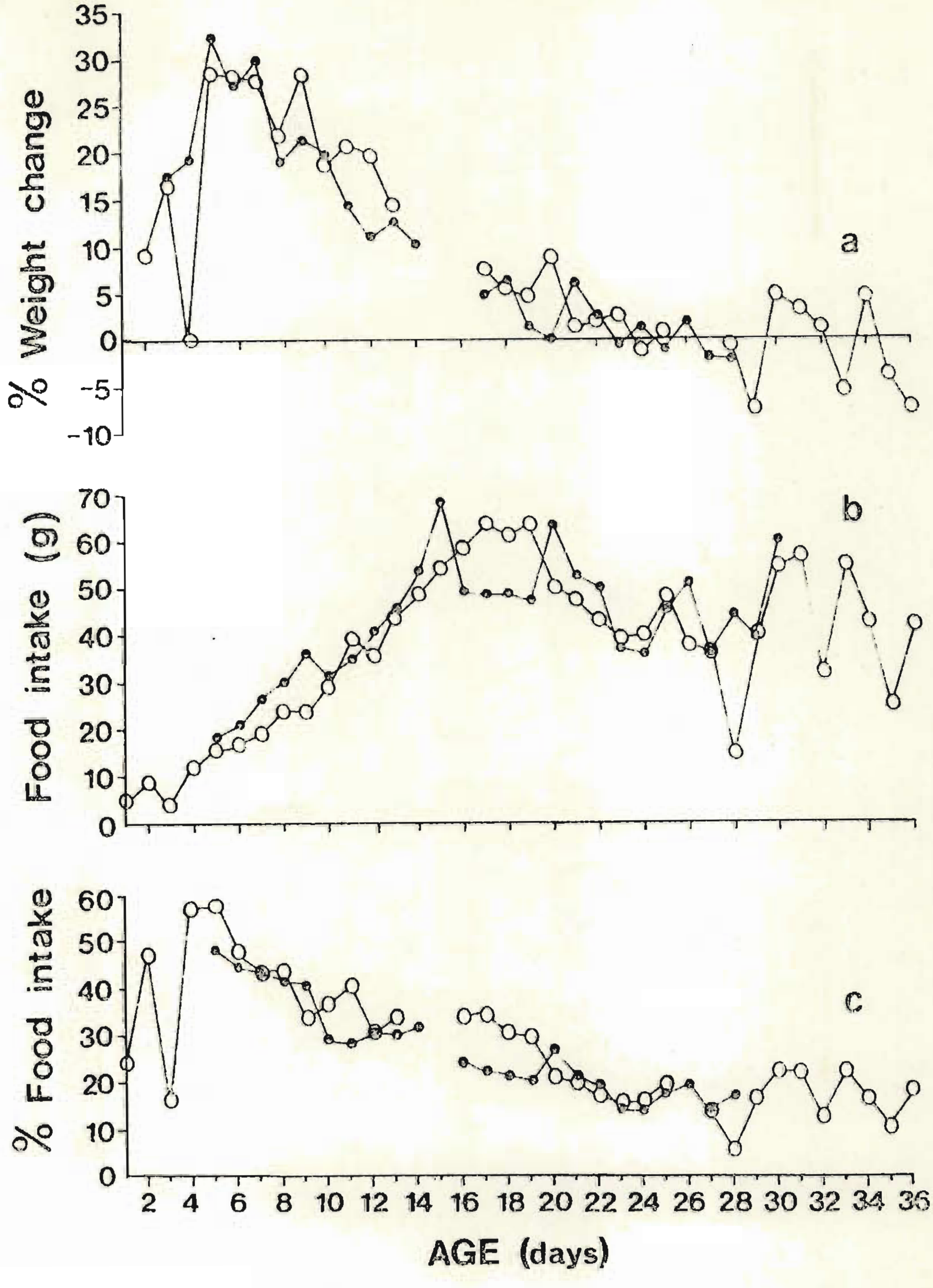


FIGURE 4.4 Growth rates and food intake of two captive female nestlings. a) percentage weight change from weight on previous day; b) weight of food consumed each day; c) food consumption relative to body weight ((food weight/body weight)(100)).

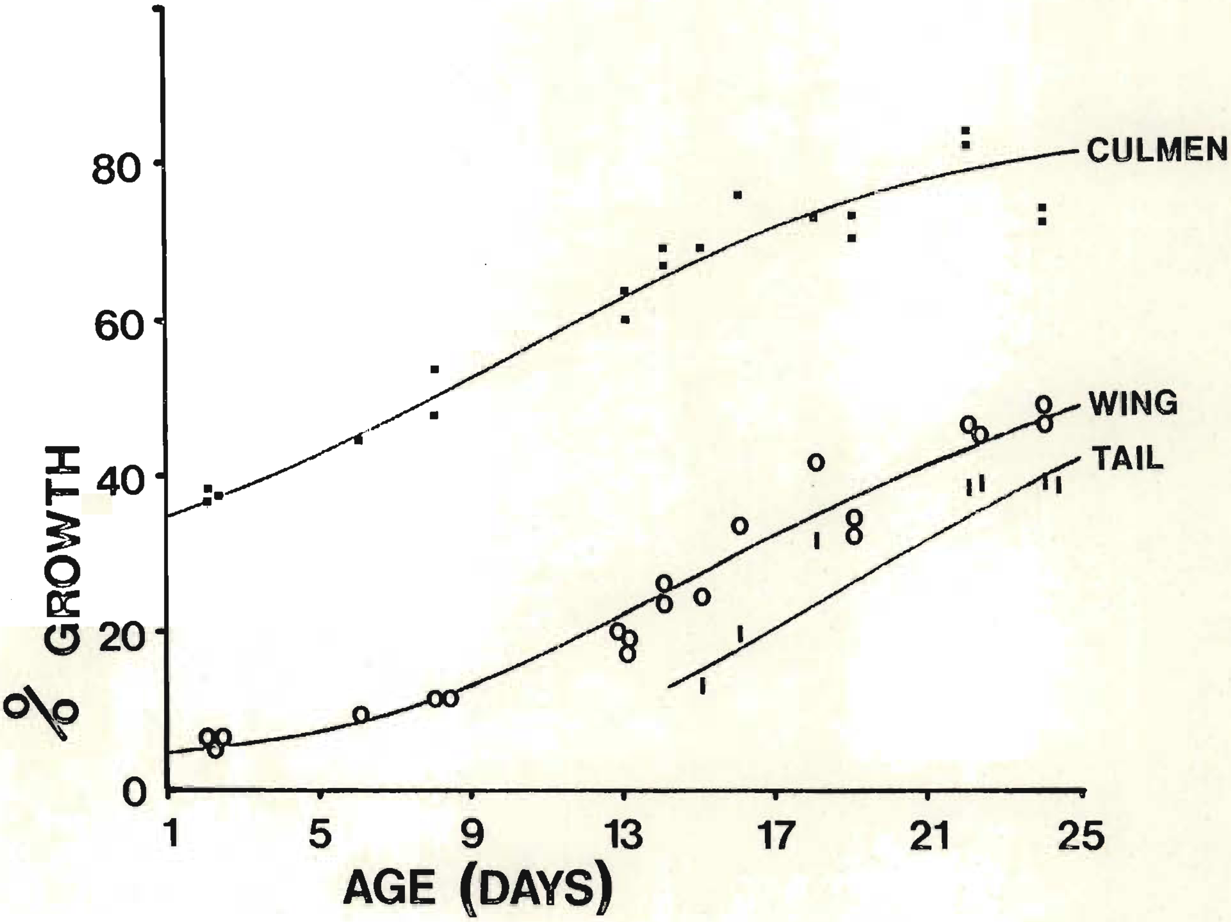


FIGURE 4.5 Changes in wing, tail and bill length during the first 25 days of the nestling period as a % of adult size. All data are for wild nestlings, and adult sizes are adapted from measurements shown in Chapter 6.

those of wild chicks, suggesting that captivity did not affect their development. Nestlings weighed about 16 g at hatching (Fig. 4.3). Relative to body weight, the percentage weight gained each day increased to a peak between five and eight days, and then decreased to the asymptotic weight at about 24 days (Fig. 4.4 a). The asymptote was then maintained, with wide fluctuations in weight, until fledging. These weight fluctuations were not due to the feeding regime since the two hand-reared females were always fed as much as they would take. Wing, tail and culmen growth was slow and, in contrast to weight, these structures probably reached their full size only at or after fledging (Fig. 4.5).

Food intake was highest at 14-21 days of age when it reached 50-60 g/day (Fig. 4.4 b). Subsequently, food intake decreased and varied around an average of about 40 g/day or 17% of body weight (Fig. 4.4 b, c). Over the whole nestling period Chick 1 consumed an average of 36,4 g/day. Between days 7 and 17, when the absolute weight increases of nestlings were greatest (Fig. 4.3), Chick 1 consumed an average of 2,79 g of prey/g weight increase, and Chick 2 consumed 2,86 g/g weight increase. Stated in calorific values (see Chapter 2, p. 60), Chick 1 took 5,13 kcal/g weight increase and Chick 2, 5,26 kcal/g weight increase. These values are lower than an average rate of 5,8 kcal/g weight increase determined for many birds (Drent & Daan 1980).

Females brooded nestlings continuously only during their first two to three days. Thereafter, nestlings were brooded or shaded at night, or during rain and extreme heat. Food brought to the nest area by males was taken by the females to the nestlings — males were never seen feeding nestlings. Nestlings were not fed skin or large bones during their first week, these being consumed by the females. Prey was torn into small pieces by females which offered the pieces individually to the nestlings until they were about 15 days old. Later in the nestling period, females left prey for the nestlings to tear up themselves.

Males supplied almost all of the food during the nestling period. Females were usually seen perched near their nests, and while they may have caught incidental prey, they were not seen to hunt intently within the nest area. Of seven females that successfully reared young, three were first seen hunting only after the young had left the nest. The remaining four were first seen hunting 1, 5, 14 and 17 days before their young had flown. Such hunting by females during the nestling period may have depended on food supply, the females hunting only when males failed to supply sufficient food. This appeared to be the case at one nest where the female was seen hunting about 900 m from the nest when the chicks were 21 days old. The nestlings (chicks A and B in Figure 4.3) were found to be very hungry and underweight. One chick was hand-reared for five days and, despite being very wild, it grabbed and ate all the offered food.

Nestling periods ended with the first flight and varied substantially: Chicks 1 and 2 (captive) 36 and 32 days, and 38, 35, 35 and 32 days for wild nestlings in different nests; mean = 34,7 days. Tarboton (MS) recorded nestling periods of 30-32 days for three siblings. As with most raptors, kite nestlings started clambering around the nest tree up to one week before first flying. Brood sizes observed near Settlers were: one young (1), two young (4), three young (7), four young (5) with a mean of 3,05 young. A larger sample from SAOS nest records gave the following sizes: one young (4), two young (7), three young (21), four young (8), and five young (3) with a mean of 3,0 young. These brood sizes were determined about midway through the nestling period.

Post-nestling period

After leaving the nest, fledglings spent most of the first two to three weeks in the nest area, returning to the nest to feed and roost.

Subsequently, they ranged further by following their parents and roosting with them elsewhere. The chicks at one nest roosted on the nest for the first 10 days, then roosted in a tree 150 m from the nest for five weeks after which they joined a communal roost 3 km away.

The youngest kite seen hunting (hovering) had been out of the nest for 12 days. It is not known what proportions of food were caught by chicks or provided by adults. However, fledglings were never seen catching prey, and an adult male was seen passing a large rodent to a chick 107 days after it had left the nest. Fledglings persistently begged food by giving BEGGIN SCREAMS (Fig. 4.2 d) and harassed their parents throughout the post-fledging period. The young birds followed the adults from perch to perch and flew up to them when they were hovering. In response, adults dive-bombed the young and TAIL WAGGED in threat (Chapter 5, p.210), or flew away to hunt elsewhere.

Table 4.5 lists details for 10 nests observed after the young had flown. Females deserted after the young had flown at eight out of nine nests — the female died at the tenth nest. The average interval between young leaving the nest and desertion by females was 19,6 days (range 0-49 days). (♀88 was last seen three days before her young flew and her departure date has been taken as the chicks' flying date.) ♀36 paired with ♂5 immediately after leaving her young and mate (see Chapter 3 — Appendix 3 All other females simply disappeared, but three (♀32, ♀51x & ♀25) returned to the same territories after absences of 61, 50 and 56 days respectively. (The mate of ♀25 and her chicks had died in the meantime, and she then occupied the territory alone for 15 days.) Before leaving, females helped feed the young, and ♀74, which did not desert, helped provision her chick throughout the post-nestling period.

The mean intervals between chicks leaving the nest and disappearing (= independence) was 81,6 days (range 54-107 days) (Table 4.5 -- "last" chicks only). The dates on which other chicks became independent

TABLE 4.5 Intervals (days) between nestlings leaving the nest (fledging), female desertion and independence.

Adults	Fledging date	Female last seen - days after young fledging	First chick last seen - days after fledging	Last chick last seen - days after fledging	Remarks
♂27 ♀32	29 Mar	30	-	94	Only one chick fledged
♂15 ♀36	12 Mar	35	?	81	Four chicks left the nest but one caught and kept captive - ♀36 paired with ♂5 on 15 Apr
♂15 ♀74	18 Oct	-	-	83	Only one chick fledged - ♀74 did not desert
♂50 ♀12	30 Nov	-	-	-	Only one chick left the nest - ♂50 and chick disappeared after 11 Dec and ♀12 found dead
♂51 ♀51x	30 Apr	10	69	69	Two chicks fledged and both remained in area after 7 Jul when ♀51 disappeared
♂51 ♀80	3 Jun	49	?	83	Four chicks fledged
♂75 ♀28	12 Jun	11	101	107	Two chicks fledged - ♂75 seen feeding chick on 20 Sep
♂44 ♀25	7 Jun	2	-	-	Two chicks fledged - first one probably died; second found dead on 8 Jul
♂55 ♀88	4 Jun	-3	42	54	Two chicks fledged - see text for independence of first chick
♂7 ♀7x	3 Jul	?	-	?	One chick fledged - ♀7x deserted but date unknown - chick remained with ♂7 for at least 49 days

were hard to determine, but the impression was that siblings left within a few days of each other. The fledgling, ♂41, set up a territory on the edge of its parental (♂27♀32) territory and remained there for 17 days. There were frequent territorial conflicts (Chapter 5) between this bird and its parents. One parent, ♂51, left his territory temporarily, and one chick remained and defended the territory for 31 days. Its sibling, ♂53, moved to a previously vacated neighbouring territory (Chapter 3 — Appendix 3.1). All other independent fledglings disappeared from the study area.

♂55 deserted his territory and was seen with his two fledglings intruding on an occupied territory about 5 km from their nest. One of the young was trapped, but by the time it had been released, its parent and sibling had been chased from the area by the resident territory-holder. Five days later the male and sibling were back on their territory but, after repeated searching, the trapped fledgling could not be found. Then, 43 days after its capture, it was seen again intruding at the place it was caught. The trapping of this chick may have caused its premature independence.

There was no significant difference between the weights of pellets produced by young successfully becoming independent ($\bar{x}$ = 1,42 g; S.D. = 0,61 g; n = 215) and those from fledglings that died ($\bar{x}$ = 1,32 g; S.D. = 0,34 g; n = 30).

Flying broods at Settlers were as follows: one young (1), two young (2), three young (2), four young (3), five young (1) (mean = 2,9 young).

<u>Success and productivity</u>

Breeding success rates were low during my study, the following rates being observed at each stage of the cycle:

- of 40 pairs copulating, 24 (60%) built nests and 16 (40%) failed to build.

- of 40 nests being built, eggs were laid in 20 (50%) and 20 (50%) were abandoned.
- of 22 clutches, 13 (59%) produced nestlings and nine (41%) failed. In those clutches in which at least one egg hatched, 43 eggs produced 37 (86%) chicks.
- of 18 broods, 12 (67%) produced flying young and six (33%) died. In those broods that produced flying young, 30 (88%) out of 34 nestlings left the nest.
- of 11 flying broods, eight (73%) produced independent young and three (27%) whole broods died. Excluding complete broods that died, 22 (96%) out of 23 fledglings became independent.

These data indicate that failure rates decreased as the breeding cycle progressed, and that high failure rates were largely due to complete losses of clutches and broods. In those nests where at least some eggs or young survived, the success rates were high.

Similar high overall failure rates have been found by A.C. Kemp (pers. comm.) and Tarboton (MS), and are indicated by data in the SAOS nest records. Kemp found 19 nests, 16 clutches were laid, but only six nests survived to produce 14 flying young. In Tarboton's study 24 nests were built, 15 clutches (45 eggs) were laid, six clutches (19 nestlings) hatched, and five broods (14 young) fledged.

Calculations using the percentage success rates observed at Settlers indicate that 0,204 independent young were produced by each breeding attempt However, this figure is misleading because many were repeat attempts following previous failures (see below). Only 15 independent young were produced in the study area during the 19 month census period; equivalent to 9,5 young/year. Against an average population of 26 residents (Chapter 3, p.110) productivity was 9,5/26 = 0,365 independent young/resident/year. A resident would therefore replace itself only every three years.

Fifty-eight breeding attempts were observed during the study; four commenced before the study started and five were in progress when the study ended. The number of attempts made by territory-holders varied between none and seven: 29 territory-holders made no attempt to breed, 10 made one, four made two, one made three, two made four, two made five, two made six, and one territory-holder made seven breeding attempts. While some attempts started soon after previous failures, ♂15 and ♂51 started breeding again 40 and 14 days respectively after successfully rearing young to independence. Intervals between independence of their fledglings and the acquisition of new mates were even shorter, eight and 13 days respectively. The second attempts were both successful (at least until young left the nest in the case of ♂51) indicating that continuous breeding was possible. ♂15 spent 346 out of 386 days breeding, and ♂51 spent 237 out of 251 days breeding.

From data given above, the average duration of each stage of the breeding cycle was: 24 days pre-laying, 31 days incubation, 35 days nestling period, and 82 days post-nestling period for parent males and 20 days for females. Totalling these periods gives 172 days for male, and 110 days for female participation in each successful breeding attempt. In one year therefore males could potentially breed twice and females three time

In 1977 and 1978 two peaks of breeding activity were observed, one starting in July 1977 and the other in March 1978 (see Breeding seasons, p. 173). From the small samples in Table 4.6 it appeared that those pairs that started breeding earliest had the best success.

Pellet weights and behavioural observations indicated that many failures were ultimately due to food shortages. Seasonal differences in success rates also suggest that kites were most productive when food was most abundant. Between March and June 1977 eight breeding attempts produced only two fledglings, between August and September 1977 10

TABLE 4.6 The breeding success of kites according to whether they started early or late during a peak of breeding activity.

Year and month	No. pairs starting to breed	No. (%) laying eggs	No. (%) producing flying young
1977			
July	2	1 (50)	1 (33)
August	6	1 (17)	1 (17)
September	5	1 (20)	0 (0)
October			
1978			
March	10	6 (60)	3 (30)
April	4	1 (25)	0 (0)
May	3	0 (0)	0 (0)
June	2	0 (0)	0 (0)

attempts produced only three fledglings, and 13 attempts started between March and May 1978 resulted in 13 fledglings. The greater success rates in 1978 were probably due to better feeding conditions than in 1977 (Chapter 2, p. 48).

Some failures were also associated with strong winds and the deaths of adults. Three eggs, in two clutches, were broken after a strong wind in October 1978. In the S.W. Cape, at least 10% of 61 nests were destroyed by strong winds (SAOS nest records). The three adults found dead during the study were breeding, but there was no evidence that breeding activity had contributed to their deaths (Chapter 3, p. 119). ♀30x was found dead on her nest, her three nestlings having disappeared. The fledgling of ♂44 was found dead two days after he had been found dead, and the mate and fledgling of ♀12 disappeared when she was found dead.

Breeding seasons

Kites started breeding throughout the year, although most breeding commenced in August-September and March-April (Fig. 4.6). The same conclusions were reached for breeding seasons over the whole summer rainfall region of southern Africa (Fig. 4.7). Pre- and post-rains peaks of breeding activity have also been recorded in Zambia (Benson *et al.* 1971). It is noteworthy that the bulk of breeding started after the rains both in the summer rainfall area and in the winter rainfall area of the southwest Cape (Fig. 4.7). Seasonality was less clear in Natal and the eastern Cape, perhaps because of the more protracted rainfall seasons in those areas.

Comparing the onset of breeding with changes in food supply (Fig. 4.8) indicates that kites started breeding before feeding conditions were optimal. This is confirmed by highly significant correlations between the proportion of pairs copulating (Fig. 4.8 a) and the food supply (Fig. 4.8 b) one month later (Spearman's $r_{16} = +0,80$; $p < 0,001$), and two months later (Spearman's $r_{15} = +0,71$; $p < 0,005$). Furthermore, there was a significant

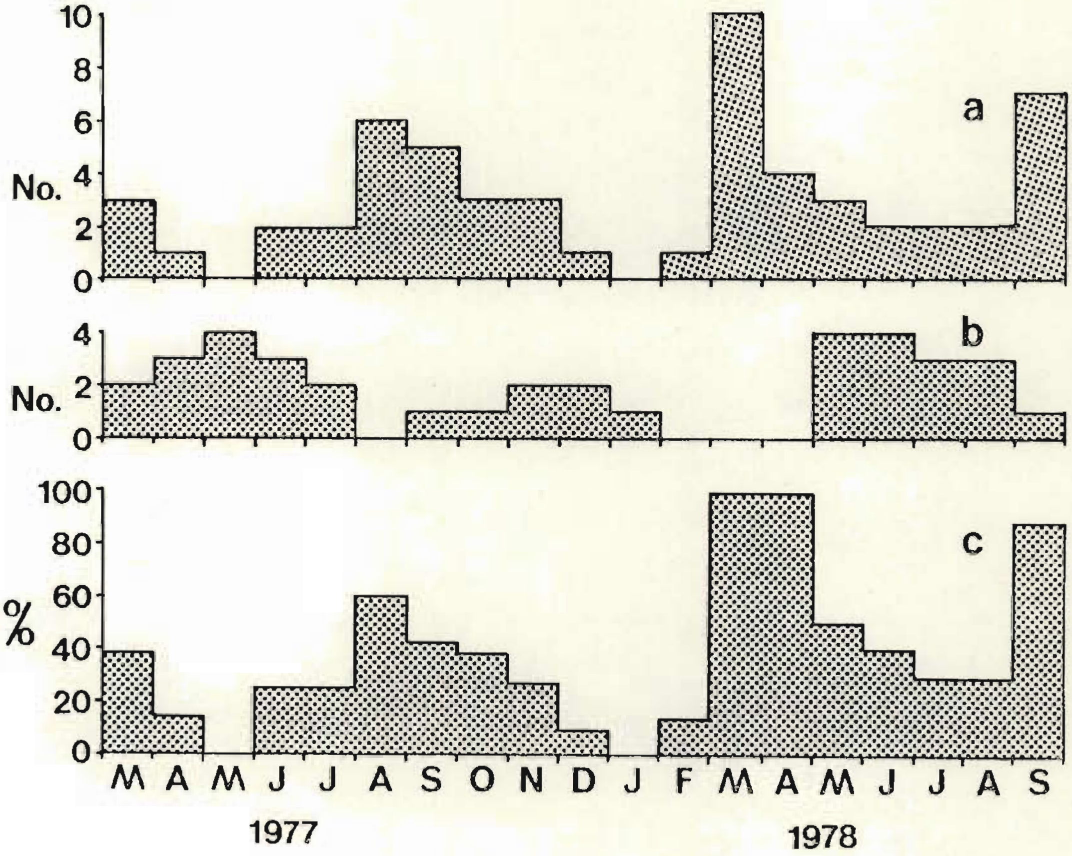


FIGURE 4.6 The timing of breeding by kites in the Settlers study area.

a) number of pairs engaged in pre-laying activity each month;

b) number of broods (nestlings and post nestlings) present;

c) number of pairs engaged in pre-laying activity as a percentage of all those pairs that could have started breeding.

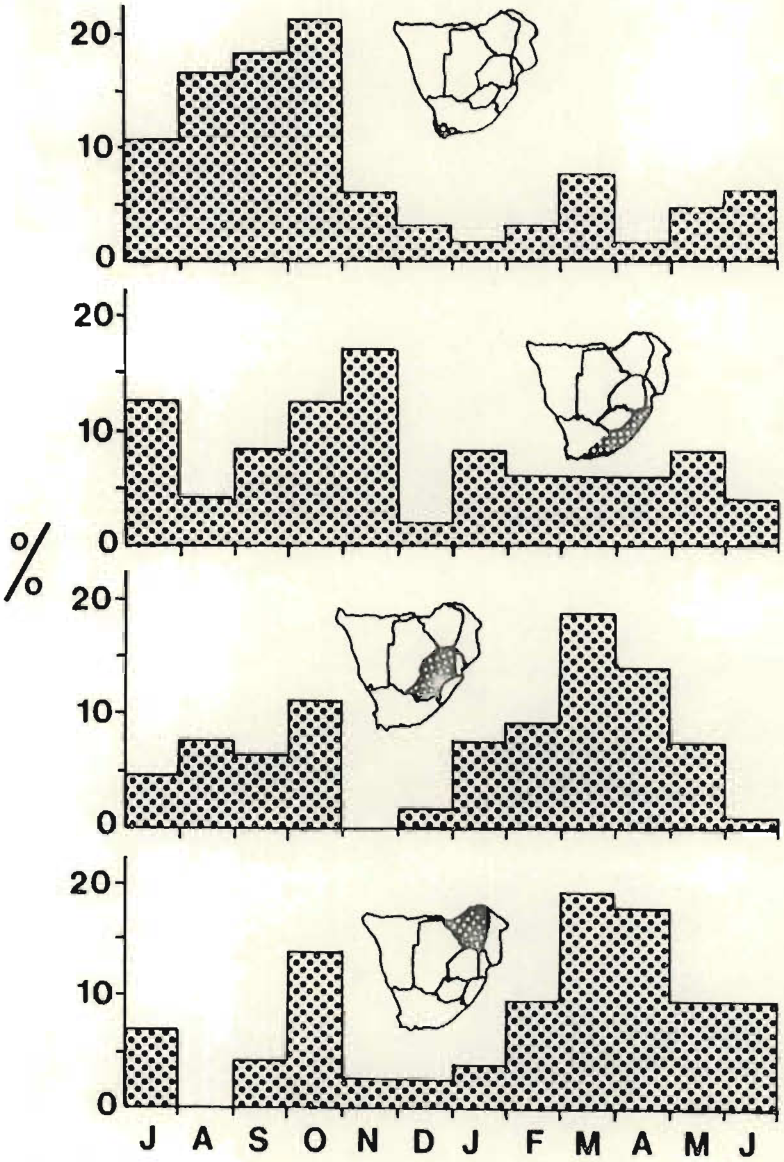


FIGURE 4.7 Breeding seasons of kites in different areas of southern Africa determined by the months in which eggs were laid. Monthly values are percentages of all nest records; southwestern Cape = 66 records, eastern Cape & Natal = 46 Orange Free State & Transvaal = 106 and Zimbabwe = 73 records.

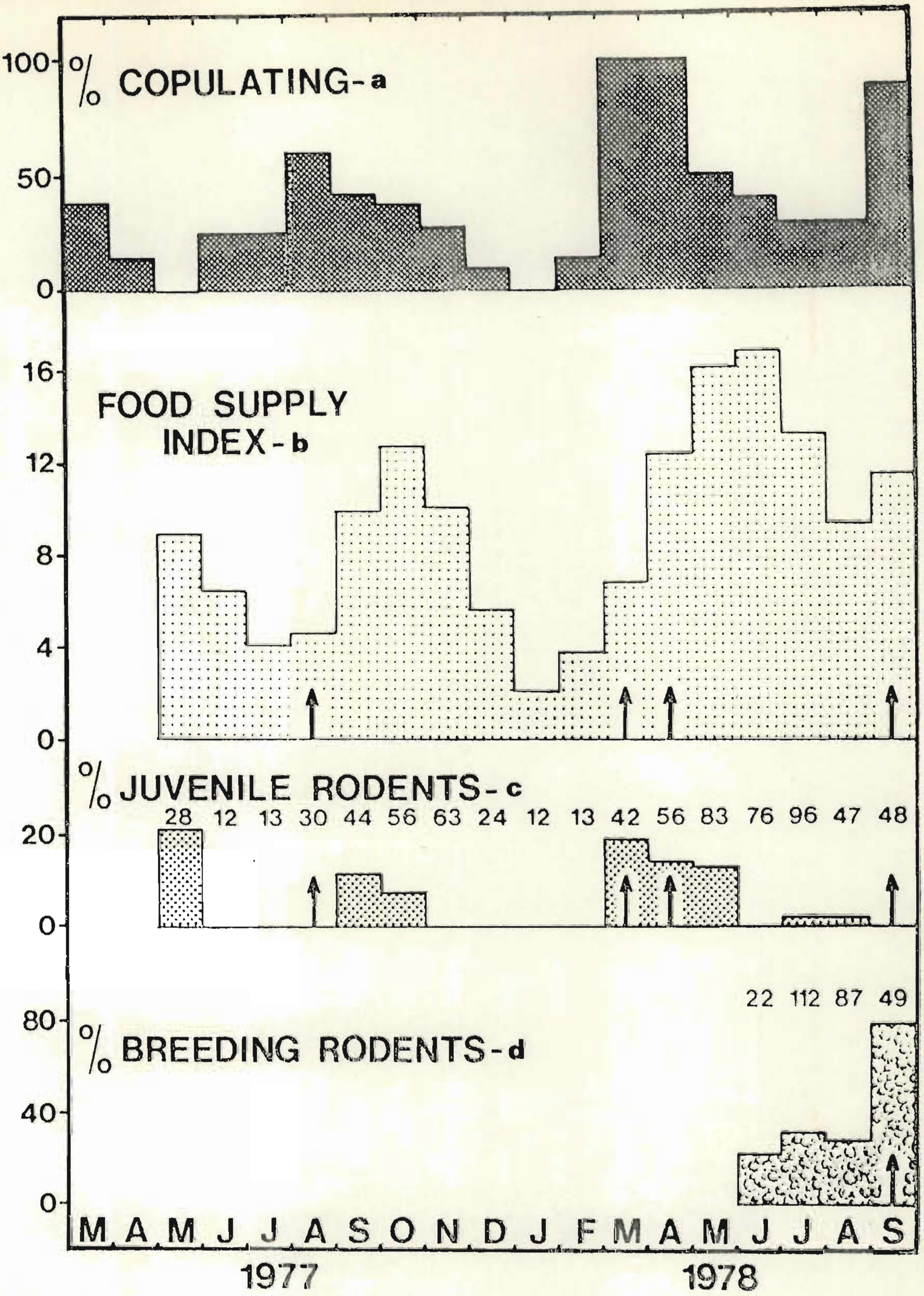


FIGURE 4.8 Seasonal changes in breeding activity and feeding conditions. a) percentage of pairs starting to breed each month (from Figure 4.7c); b) index of food supply (from Chapter 2 - Figure 2.8c); c) percentages of juvenile Rhabdomys and Praomys in trapped samples (adapted from Chapter 2 - Figure 2.4); d) percentage Rhabdomys and Praomys in breeding condition in trapped samples (adapted from Chapter 2 - Figure 2.4). Sample sizes are given for (c) and (d), while arrows in (b), (c) and (d) show months in which most breeding started (from (a)).

TABLE 4.7 Estimates of prey size for kites in their first month of breeding and at all other times (see Chapter 2 for methods concerning prey).

Variables	Kites during their first month of breeding	All other kites
Mean weight of[a] prey items seen caught		
Hovering (n)	27,3 (11)	21,5 (78)
Perched-hunting (n)	26,7 (9)	28,9 (105)
Mean pellet weight (n)	1,45 (133)	1,26 (1857)
Mean food[b] weight (g)	44,61	38,53
No. prey items/pellet (no. pellets)	1,28 (144)	1,33 (2429)
Mean prey[c] weight (g)	34,9	29,0

a - estimated weight of prey seen caught by kites (see Chapter 2, p. 37)

b - calculated by ((mean pellet weight - 0,056)/0,025)(0,8)) from Tarboton (1977) and Chapter 2, p. 56

c - "mean food weight/no prey items/pellet" relationship between the number of broods (Fig. 4.6 c) and food supply (Spearman's $r_{17} = +0{,}59$; $p < 0{,}01$) suggesting that nestlings were present when feeding conditions were best (see Feeding and energetics, below). The proportion of pairs copulating was not significantly related to the food supply three months later (Spearman's $r_{14} = +0{,}27$; NS). A low level of significance between pairs copulating and food supply in the same months (Spearman's $r_{17} = +0{,}44$; $p < 0{,}05$) suggests that at least moderate food abundance was required for breeding to start. It is notable, however, that few pairs started breeding when prey densities were greatest in October-November 1977 and May-July 1978 (Fig. 4.8 b).

The close agreement between peaks in Figures 4.8 a and Figure 4.8 c & d suggests that the onset of kite breeding was associated with rodent breeding activity. Most kites started breeding either one month before (August 1977 and September 1978), or in the same month that juvenile rodents appeared (March-April 1978). Although not shown in Figure 4.8 c, great numbers of young rodents were seen during random fieldwork in October 1978 after the study had ended. This agreed with the high proportion of rodents breeding in the previous month. It is possible that kite breeding was stimulated by the appearance of juvenile rodents. However, kites starting to breed did not catch smaller (= younger) prey than other kites (Table 4.7).

Feeding and energetics

Table 4.8 shows the weights and energy values of food consumed by adults and young (average brood of three) at various stages of the breeding cycle. Since adult males supplied virtually all the food before the young left the nest (see above), they provided both the minimum (81,6 g/day during incubation) and maximum (236,8 g/day when large nestlings were present) quantities of food during the breeding cycle. The average weight of food supplied by males was probably about 121 g/day — calculated from data in Table 4.8 and assuming that they provided half the food requirements of

TABLE 4.8 Daily food (g) and energy (kcal) intakes per adult, per chick and per breeding unit at different stages of the breeding cycle. Only data for pairs successfully completing each stage are given. The number of chicks was taken as three (modal number, see p. 166 & 169) and their food weights were estimated from Figure 4.4b.

Stage and (duration)	Adults					Chicks		Family total	
	Pellet weight			Food[a] weight	Energy[b] intake	Food weight	Energy intake	Food weight	Energy intake
	mean	S.D.	n						
Pre-egg laying (24 days)	1,53	0,79	78	47,3[a]	87,0	-	-	94,6	174,0
Incubation (31 days)	1,33	0,66	127	40,8	75,0	-	-	81,6	150,0
Small chicks < 14 days (14 days)	1,44	0,63	86	44,2	81,3	22,9	42,1	157,1	289,0
Large chicks > 15 days (21 days)	1,67	0,95	81	51,8	95,0	44,4	81,7	236,8	435,6
Post-nestling (82 days)	1,41	0,61	245	43,3	79,6	43,3	79,6	172,8	317,9

a - food weight = (pellet weight - 0,056/0,025)(0,8). (See Chapter 2, p. 56)

b - energy intake = (food weight)(0,35)(5,84)(0,9). (See Chapter 2, p. 60) flying young, the other half being obtained by the young themselves and by females.

Taken individually, the food intakes of adult males and females also changed during the breeding cycle. Although data in Table 4.8 do not show independent changes for the sexes (pellets from males could not be separated from those of females), such changes may be inferred from activity budgets (Table 4.9) and the distribution of pellet weights (Fig. 4.9). For females there were chiefly two levels of food intake, one during the incubation and nestling periods and the other during the pre-laying period. Females were largely inactive during the incubation and nestling stages (Table 4.9) and their food intake was probably low, as reflected by low pellet weights during incubation (Table 4.8). In contrast, pre-laying females probably needed large quantities of food to meet their high energy requirements for egg production and the accumulation of body reserves. Three females trapped during egg-laying (one at Settlers and two by Tarboton (MS)) weighed 320, 320 and 333 g respectively. These high weights (<u>cf</u>. mean female weight of 256,4 g; Chapter 6 — Table 6.3) indicated that females stored large reserves of 25-30% during the pre-laying period. A bimodal distribution of pellet weights collected during the pre-laying period (Fig. 4.9) might indicate a marked difference in food intake between the sexes — the higher rate being that of females.

Food consumption by males was probably highest during the nestling period. Their energy expenditure was highest at this time as a result of the long periods they spent hunting to provision their mates and young (Table 4.9). An increased food intake, concomitant with an increased provisioning rate, is indicated by pellets being heavier during the late than the early nestling period (Table 4.8). A higher feeding rate by males than relatively inactive females is suggested by a bimodal distribution of pellet weights collected during the nestling period (Fig. 4.9). Unimodal weight distributions during

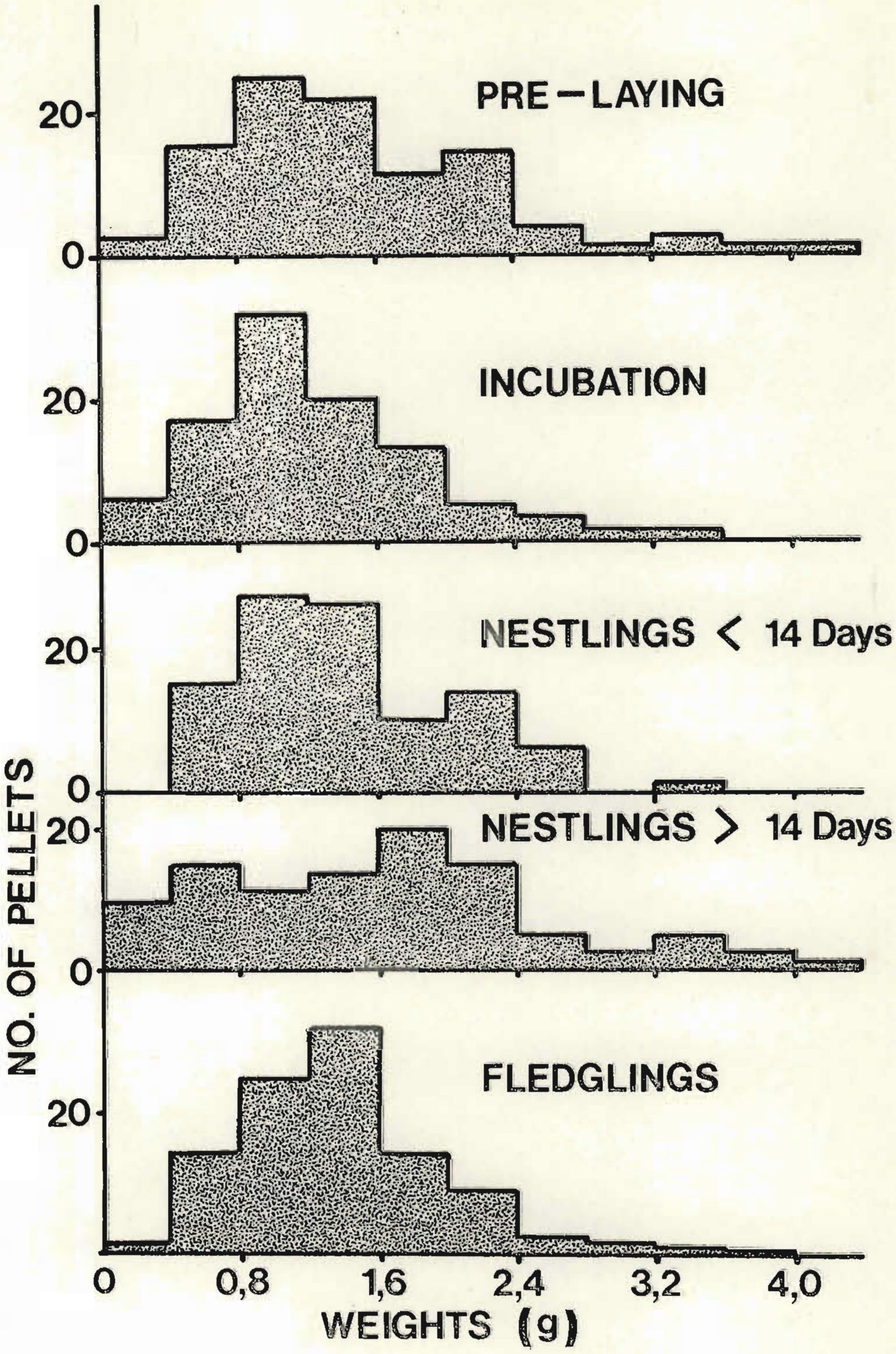


FIGURE 4.9 Weight distributions of pellets obtained from kites at various stages of the breeding cycle. Pellets during the post-nestling period include those of adults and post-fledglings; all others are from adults.

TABLE 4.9 Activity and energy budgets for inactive females during the incubation and nestling periods, and for males catching an average of 121 g of prey/day (see p. 178). Methods used to obtain the estimates are explained in the text (see p. 183 and Chapter 2, p.60; Table 2.15 & Appendix 2.1). Basal metabolic rates were calculated for average female (256,4 g) and male (235,2 g) weights (Chapter 6 - Table 6.3).

Activity	Total hours spent		Total kcal spent	
	Females	Males	Females	Males
Perched				
Inactive - night (1,7 BM)	10,40	10,40	21,7	18,7
Inactive - day (1,7 BM)	9,57	5,05	31,5	19,4
Low activity (1,7 BM)	3,05	3,05		
Feeding (1,7 BM)	0,52	0,52		
Hunting (3,5 BM)	0	2,88	0	13,3
SUBTOTAL	23,54	21,90	53,2	51,4
Flying				
Soaring (7,5 BM)	0,20	0,35	2,1	3,5
Directional (11,5 BM)	0,26	0,52	4,2	7,9
Hovering (11,5 BM)	0	1,23	0	18,7
SUBTOTAL	0,46	2,10	6,3	30,1
GRAND TOTAL	24,00	24,00	59,5	81,5

the incubation and post-fledging periods suggest that food intake did not differ as substantially between family members during these periods.

Time and energy budgets are presented in Table 4.9 for inactive females that did not hunt during the incubation and nestling periods, and for males providing an average 121 g of prey daily. Activity periods were based on Tarboton's (1978 a) measurements for "low activity" (see Chapter 2, p. 60), feeding, soaring and directional flight, my estimates, and calculated periods required to catch prey (from data in Chapter 2 and Table 2.16). Energy budgets were estimated using a model developed by Wakeley (1978 a,c) (see Chapter 2 — Appendix 2.1).

The estimates in Table 4.9 indicate that females spent most of their time (98%) perched, and that perched activity accounted for 89% of their daily energy budget (DEB). Males, however, spent 90% of their time but only 59% of their DEB in perched activities. Differences in DEB between males (81,5 kcal) and females (59,5 kcal) were therefore mainly due to differences in flying and hovering time. The DEB of females was about 27% lower than that of males. Both sexes spent large proportions of the day inactive. Of a 24-h day, females spent 83% and males 64% of the time inactive, and of an average 13,6 h of daylight (Chapter 1, p. 9), females spent 70% and males 37% of the day inactive.

DISCUSSION

Food, time and energy

Breeding birds are likely to be adapted to withstand energy shortages. The adaptations may vary according to how energy shortages arise, how often they are likely to occur, and when the birds are most vulnerable to shortages. Kites, and many other raptors, take relatively large prey with considerable time intervals between successive prey captures (Chapter 2 — Table 2.4). The capture of prey therefore tends to be unpredictable and temporary food shortages and gluts may arise at any time. Predators taking small items are more likely to obtain some food predictably because of the more even distribution of their prey, but being usually small, they are less able to take advantage of brief periods of super-abundant prey.

Female European Sparrowhawks Accipiter nisus, European Kestrels Falco tinnunculus, Greater Kestrels F. rupicoloides and Tawny Owls Strix aluco accumulate fat and protein reserves during the pre-laying period (Hirons 1976; A.C. Kemp pers. comm.; Newton 1979; Village 1979). The excessively high weights of three females trapped during laying suggests that female kites also store reserves during the early stages of breeding. Newton (1979) suggests that reserves not only provide energy for egg production, but also enable females to withstand sporadic food shortages during the incubation and nestling periods. Newton supports this argument by showing that incubating female European Sparrowhawks retain part of the reserves accumulated before laying. While reserves obviously benefit the female, there may be more important advantages for the nestlings. Food obtained during lean periods is likely to be eaten by the adults themselves. However, if an adult (in this case the female) can survive without food for a while, then whatever prey is caught can be passed to the young. The effects of temporary food shortages are probably more critical for developing nestlings than for adults.

Pairs of kites with a poor food supply either failed to lay or laid only after a longer pre-laying period than other pairs (Table 4.4). Similar results have been obtained for many birds (Cody 1966; Murton & Westwood 1977; Newton 1979) and there is some evidence that food shortages directly prevent egg production (Cave 1968; Drent & Daan 1980; Jones & Ward 1976). However, food supply may influence laying in other ways, especially if food reserves obtained before laying are used only later in the cycle. Insufficient reserves accumulated initially could predict poor feeding conditions in the future. It would seem logical to terminate, at an early stage, a breeding attempt that has a poor chance of success.

Pairs of kites that failed during incubation had a poorer food supply than those that hatched their eggs. An apparent lack of interest in nests displayed by females may have been among the first symptoms of food stress. Under more extreme conditions, females probably deserted the nest area to hunt for themselves. Similar inattentiveness by incubating female Tawny Owls has been noted during food shortages (Hirons 1976). Incubation attem by mates of inattentive female kites resemble behaviour recorded for severa raptors in which males fed nestlings after females had died (Snyder 1974; Tinbergen 1940).

In European Sparrowhawks, nestling growth rates and female attendance rates at nests during the nestling period were highest in good feeding area and lowest in poor areas (Moss 1979). Females probably left their nests to forage only when males were unable to provide adequate food, and these observations and conclusions seem to agree with the meagre data available f kites. However, nestling predation may be another factor influencing female hunting. In leaving the nest area to hunt, the advantages of obtaining food might be weighed against the potential loss of the nest contents to predators. During the nestling period, the food requirements of nestling sparrowhawks remained roughly constant (Newton 1978) and therefore did not match a linear increase in female hunting activity (Moss 1979). If females hunted only in response to food demands, a closer relationship between the two variables would have been expected. Instead, females may hunt increasingly because nestlings become progressively better at defending themselves.

Activity and energy budgets have been poorly studied in raptors (Moshe 1976). Most energy studies have concentrated on body size and thermodyna relationships, while activity has usually been studied during the incubati and nestling periods (reviewed in Chapter 2, p 64). Although energy and activity data in Table 4.9 are largely estimates, when compared with similar data for non-breeders (Chapter 2 — Table 2.15) they indicate some of the changes in time and energy use that occur during breeding. Non-breeding males and females spent 14% of daylight time hunting, while breeding males hunted for about 30% of the day and breeding females normally did not hunt (Table 4.9). Although breeding males were inactive for shorter periods than non-breeders, the average of five hours of each day spent loafing also represents a substantial proportion (37%) of their daily activity; this is discussed in Chapter 2 (p. 65). The daily energy budget (DEB) of non-breeders was about 67 kcal, compared with 59,5 kcal for females during the incubation and nestling periods. The average DEB of breeding males (81,5 kcal) was about 22% higher than their DEB as non-breeders. Changes of a similar order between non-breeding and breeding have been recorded for several other birds (Bryant & Westerterp 1980; Ettinger & King 1980; Kendeigh 1973).

Breeding males provided average maximum and minimum food weights of 237 and 82 g/day (Table 4.8). The ratio between these quantities was 237/82 = 2,9 times. It may be expected that males incurred different daily energy costs in hunting to obtain these amounts. However, the difference in DEB was probably substantially lower than the 2,9 times change in provisioning rate. Using average periods (Chapter 2 — Table 2.16) required to catch 237 and 82 g and adjusted activity and energy budgets (as in Table 4.9), the DEB of breeding males was about 112 and 71 kcal for maximum and minimum provisioning rates respectively, a ratio of 112/71 = 1,6 times. This ratio may in fact be too high. The calculations are based on constant rates of prey capture and therefore do not take into account changes in food availability (Fig. 4.8 & Chapter 2, p. 48). Because food supplies were poorest early in the breeding cycle, males probably spent more than 71 kcal/day while catching 82 g of prey during incubation periods. Similarly, males may have had lower DEB's than 112 kcal on days when they were catching maximum food quantities to supply their nestlings.

Sexual roles and reversed size dimorphism

Although parental roles and sexual size dimorphism vary greatly, in most birds larger males relieve smaller females at the nest (Kendeigh 1952; Skutch 1957). This enables one bird to forage while the other attends the nest. As a group, raptors are quite distinct in that normally smaller males provide most food while the larger females remain at their nests. Reversed size dimorphism in raptors and other predatory birds (e.g. owls, skuas and boobies) has attracted much theoretical interest (reviews in Amadon 1975; Balgooyen 1976; Newton 1979; Snyder & Wiley 1976). Newton (1979) has indicated that the degree of size dimorphism is related to prey size and agility. Those species that take the largest and most agile prey tend to be most dimorphic in size (Fig. 4.10). There has, however, been little agreement as to why females should be so large and males so small in these species.

While there need not necessarily be a causal relationship between parental roles and size dimorphism, I suggest that the storage of energy reserves during breeding affects both aspects in raptors. In addition, among raptors as a group, differences in energy storage are probably matched by proportional differences in size dimorphism.

Fat and protein reserves are likely to be most useful for those predators taking large prey items and therefore having the highest chances of encountering sporadic food shortages. Vultures and European Sparrowhawks take large prey and accumulate energy reserves during breeding (Houston 1976; Newton 1979). In Rüppell's Vulture *Gyps rueppellii* and the Whitebacked Vulture *G. africanus*, males and females store energy and share incubation and nestling duties equally. In contrast, only female

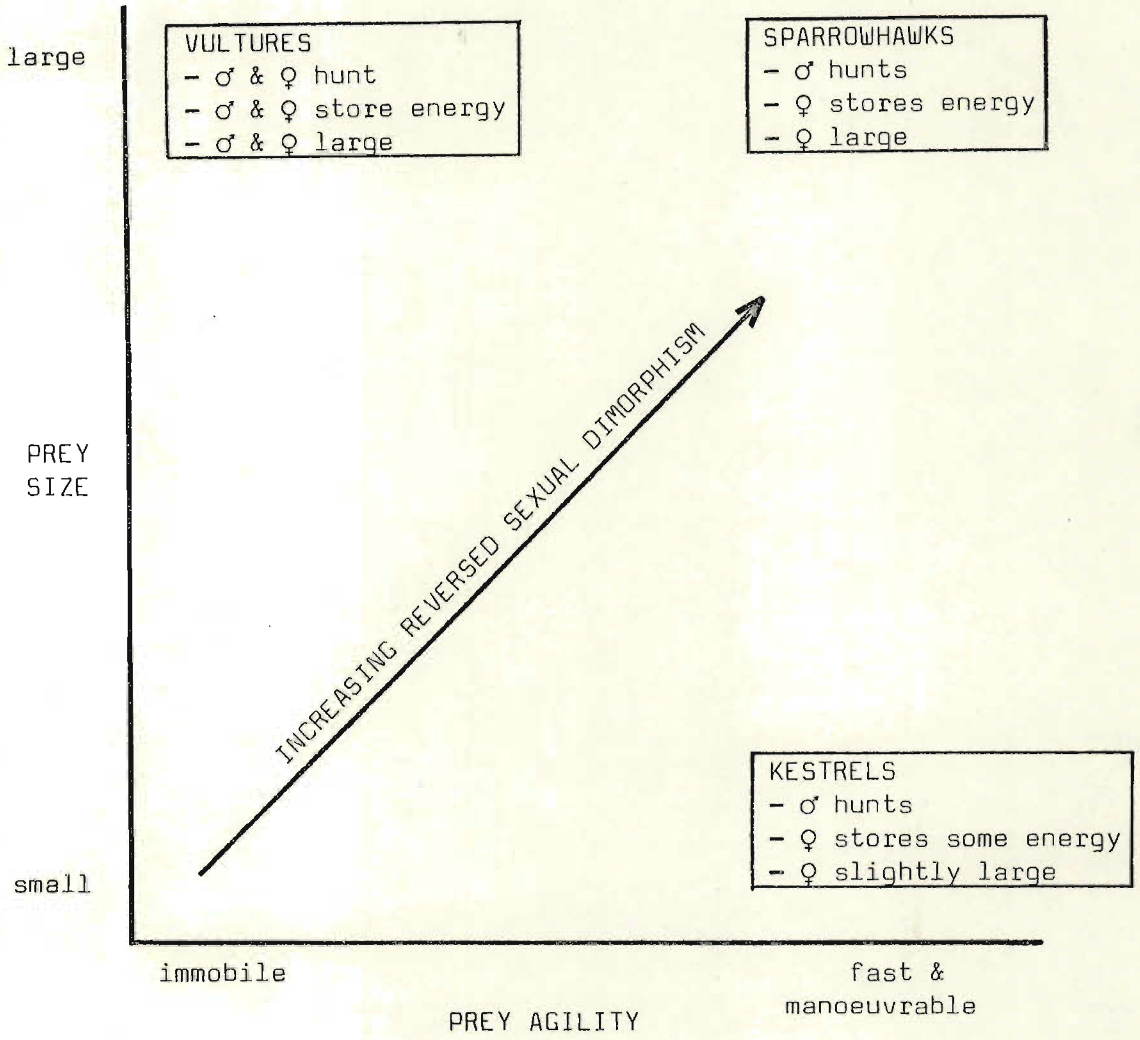


FIGURE 4.10 Hypothetical relationships between prey size and sexual size dimorphism and roles during breeding. The degree of reversed size dimorphism (females increasingly larger than males) increases as prey size and agility increases.

European Sparrowhawks maintain reserves and remain inactive at the nest. This raises the question — why do male European Sparrowhawks not help counter food shortages by also storing fats and proteins? The relevant difference between vultures and sparrowhawks probably lies in the mobilities of their preferred prey. Vultures take immobile prey and the increased weight of energy reserves may not affect their ability to exploit carcasses — they simply soar around and glide down to the prey. Sparrowhawks, however, catch fast-moving and manoeuvrable birds. A substantial weight increase probably affects their flight dimensions (wing loading *etc*.) and therefore reduces their efficiency in taking agile prey. For these reasons, the functions of energy storage and provisioning are separated in sparrowhawks, one bird acts as an energy reservoir while the other forages. Females probably take the former role because they accumulate reserves for egg production in any case.

These arguments can be pursued to explain reversed size dimorphism by now considering the influence of prey size. Where prey is large and the storage of energy reserves most important, selection will favour large size. This is because large birds can accumulate greater reserves than smaller birds (Cade 1980; Downhower 1976; Marcström & Kenward 1981; Ralls 1976), and since female sparrowhawks store energy reserves, they are larger than males. In vultures, with both sexes storing energy, males and females are equally large. Where prey is small and numerous and the chances of food shortages lower, selection for energy storage and therefore large size is probably not as strong. Insectivorous raptors are thus only slightly dimorphic, or even monomorphic in size (Newton 1979).

The suggested relationships between prey size, agility and energy storage are summarised in Figure 4.10. Selection pressures for accumulating energy reserves and hence large size, probably increase directly with increasing prey size. However, if the extra weight of reserves causes any reduction in prey capture efficiency, parental roles are likely to be separate. Since the prey of most raptors is to some degree agile, most males and females perform different roles in breeding.

Females may obtain several other benefits from being large. For example, they may produce bigger eggs at relatively lower energy costs, they can defend their nests more effectively, they may incubate more efficiently and they can provide bigger prey for their young (Downhower 1976; Ralls 1976; Schantz & Nilsson 1981). These advantages, however, are probably effects and not evolutionary causes of reversed size dimorphism. This is because they do not explain why females are largest in those species that take the biggest and most agile prey. Females of most species would be large if these benefits were so advantageous, but most females are small, at least relative to their mates.

The overall breeding strategies of a species may also influence the degree of reversed size dimorphism, *r*-selected birds being less dimorphic than *K*-selected ones. Species that breed opportunistically and frequently (*r*-selected) may be less adapted to countering food shortages and better geared to making repeat breeding attempts. In being able to start breeding attempts as rapidly as possible, they may store smaller reserves and thus avoid the long periods that females probably need to accumulate substantial reserves. This may explain why Blackshouldered Kites are only slightly dimorphic in size (Chapter 6 - Table 6.3), their ability to make frequent, opportunistic breeding attempts being possibly more important than withstanding food shortages. *K*-selected birds, in contrast, make fewer breeding attempts and are probably seldom able to make repeat attempts. They are probably better geared to withstanding food shortages and large energy reserves are therefore probably most important in ensuring the success of their infrequent breeding attempts.

Duration of the breeding cycle

A number of factors probably determined the duration of the breeding cycle, or any stage of it. Several factors may have operated to shorten the cycle while others tended to prolong it. Food availability was probably important throughout breeding in that selection favoured the compression of the whole cycle into those periods most favourable for breeding. In this respect, food supply was an ultimate factor, but feeding conditions may also have had proximate effects on each stage of the cycle, particularl the pre-laying and post-fledging periods. Incubation and nestling periods were probably less affected by feeding conditions (although see Moss (1979) and discussion above).

Pairs with a poor food supply laid after longer pre-laying periods than pairs with better feeding conditions (Table 4.4). Several factors may have caused such delays. It is possible that accumulated fat and protein reserves had to reach minimum thresholds before laying commenced. Laying may have been prevented because a) there was insufficient energy for egg production and, b) the reserves were inadequate to counter food shortages later in the cycle and females were therefore 'reluctant' to continue breeding attempts that would probably have failed. Pairs with poor food supplies may also have had insufficient time and energy to prepare nests rapidly.

There are two feeding strategies open to fledged young: self-feeding and begging food from parents. Davies (1978) showed that, irrespective of age, young Great Tits Parus major change strategy according to profitability. The young become independent once the benefits of self-feeding exceed those of begging. Since the profitabilities of the strategies can vary independently, post-fledging periods are likely to vary markedly. There are several possible ways in which feeding conditions could have caused the observed variation in the duration of kite dependence periods (Table 4.5). The periods might have been shortened if a) food was scarce and parental meanness reduced the rewards of begging or, b) food was abundant and the young soon profited more by catching their own prey. Conversely, post-fledging periods might have been prolonged by good feeding conditions (parents remained generous), or by food shortages (self-feeding remained unprofitable). Ultimately, though, long post-fledging periods would have benefited young by giving them added hunting experience in the relative protection of their parental territories. Young raptors evidently lead a precarious existence since mortality rates in the first year are high (between 50 and 83% in all populations studied (Newton 1979)).

Independence was probably not a fixed event that was achieved on a certain day. In several cases I missed seeing pre-independent young for a few days before resighting them on their parental territories. It was not certain that these young had left temporarily, but in a telemetry study of Redtailed Hawks Buteo jamaicensis, Johnson (1973) found that pre-independent young wandered far (1-35 km) from their parents and returned one to seven days later. Johnson concluded that the hawks gradually became independent.

Incubation and nestling periods vary according to raptor size, the largest birds have the longest, and the smallest ones the shortest periods (Newton 1979; Ricklefs 1968). Regression equations comparing female weight with incubation and nestling periods in Newton (1979) are convenient for comparing periods recorded for kites with those of other raptors. Using a mean female weight of 256,4 g (Chapter 6 — Table 6.3), the equations predict incubation and nestling periods of 31 and 33,5 days respectively. The incubation period agrees with that recorded, while a mean nestling period of 35 days suggests that kites spent slightly longer in the nest than expected on the basis of size. There was, however, substantial variation in the duration of the nestling period (see p. 166).

The duration of the post-nestling period also varies with body size (Fig. 4.11), although in any one species there tends to be much variation

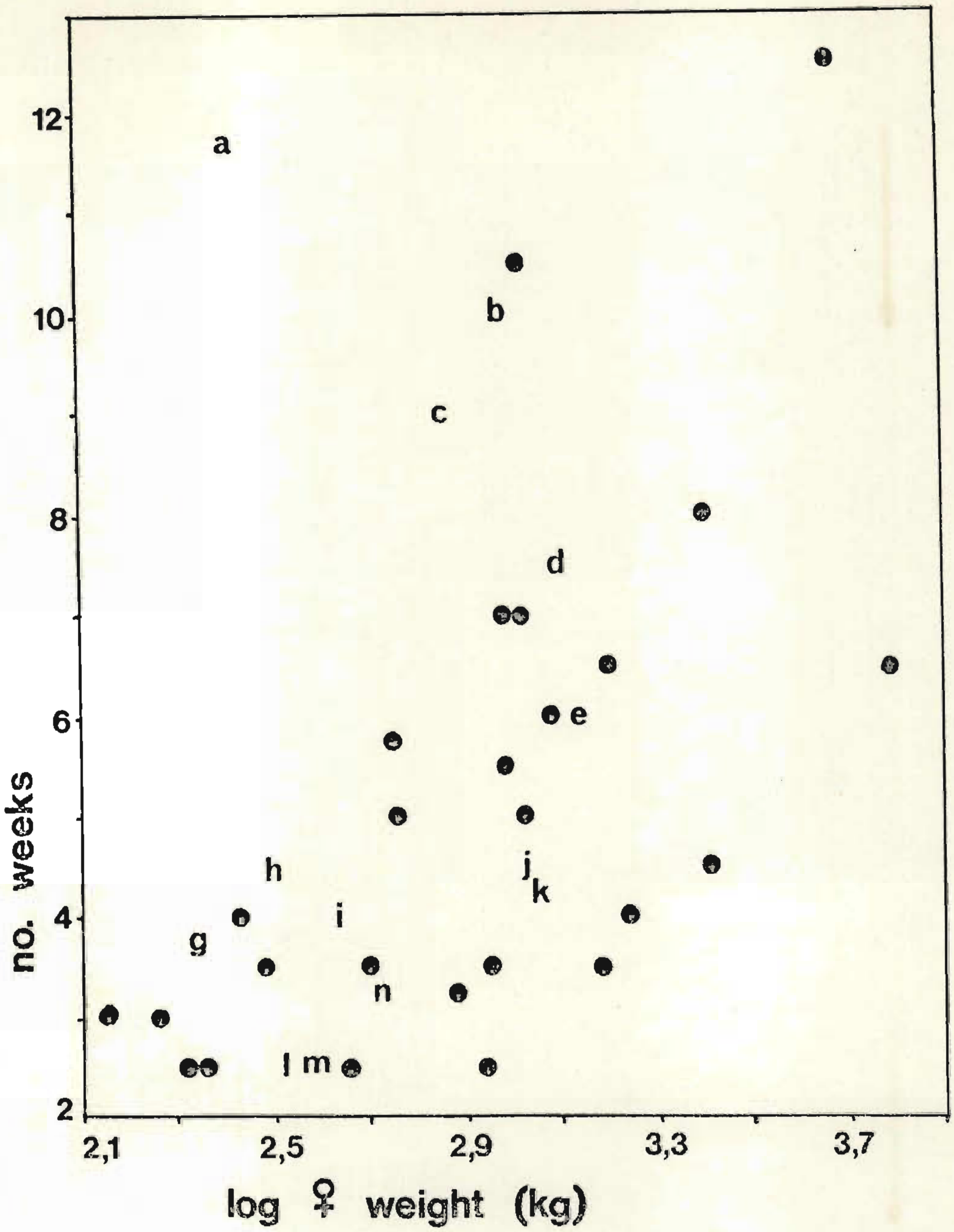


FIGURE 4.11 Post-nestling dependence periods compared with female body weight for specialist rodent predators (letters) and other raptors (●). a - Blackshouldered Kite; b - Buzzard Buteo buteo; c - Redshouldered Hawk B. lineatus; d - Redtailed Hawk B. jamaicensis; e - Longlegged Buzzard B. rufinus; g - Kestrel Falco tinnunculus; h - Whitetailed Kite Elanus leucurus; i - Aplomado Falcon F. femoralis; j - Roughlegged Buzzard B. lagopus; k - Swainson's Hawk B. swainsonii; l - Montagu's Harrier Circus pygargus; m - Pallid Harrier C. macrourus; n - Hen Harrier C. cyaneus. Based on data in Newton (1979).

(Table 4.5; De Vries 1975; Davies & Davies 1973; Johnson 1973; Newton 1979). From Figure 4.11 it is apparent that kites spend far longer dependent on adults than expected on the grounds of size alone. This may be connected with a preference for rodents: variation in strike success rates, intervals between kills and hunting methods (Chapter 2 — Table 2.4) suggest that there is abundant scope for errors in hunting. Long post-fledging periods probably allow young kites to learn hunting skills. Rodents may be harder prey to catch than fishes, reptiles, insects and other prey, since there is a tendency for specialist rodent predators to have longer post-fledging dependence periods than other raptors (Fig. 4.11).

Multiple broods and polyandry

A bird can raise more than one brood each year in two ways: it may either produce one brood and then start another, or it can raise different broods simultaneously (= polygamy). Kites show both tactics and possible reasons for males adopting the former and females the latter strategy are discussed in Chapter 3, p. 127.

Few raptors raise second broods (Table 4.10), probably because in most areas the favourable season is short. Not surprisingly, therefore, most records of successive broods come from places where long periods of abundant food are possible. Equally few raptors engage in polygamy. Polygynous breeding units have been observed in 12 species and polyandry in five raptors (Table 4.10).

Polyandry is conventionally divided into two forms: simultaneous and sequential polyandry in which a female pairs either simultaneously or successively with two or more males (Jenni 1974; Lack 1968). Galapagos and Harris's Hawks and Augur Buzzards practise simultaneous polyandry, but instead of attending their own separate nests, males cooperatively attend one female on one nest. This type of polyandry has been termed "cooperative polyandry" (Faaborg et al. 1980). Blackshouldered and Whitetailed Kites

TABLE 4.10 Birds of prey in which polygyny, double-brooding and polyandry have been recorded. After Brown 1980, De Vries 1975, Hollands 1977, Howell 1932, Lendrum 1979, Macdonald 1980, Maclean 1970, Mader 1975, Newton 1979, Smeenk & Smeenk-Enserink 1975, Waian 1973.

Polygyny	Polyandry	Double broods
Osprey *Pandion haliaetus*	Harris's Hawk *Parabuteo unicinctus*	Harris's Hawk
Marsh Harrier *Circus aeruginosus*	Galapagos Hawk *Buteo galapagoensis*	Galapagos Hawk
Montagu's Harrier *Circus pygargus*	Whitetailed Kite *Elanus leucurus*	Whitetailed Kite
Sparrowhawk *Accipiter nisus*	Blackshouldered Kite *Elanus caeruleus*	Blackshouldered Kite
Shikra *Accipiter badius*		Letterwinged Kite *Elanus scriptus*
Redtailed Hawk *Buteo jamaicensis*		Black Kite *Milvus migrans*
Buzzard *Buteo buteo*		Chanting Goshawk *Melierax poliopterus*
Augur Buzzard *Buteo augur*	Augur buzzard	Pygmy Falcon *Polihierax semitorquatus*
Kestrel *Falco tinnunculus*		American Kestrel *Falco sparverius*
Peregrine *Falco peregrinus*		Fish Eagle *Haliaetus vocifer*
Merlin *Falco columbarius*		

probably engage in sequential polyandry. Although successful second breeding attempts by females with new mates were not recorded during this study (see p. 167), these probably occur when feeding conditions are suitable. Data for Whitetailed Kites are unclear; Waian (1973) simply states that in the post-fledging period breeding females may "leave the territory, start another nest, or remain at the edge of the territory". The statement suggests behaviour similar to that recorded for Blackshouldered Kites.

Graul _et_ _al_. (1977) suggest that the evolution of polyandry is linked with temporal variations in food supply, polygyny being associated with spatial variations in feeding conditions. In particular, they suggest that unpredictable increases in food abundance late in the breeding season would allow females to produce repeat clutches. Their hypothesis is superficially supported by evidence from raptors. Four of the five species in which polyandry occurs may also produce successive broods (Table 4.10). None of the four species regularly breeds more than once a year, suggesting that their food supply may vary unpredictably. The relationship between polyandry and double brooding may be obvious for sequential polyandrists, but it is noteworthy that two cooperatively polyandrous raptors may also breed twice a year (Table 4.10).

Breeding rates and productivity

Productivity during this study (0,365 independent young/resident/year) was very low and probably unrepresentative of kites. Marked variation between years and different areas probably occurs in relation to uneven feeding conditions. If kites had bred maximally (two breeding attempts/year/territory), productivity could have been 11 times higher than the rate observed. In addition, kites might make more breeding attempts each year by reducing the duration of the pre-laying and post-fledging periods. During a rodent plague, Malherbe (1963; pers. comm.) observed kites starting second clutches while still feeding fledged young. Similar rapid breeding has been indicated for Whitetailed and Letterwinged Kites (Dixon et al. 1957; Hollands 1977; Waian 1973).

Using recorded periods of male and female participation in breeding attempts, calculations indicated that males could breed twice and females three times each year. The ratio of attempts (2 : 3) is the reciprocal of the observed sex ratio of males to females (3 : 2) (Chapter 3, p. 88). This means that three males, each breeding twice, could make six breeding attempts in a year; and two females, each breeding three times, would also make six attempts. Thus, although numbers of males and females and their breeding rates differed, the sexes ultimately might have made equal numbers of monogamous breeding attempts.

Nest sites

The height of kite nests appeared dependent only on the heights of available trees. Elsewhere in southern Africa, nests in Eucalyptus and Pinus trees may be 10-25 m above ground (S.A.O.S. nest records; pers. obs.), and one ground nest has been recorded (Cairns 1940). Kites also nest on telegraph and electricity pylons (Broekhuysen & Broekhuysen 1974; pers. obs.), sites which would seem to provide little protection against wind and direct solar radiation. This contrasts with sites at Settlers which seemed to provide shading and relative protection against prevailing ENE winds (Chapter 1, p. 9). The predominance of nests placed between west and south was equivalent to the nest orientation of Whitebrowed Sparrow Weavers Plocepasser mahali and Marsh Owls Asio capensis in the Settlers area (Mendelsohn 1968; pers. obs.). Of 17 Marsh Owl nests placed on the ground, 15 either faced south, south-west or west. Shading is probably an important aspect of nest site selection, particularly in hot climates. Of 25 deaths among Golden Eagle Aquila chrysaetos nestlings in Idaho, eight were attributed to over-heating (Beecham & Kochert 1975). Heat would probably also affect the incubating bird lying in the sun for hours on end.

Breeding seasons

Kites appear opportunistic in probably being able to breed whenever suitable feeding conditions arise. This flexibility is probably related to their strong dependence on rodent prey.

Rodent population dynamics in southern Africa are seldom predictable, with densities changing at different times and rates each year (Brooks 1974; Choate 1972; Coetzee 1967; Davis 1973; De Wit 1972; Perrin 1980). This is partly because rodent breeding is linked with rainfall (Coetzee 1965, 1967; Perrin 1980; Taylor & Green 1976). While rainfall is broadly seasonal over much of southern Africa, its timing and extent locally vary markedly (Schulze 1974).

Similar peaks in the onset of breeding (Figs. 4.6 & 4.7) suggest that changes in food supply at Settlers were similar to those usually experienced by kites in summer rainfall areas. Rodents generally breed in summer in southern Africa and densities become greatest between late summer and early winter (Brooks 1974; Coetzee 1965, 1967; Davis 1973; De Wit 1972; Perrin 1980). Egg-laying during March and April is therefore probably related to prey usually being abundant after summer. The egg-laying peak before the summer rains may also be linked with increased food availability, as suggest by the Settlers data (Fig. 4.8 b). Rodent populations are usually low at this time of the year, but the early production of young (Fig. 4.8 c), poor grass cover and extensive foraging by rodents may result in an increased available food supply (Chapter 2, p. 77).

Breeding seasons in the S.W. Cape winter rainfall area (Fig. 4.7) are less easily interpreted. David (1980) found that <u>Rhabdomys pumilio</u> densitie are lowest in September and highest between February and April as a result o summer breeding. Most kites, therefore, start breeding when prey populations are lowest and about six months before they peak.

The breeding seasons of most birds are probably timed so that periods of greatest food availability and demand coincide (Perrins 1970). This probably explains why kites started breeding before prey densities reached a peak. Breeding males had to catch the greatest quantity of food when chicks were present, two to four months after the onset of breeding (Table 4.8). In the light of these periods, a significant correlation was expected between the proportions of pairs copulating and food supply three months later. The absence of this relationship suggests that kites did not respond to predicted prey increases as efficiently as they might have done. Two factors may have prevented kites from timing their breeding more closely with changes in food supply. Firstly, food shortages may have prevented breeding from starting earlier, e.g. in January and February 1978 (Fig. 4.8 b). Secondly, rodent density often decreased unpredictably as a result of fire, grazing and other agricultural practices.

While an explanation is available for why kites start breeding before prey becomes abundant, it is less clear what stimulates breeding proximately. Most birds breed at the same time each year, their breeding being triggered by changing environmental factors such as daylength and rainfall. Variation in kite breeding seasons (Figs. 4.6 & 4.7) indicates that such proximate stimuli could not trigger breeding. The close link between breeding and food supply suggests that some feature of food itself may stimulate breeding. Four aspects of food supply may be considered.

Firstly, kites could start breeding whenever prey abundance, and therefore body condition, are above a certain threshold. A good food supply is certainly required during the pre-laying period for males to feed females and the formation of eggs (Table 4.8). However, data from Settlers do not suggest that a good food supply stimulated breeding. The correlation between food supply and the proportion of pairs copulating was weak, and few pairs started breeding when prey densities were greatest (Fig. 4.8 b).

Secondly, kites might respond to increasing food supply, gonad activity being stimulated by improving body condition. This idea assumes some mechanism in kites that measures changing body condition or food supply. Because environmental conditions during a period of rodent population growth are evidently favourable for rodent survival, it is probable that either similar densities or increases would be sustained for a while. The few data available do not support this second idea. There were nine months in which food supply increased from one month to the next (Fig. 4.8 b), but in four of these months less than half of the available pairs were starting to breed.

Thirdly, the proportion of juvenile rodents could be predictive of greater food availability in the near future. While there is good agreement between the onset of breeding and the appearance of juvenile rodents (Fig. 4.8 a, c), data in Table 4.7 do not suggest that more juveniles were caught in the pre-laying period than at other times. Kites would also face a problem of distinguishing the young of large species from adults of small species.

Finally, breeding may be stimulated by gonadal activity in their rodent prey. The presence of reproductive steroids in rodents could trigger similar hormonal activity in kites. Similar suggestions are made for rodents and fleas — plant oestrogens probably stimulate the production of reproductive hormones in rodents, and mammalian reproductive hormones stimulate breeding activity in fleas (Bodenheimer & Sulman 1946; Field 1975; Reynolds 1960; Rothschild et al. 1970; Taylor & Green 1976). A threshold response, based on numbers of breeding rodents, might provide an efficient index of future prey abundance. Consumption of a great number of breeding rodents would result in a high concentration of ingested gonadal hormones and predict a high rodent density in the near future. Conversely, smaller densities would be forecast by lower numbers of breeding rodents.

This hypothesis would be easy to test in the field or laboratory. Data in Figure 4.8 c & d provide some support for it by suggesting that great numbers of breeding rodents were present in August-September 1977, February-April and September 1978. Except for February 1978, most kite breeding started in these months. A poor food supply may have prevented kites from starting to breed in February 1978 (Fig. 4.8 b).

SUMMARY

The basic breeding behaviour and performance of kites is described. Attempts are made to relate breeding to feeding conditions.

The pre-laying period lasted an average of 24 days; some variation in the length of the period was related to food supply. Males fed females, and both sexes participated in building nests that were mostly sited on, and between the west and south sides of *Acacia* trees. Copulation and feeding were most frequent in the morning and afternoon, while nest building activity was greatest in the morning.

Incubation periods lasted an average of 31 days. Females normally did all the incubation. Incubation by males was probably related to poor feeding conditions, as was nest desertion.

Nestlings spent about 35 days in the nest. Growth rates were probably partly related to food supply. Females remained largely inactive around nests, while males provided most of the food for the family. Food intake by chicks was greatest between 14 and 21 days, and for one bird averaged 36 g/day over the whole nestling period.

Flying young remained in their parental territories for an average of 82 days. Adult females at most nests deserted after (average 20 days) the nestlings had left the nest. These females probably attempted to pair and breed with non-breeding males.

Breeding success was poor, most failures being due to nest desertion. Kites made many breeding attempts, up to seven in 19 months. At observed breeding rates, males could make two, and females three successful breeding attempts each year.

Kites started breeding throughout the year, but most attempts commenced in August-September and March-April. The timing of breeding varies between years and different areas of southern Africa.

The total feeding requirements of a family were lowest during incubation and highest in the nestling period. The daily energy expenditure of females was estimated to be 59,5 kcal during the incubation and nestling periods. The average energy spent by males over the whole cycle was about 81,5 kcal/ day.

The results are discussed and compared with those for other raptors. The accumulation of energy reserves by females during the pre-laying period appears to be a critical factor influencing the success and duration of breeding at most stages.

It is suggested that females remain inactive at their nests and are larger than males because they must maintain energy reserves to withstand sporadic food shortages.

Sequential polyandry is probably possible only because there are more males than females and because feeding conditions may sometimes allow females to start breeding again.

Productivity at Settlers was low, but many more young could have been produced if the food supply had been better.

Kites probably start breeding before their food supply reaches a peak. Several methods are suggested which kites might use to anticipate increasing rodent populations.

Chapter 5

GENERAL BEHAVIOUR

INTRODUCTION

This chapter considers the general behaviour of kites, particularly daily activities, maintenance behaviour, territorial defence, and roosting. Feeding and breeding behaviour are described in Chapters 2 and 4 respectively.

Comparative data on these topics are scarce for other raptors. For most species only general accounts are available, mostly as summaries in Brown & Amadon (1968). Correct interpretation of these accounts is often difficult, since almost all studies have been of unmarked individuals. It is thus often impossible to know if a raptor is interacting with its mate or an intruding competitor.

Roosting, particularly communal roosting, has attracted considerable attention and several species are known to congregate at night (review in Newton 1979). The function of communal roosting has variously been suggested to be anti-predator behaviour (Lack 1968) or facilitating the location of patchy food sources (Ward & Zahavi 1973).

METHODS

Data in this chapter were assembled largely from "instantaneous sampling" (Altmann 1974; Chapter 1), dawn-to-dusk watches and shorter observations of focal birds. The results were biased towards those periods of the day usually spent observing kites in the field (Chapter 1).

All conflicts of an apparently "territorial" nature were noted. Some conflicts were induced by chasing neighbouring birds towards each other. In addition, captive kites were tethered or flown (using falconry methods) in the territories of wild kites.

Calls were recorded on a Uher 4000C and displayed on sonagrams produced by a Kay Electric Sona-graph.

Nocturnal roosts were found by following kites at dusk or by systematically inspecting trees for accumulations of faeces and pellets. Analysis of pellets is described in Chapter 2.

RESULTS

Daily activity patterns

The main activities of five kites during dawn-to-dusk watches are shown in Figure 5.1. Hunting and inactivity accounted for 95, 96, 84, 96 and 95% (mean 93%) of the activities of the five kites, A - E, respectively. The balance of their activity was made up of short periods of feeding, flying and other miscellaneous behaviour. Not indicated in Figure 5.1 were 21, 4, 25, 11 and 22 min (mean 16,6 min) of feeding, and 37, 68, 51, 24 and 79 (mean 51,8) short flights made by the five kites in A - E respectively. Most of these flights lasted 5-20 s. The five birds also spent 0, 14, 2, 2 and 5 min (mean 4,6 min) soaring. ♂59 (C) also made four visits to his nest, spent a total 38 min on the nest, and made two FLUTTER display flights (Chapter 4, p. 148). All the kites preened intermittently during spells of inactivity. The general sequence of events for three kites, A, B and C, resembled the pattern seen on most days.

Percentages in Figure 5.2 are based on 3055 sightings. These data strongly favour activities readily observable from roads. Thus, kites perched on utility poles were conspicuous and over-represented in the counts, while birds perched inside trees or flying high were seldom recorded.

Kites usually spent their days in the following way. They left

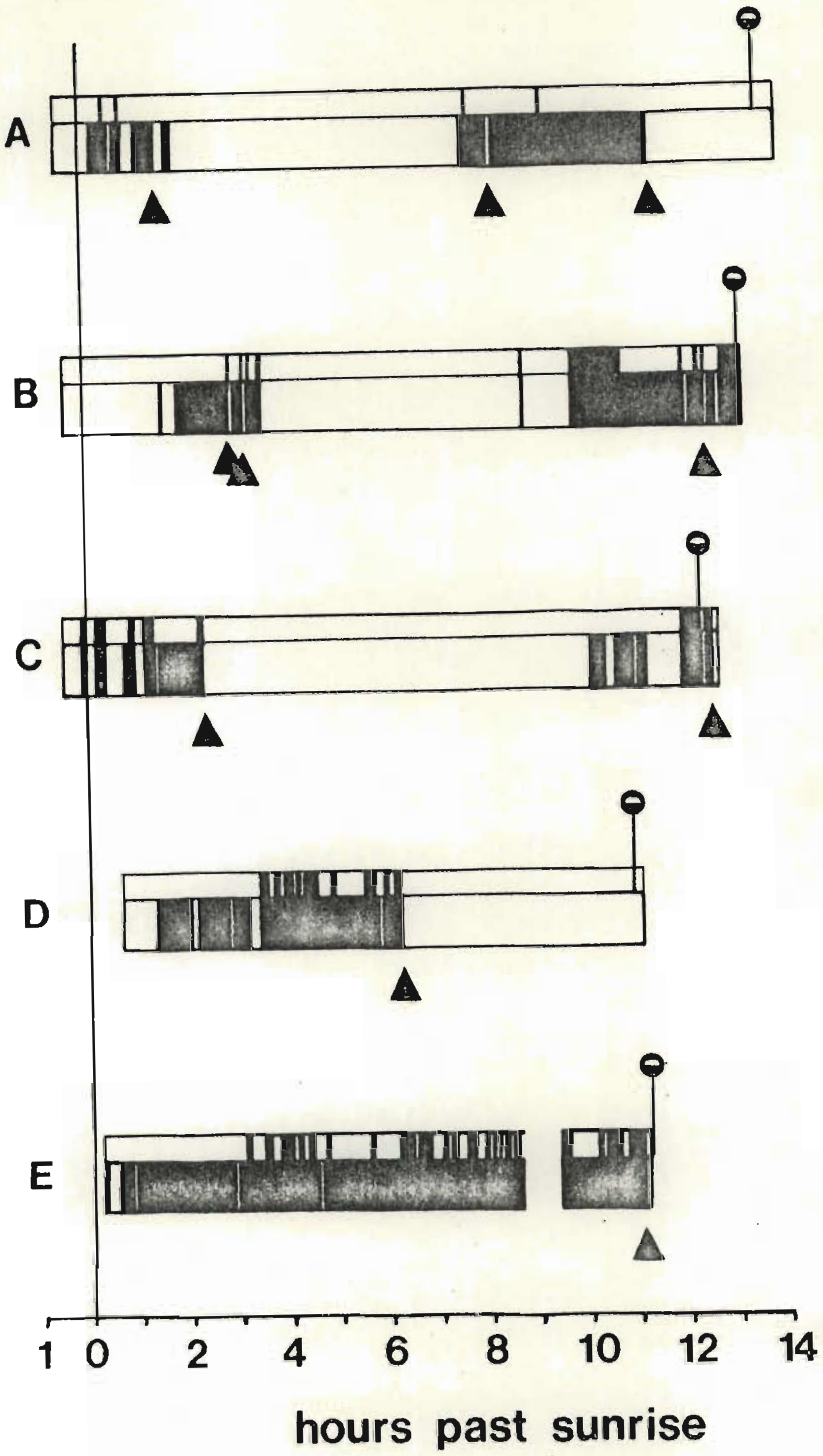


FIGURE 5.1 Distribution of hunting and other activity for five kites during dawn-to-dusk watches. Time spent hunting is shaded - upper bar for hovering, lower bar for all hunting. Sunset (●) and kills (▲) are shown. (A) - 20 Jan 1978, paired female; (B) - 9 Feb 1978, unpaired male; (C) - 16 Mar 1978, breeding male; (D) - 4 Aug 1975, female; (E) - 17 Aug 1975, same female as in (D). (D) and (E) from W.R. Tarboton (pers. comm.).

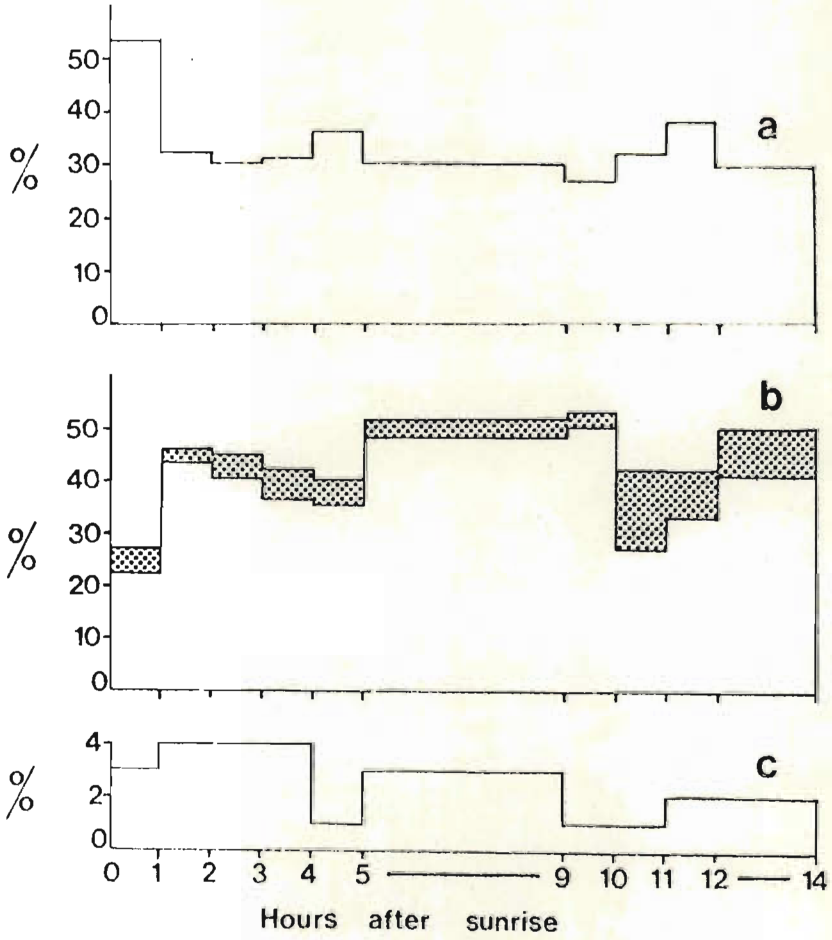


FIGURE 5.2 Percentages of kites inactive (a), hunting (b) and preening (c) during the day determined from 3055 sightings (Chapter 1, p. 13). Hovering kites (shaded) and perched-hunting birds (unshaded) are shown separately. Sightings between 05s00 and 08s59, and from 12s00 onwards were pooled.

their roosts 15-30 min before sunrise; four birds were timed at 29, 27, 25 and 19 min before sunrise. While some birds started hunting immediately (usually by hovering), most then flew to the focal areas of their territories (Chapter 3 p. 97). The kites then remained inactive for the next 30-120 min, sunning themselves and preening sporadically (Fig. 5.1 & 5.2 a).

Kites started hunting after this spell of inactivity. Perched-hunting predominated, interspersed with short bouts of hovering (Fig. 5.1). Short periods of inactivity and soaring were also observed during the morning hunting period. Soaring was normally associated with hovering (Chapter 2). Hunting usually ceased after prey had been caught (Fig. 5.1) and kites then returned to the focal areas of their territories, where they perched in the shade of large trees. On hot days, or often late in the morning, kites flew directly to shade before starting to feed. At lower temperatures they first fed and cleaned their bills and feet before flying off. Those kites that hunted unsuccessfully often continued hunting into the late morning and early afternoon (Fig. 5.1).

Most kites then spent the next several hours perched inactive in the shade. Three birds (Fig. 5.1 A, B & C) spent the midday siesta perched for unbroken periods of 5 h 59 min, 4 h 20 min, and 5 h 32 min respectively. The high percentage of hunting activity during midday indicated in Figure 5.2b is an exaggeration. Because most birds were perched inside trees, few kites were seen during this period; those that were seen tended to be hunting.

Hunting usually started again in the mid-afternoon, at first from perches, but later by hovering (Fig. 5.1 and 5.2b) as dusk advanced and nocturnal rodents became active (Chapter 2). The kites continued hunting until they caught prey or it became very dark. Those that caught prey early flew to roost early, while late hunters often arrived at roosts in virtual darkness (see Roosting, p. 221).

Of 1352 kites seen hunting (Fig. 5.2b), 14% were hovering and 86% perched-hunting. To the observer, kites hunting along roads from perches were, however, far more conspicuous than hovering birds, especially those hovering at great heights. Kites were carrying prey in 135 (4%) of all sightings, and 774 (25%) birds were flying, of which 25% were hovering and 75% were flying directionally or soaring. Tarboton (1978a) recorded kites flying in 18% of 849 sightings.

Territorial behaviour

The spatial and temporal properties of defended areas were described in Chapter 3. This section considers the advertisement and defence of territories.

Territorial advertisement was probably largely passive. Hunting birds hovered and perched prominently on telephone poles, trees etc. These positions and the white underparts of kites probably helped to make territorial kites conspicuous and to discourage potential intruders. The area of white on the underparts changed when kites altered their feather positions (Fig. 5.3f, g), suggesting that they might change their conspicuousness.

FLUTTER display flights (Chapter 4, p. 148) by males during the early stages of breeding probably served to advertise the positions of nest areas, if not the whole defended territories. One FLUTTER flight, at about 150 m above the ground, by an unpaired male (♂63) was observed. Ten minutes before this flight the male had been TAIL WAGGING (see below) in response to the presence of a captive female tethered in his territory. The flight may have been associated with mate attraction and/or the

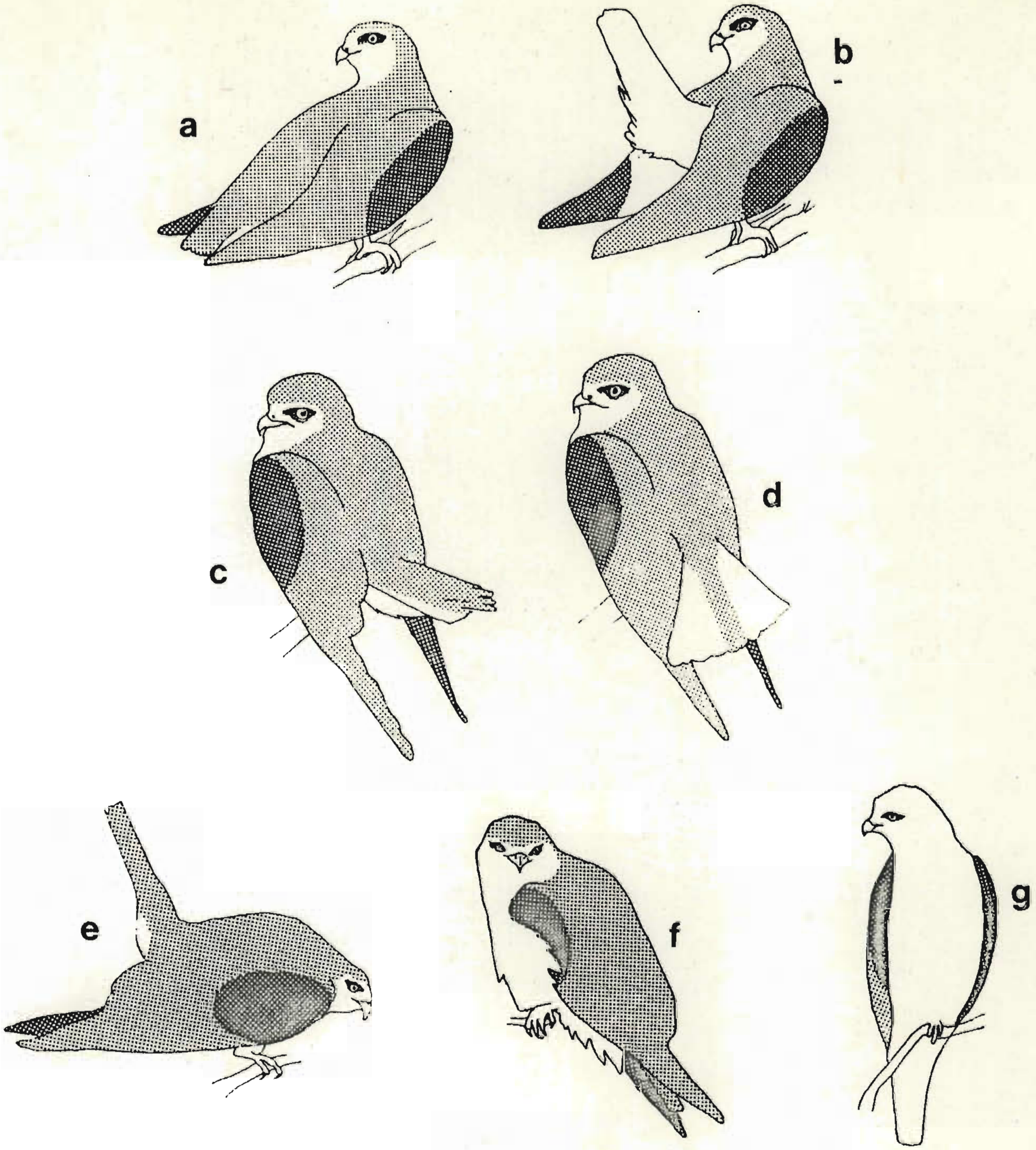


FIGURE 5.3 Kite postures drawn from photographs ((e) from Steyn (1963)). (a) and (b) - TAIL WAGGING, (c) and (d) - TAIL FANNING, (e) - TAIL WAGGING showing dropped wings, (f) - relaxed posture with body feathers fluffed, (g) - ANXIETY with crown feathers raised and body plumage sleeked.

advertisement of his territory. The former alternative seems probable since paired males (non-breeding) did not make FLUTTER flights. Similar high level flights by unpaired territorial raptors have been observed in several species (Newton 1979).

Residents repelled nomads and intruding neighbours from their territories. Even neighbours that moved as little as 10 m into a territory were attacked. Several patterns of behaviour were observed during conflicts and these are described below. Behaviour during territorial conflicts depended partly on whether intruders were neighbours or nomads (Table 5.1). "Undisputed" conflicts usually involved intruding nomads which simply flew off when residents TAIL WAGGED and TAIL FANNED and pursued them. Conflicts between neighbours were usually more contentious ("Disputed" — Table 5.1) but started with the same preliminaries as "Undisputed" encounters. However, they later involved dive-bombing or stooping, SHALLOW FLAPPING displays, and displacement preening. "Violent" conflicts (Table 5.1) included the same actions in addition to cartwheeling and one bird being struck to the ground by the other.

Territorial defendants always appeared to be winners. Table 5.1 suggests that half (35) of all encounters were 'undisputed'. This may be an underestimate since I probably missed some encounters in which the birds were far apart, _i.e._ I may have missed seeing one of the contestants. In conflicts in which the territorial defendants could be identified, 42 males and 17 females were defendants, and males and females jointly repelled intruders on six occasions. These figures suggest that males may have been more active in territory defence than females, but males were more often residents (Chapter 3) and females spent time restricted to their nest areas during breeding (Chapter 4).

TAIL WAGGING (Fig. 5.3a & b), in which the tail was cocked up and down repeatedly, was observed in all territorial conflicts. Viewed from

TABLE 5.1 Number of territorial conflicts involving intruding nomads and neighbours. The kind of conflict depended on the birds' behaviour (see text).

Type of intruder	Nature of conflict			Total
	Undisputed	Disputed	Violent dispute	
No. involving neighbours	8	27	7	42
No. involving nomads	27	1	0	28
Total	35	28	7	70

behind, the effect of the movement was similar to a white flag being flashe the white under-tail and crissum appearing and disappearing with each stroke TAIL WAGGING kites drooped their wings (Fig. 5.3e). The tail was moved mos rapidly and through the greatest arc (about 80°) during intense threat. In addition, the tail was occasionally held momentarily (about 0,5 s) at the top of the upstroke during intense threat. Normally the movement was stead with about one beat per second.

During intense threat kites also TAIL FANNED (Fig. 5.3c, d) The tail was spread progressively during the downstroke and closed on the upstroke. This movement exposed the white vanes of the five outer pairs of rectrices and, viewed from above, also had the effect of a white flashing flag.

TAIL WAGGING and FANNING were usually the first responses to intruders, and were often the only reaction to intruders flying overhead, particularly those flying high (above about 50 m). In some cases, however, residents did attempt to chase high flying trespassers, but the intruders had usually moved off by the time the defenders had soared to the same heights.

Most pursuits were directed at perched or low flying intruders and consisted of approach flights and subsequent chases. The approach flights were characteristically fast and low (1- 4 m), some of which were over considerable distances (200-1000 m). Most intruders flew off before being reached by approaching residents, which then either gave further chase or flew to perch on the sites last occupied by the intruders. The residents invariably TAIL WAGGED and TAIL FANNED while perched on these sites. Intruding nomads were often chased beyond territorial boundaries, but intruding neighbours were usually pursued until they reached their own territories. In some conflicts between neighbours pursuits continued across the boundaries, resulting in the pursuers being in turn chased back again.

Aerial fighting consisted mostly of dive-bombing or stooping, and normally occurred near boundaries during conflicts between neighbours. These disputes seemed more contentious than those involving only tail wagging and pursuits. During the flights there appeared to be continual contests for height superiority, since the higher bird could repeatedly stoop at the one below. Dive-bombing birds were usually able to maintain their advantage by swinging up again in pendulum fashion. The lower bird frequently attempted to gain height by flying upwards with rapidly flappin wings. A stooping kite that did not return to its higher position was the often attacked.

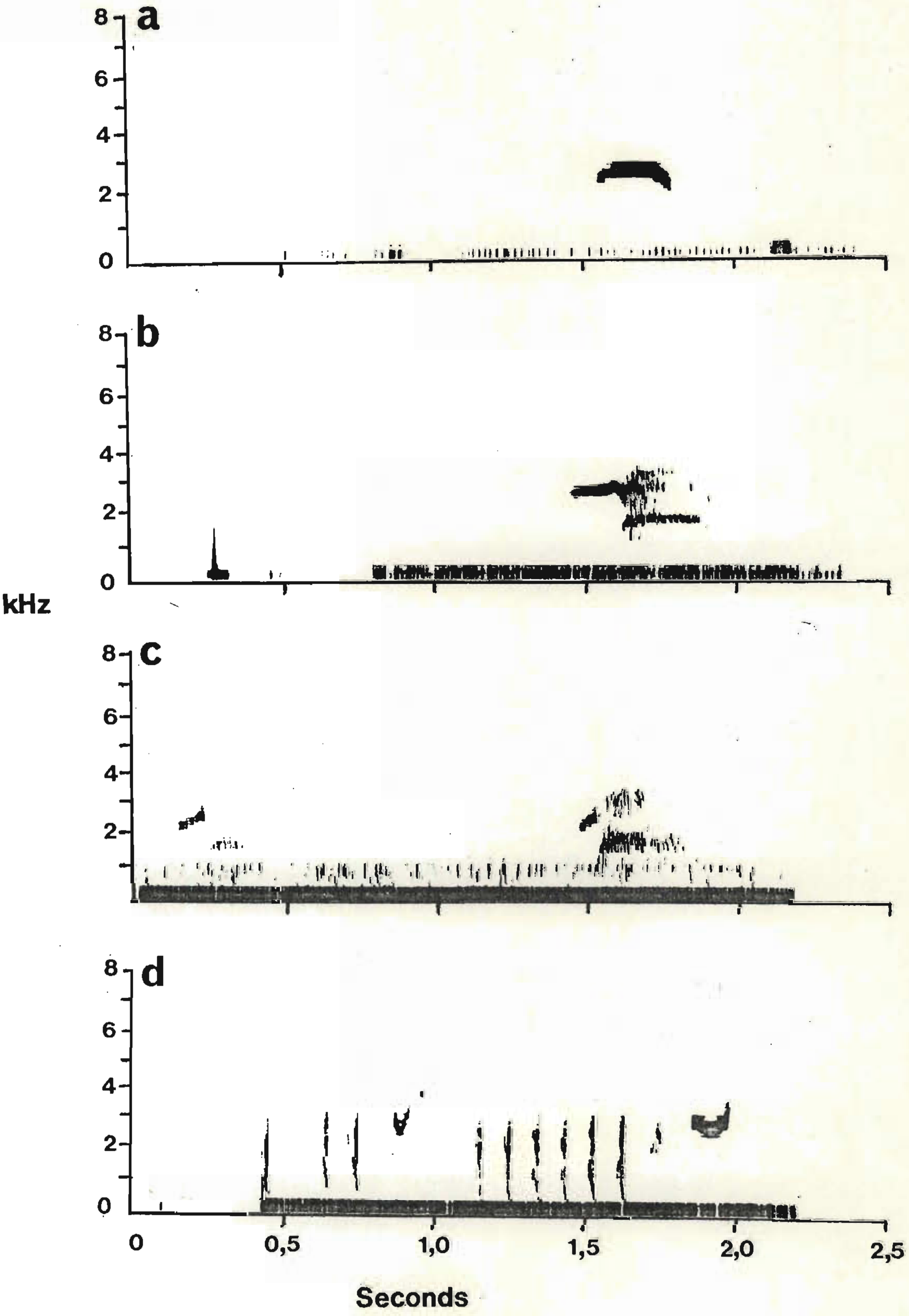
As a stooping bird approached, the lower bird normally turned and extended its feet to the attacker. Contact between the birds was frequent and in five cases the kites locked their feet and cartwheeled down. Three times the birds broke loose after falling 5-20 m, but twice they fell to the ground. None of the birds appeared injured; once they flew off immediately, and once they continued grappling on the ground for 15 s.

Contestants were forced to the ground during several aerial fights. This was first observed while flying a captive kite in the territory of a wild kite. The captive was repeatedly stooped at and struck until eventually it was lying on its back. The wild kite then ceased diving, but, as soon as the captive stood or attempted to fly, it was forced down again. In another conflict, a nomad was forced into a wheat field by a pair of territorial birds. The pair circled above the grounded bird and stooped only when it attempted to fly off.

Similar observations were made during attacks on tethered captives. The captives were usually placed on perches about 1 m high, and were repeatedly attacked at this height. Few attacks occurred, however, if they perched on the ground, often after being forced off their perches.

After bouts of stooping kites often started SHALLOW FLAPPING which was similar to the flight of kites inspecting potential nest sites (Chapter 4 p. 150). The wings were flapped through a shallow arc near the horizontal and the legs were extended below the bird. This display was often performed by both contestants, simultaneously or separately. However, display by one bird did not necessarily stop the other from stooping and attacking it. The contestants usually displayed as they flew in opposite directions to settle on nearby perches. Whistling (see below) was often heard during SHALLOW FLAPPING.

Calls heard during territorial conflicts were given with TAIL WAGGING and FANNING and SHALLOW FLAPPING displays. Most calls consisted partly or fully of whistles and screams. There was a range of intermediate WHISTLE-SCREAMS between full whistles (LONG WHISTLES) and screams (SHORT SCREAMS) (Fig. 5.4 a, b, c). The lengths of the whistle and scream components in WHISTLE-SCREAMS varied inversely so that some calls contained long whistles and short screams while others consisted of short whistles and long screams. SHORT SCREAMS that were not preceded by whistles were heard occasionally but were not recorded on tape. Both LONG WHISTLES and SHORT SCREAMS were heard only when contestants were close to each other (5-50 m), but WHISTLE-SCREAMS usually seemed to be directed at kites at greater distances. Calls containing scream components were heard only from perched kites and may have indicated intense threat since LONG SCREAMS were used at close range in extreme threat conditions (Chapter 4, p. 156 & Fig. 4.2e). LONG WHISTLES were the most frequent calls during conflicts and were given by perched and flying kites. Compared with other whistles (Fig. 5.4 d & Chapter 4 — Fig. 4.2a, b), LONG WHISTLES lasted longer and were spaced at



continued on p. 216

continued from p. 215

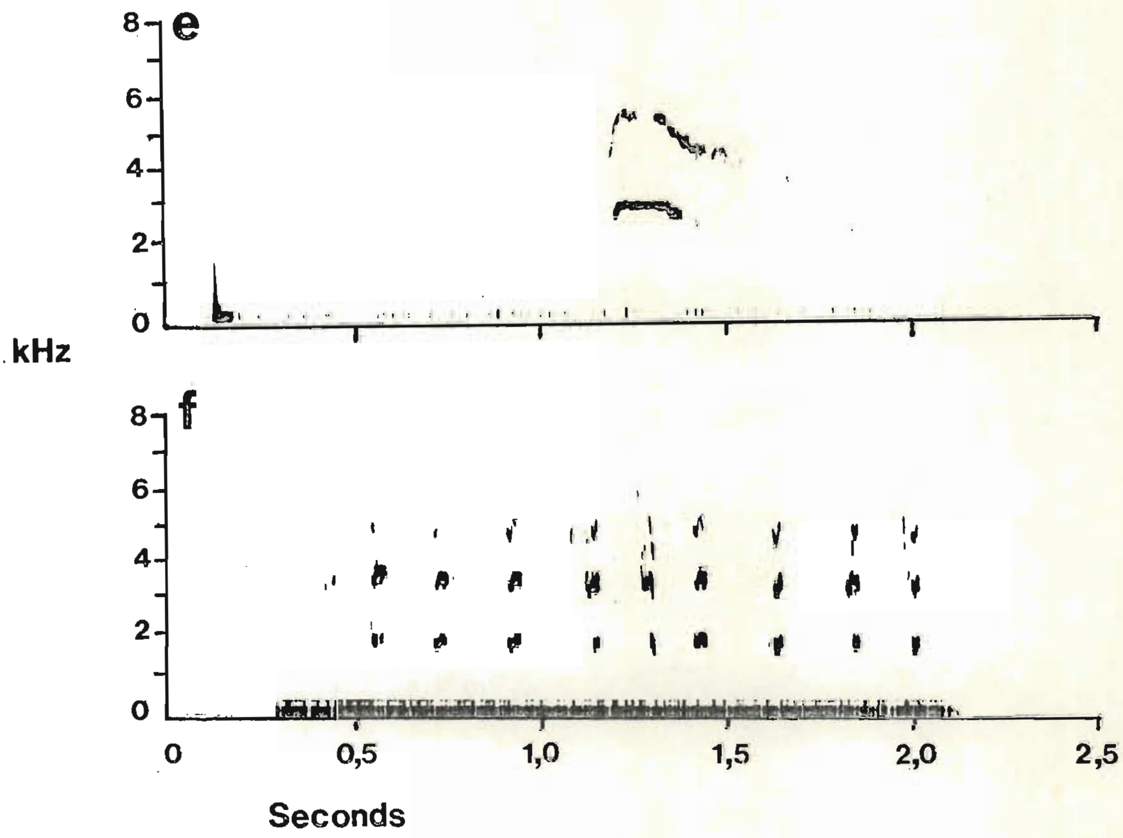


FIGURE 5.4 Wideband sonagrams of calls heard during intraspecific (a-d) and interspecific conflicts (e & f). (a) LONG WHISTLE, (b) and (c) WHISTLE-SCREAMS showing different lengths of 'whistle' and 'scream', (d) HIGH WHISTLES and CHATTER calls, (e) SHRILL SCREAM, and (f) YELP call. See text for further explanation.

greater intervals of about one whistle/2 s. HIGH WHISTLES were given at about 1-s intervals and were shorter and higher pitched.

HIGH WHISTLES were often given by kites performing SHALLOW FLAPPING displays but were also interspersed with CHATTER calls given by kites perched close to each other (5-10 m) (Fig. 5. 4d). CHATTER calls were given in conjunction with a BOWING display in which the calling kites bowed their heads and held their bodies horizontally. A captive kite uttered a CHATTER when it viewed itself in a mirror. The duration of CHATTER calls varied greatly, occasionally lasting only 2-3 s and at other times continuing for 10-20 s.

TIP..TIP calls (Chapter 4 – Fig. 4.2c) were twice heard during territorial conflicts when contestants were displacement preening. This call was frequently heard from males during the early stages of breeding.

Kites displacement preened intensely after spells of aerial fighting when they perched opposite each other across territorial boundaries. While all feather regions appeared to be preened, the kites did not stretch their wings or scratch their heads (activities seen during normal preening), see p. 219. In addition, they also often cleaned their bills and feet, movements which were usually associated with feeding (p. 219). The contestants often called and TAIL WAGGED and FANNED during displacement preeni

Interspecific relations

Kites usually showed fear of large raptors and crows, and adopted a distinctive ANXIETY posture — upright stance, sleeked plumage and raised crown feathers (Fig. 5.3g) — when these birds approached or soared overhead. The kites did not move in this posture which appeared to reduce their conspicuousness. But kites also regularly attacked the same large birds that approached their nests or fledged young. Their attacks mostly consisted of repeated stooping and chasing until the intruder left the area.

Steppe Buzzards Buteo buteo often flew up to hunting kites and sometimes attempted to pirate prey. One buzzard pursued a kite carrying an *Otomys angoniensis* which it subsequently dropped after a chase of about 500 m. Kites were particularly aggressive towards Pied Crows *Corvus albus* which probably took the contents of unguarded kite nests. Once, four crows harrassed a female kite covering her eggs. Her mate repeatedly stooped at the crows but for 10 min they refused to leave the nest tree. Lanners *Falco biarmicus* were usually pursued if they approached nests or fledged young. At other times, kites showed fear of Lanners by adopting their ANXIETY posture. Greater Kestrels *F. rupicoloides* were also attacked near kite nests. The kestrels probably dominated kites because one pair occupied a kite nest, and one pair of kites left their nest area when kestrels began nesting in the same area. Four Marsh Owl *Asio capensis* nests were found within 50 m of active kite nests, in one case only 10 m away. Occasionally kites stooped at owls flying during the day, but usually there was little aggression between kites and the many (about 200) owls in the study area.

Perched kites gave SHORT SCREAMS or WHISTLE-SCREAMS (Fig. 5.4b,c) when large birds approached. Stooping kites, however, uttered a distinctive SHRILL SCREAM (Fig. 5.4 e) which was given when the stooping birds passed closest to the intruders. Captive kites held in the hand emitted a YELP call (Fig. 5.4 f) and some wild birds caught for ringing gave LONG SCREAMS (Fig. 5.4 c). Both calls suggested distress at the hands of a potential predator.

Maintenance behaviour

Display flights, hovering and other special flights have been described elsewhere (see p. 214 Chapters 2 (p. 21) & 4 (p. 148)). Directional flight from one place to another was usually in a straight line with a regular wing beat. Kites usually flew low over the ground while flying into wind, probably to benefit from the lower wind speeds. Long flights over distances of more than 2 km were normally at heights of 50-150 m, and kites soared initially to reach these heights. Recently fledged young often performed an undulating flight. They flew at heights of 10-20 m and at intervals of 40-100 m, diving obliquely to just above the ground before rising again. The same flight was seen several times in adults but no function could be recognised.

Feeding and the collection of nesting material accounted for most activity on the ground. Kites either walked a few steps or jumped and flew over greater distances.

Stretching usually occurred during preening or in a spell of inactivity during hunting. The actions were similar to those of other birds and consisted of single wing, leg and tail stretch; double-wing stretch; and jaw stretching or "yawning".

Rousing, or vigorous shaking of the feathers, occurred during preening or after a spell of inactivity just before a kite flew off. A kite was certain to take off within 1-2 min (usually sooner) if it roused and defaecated in quick succession. Faeces were muted (simply dropped) rather than sliced (squirted away from the tail).

Claws II and III were used to scratch the sides of the head and base of the bill directly. The bill was held slightly ajar with the lower mandible slightly retracted while scratching near the base of the bill.

Kites preened sporadically throughout the day, but most frequently during the morning and midday (Fig. 5.2 c). Preening was often intense for 10-30 min during spells of inactive perching, but they frequently preened sporadically during bouts of hunting. Preening birds nibbled at powder down patches on the sides of the pelvis.

After feeding on prey items that had been torn into pieces, kites spent some time (20-120 s) cleaning their bills and claws. The bill was pulled over the claws, any scraps of flesh being removed and eaten. Claws II, III and IV were cleaned in this way with II being cleaned most. Claw I was cleaned by nibbling at pieces of adhering flesh. The bill was

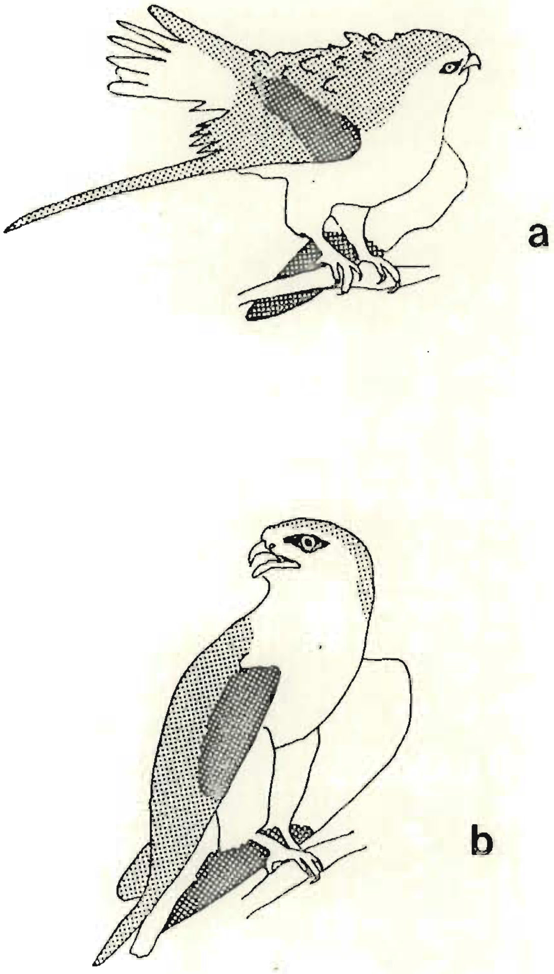


FIGURE 5.5 Comfort postures drawn from photographs. (a) - bathing in rain, (b) - cooling.

cleaned by rubbing it rapidly along the edge of the feeding perch.

Four wild kites were seen bathing during rain showers, and my tame birds regularly bathed under lawn sprinklers. Bathing occurred only during soft downpours and after hot and dry periods. The kites perched horizontally with wings and tail spread and the dorsal contour feathers raised (Fig. 5.5 a). The wings were flapped slowly and the birds moved up and down and around, presumably to allow water penetration. Bathing continued for 2-5 min.

In the early mornings, especially in winter, kites perched low down (1-2 m) in the sun. Their feathers were fluffed and the birds were probably warming themselves. True sunbathing was observed once: a captive kite hopped down onto the floor of my truck, spread its wings and tail and lay resting on its tarsometatarsals. The floor of the open truck was warm after standing in the sun.

At shade temperatures above about 25°C kites attempted to cool themselves by standing high on their legs, holding their wings away from their bodies, sleeking their contour feathers and panting (Fig. 5.5b).

Roosting

Most kites arrived at roosts 10-35 min after sunset (Fig. 5.6). Early arrivals usually perched in trees near roosts and then flew from tree to tree and occasionally chased each other. They flew to the roost tree later and often hopped from perch to perch before finally settling. Late arrivals went directly to their roosting sites. Discrete accumulations of faeces and pellets suggested that certain perches were favoured and probably occupied by the same individuals.

Roosts in the study area were in Acacia nilotica (eight), A. caffra (three), A. flecki (two), A. karroo (one), Rhus pyroides (six) R. lancea

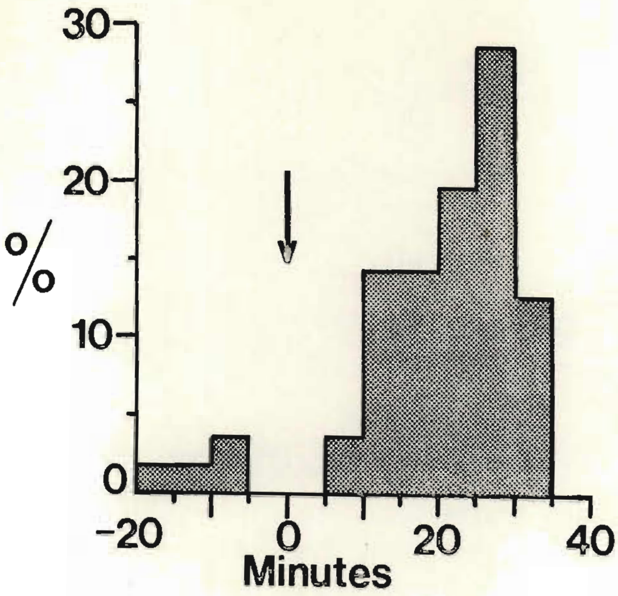


FIGURE 5.6 The number of minutes before and after sunset (arrowed) that 56 kites arrived at their roosts.

FIGURE 5.7 The number of kites in roosts observed each month. Each dot shows an active roost.

(one), Zizyphus mucronata (two), Eucalyptus sp. (one) and Melia azedarach (one). The paucity of roosts in Acacia tortilis and A. flecki, the two commonest trees and those used most often for nesting (Chapter 4 — Table 4.2), was notable. These two species lacked exposed dead branches that were favoured roosting perches for most of the year. Most A. nilotica, in contrast, had many suitable perches. During the winter months of May to August kites roosted within the foliage of Rhus pyroides, R. lancea and Melia azedarach trees, the perches being sheltered by surrounding leaves.

Kites roosted alone, in family parties, or communally with neighbouring residents and occasional nomads being drawn to group roosts. The number of kites in different roosts varied between one and 22. When first found, six roosts had one kite, 11 had two birds, seven roosts had three or four kites, five had five to eight birds and two roosts had more than nine attendant kites. Kites that roosted alone were either unpaired birds or breeding males (females roosted on the nest). Those in larger roosts of up to six birds were pairs, family groups or neighbouring residents. Numbers also varied from night to night as some birds joined and others left the roost. The largest roosts were usually observed in summer and winter (Fig. 5.7) when few birds were breeding (Chapter 3 — Fig. 3.7). As autumn and spring approached the numbers dropped when breeding birds started roosting on their territories. With most roosts being small, kites seldom had to fly more than 3 km from their territories to roost. Most probably flew 1-2 km on each journey, which would have taken only 5-10 min of flying.

Kites that roosted communally had a poorer food supply (lower pellet weights — Chapter 2) than those that chose to roost solitarily on their territories (Table 5.2). There was also a tendency for food supply to become poorer as roosts became larger, i.e. roost size and food supply

TABLE 5.2 The weights (g) of pellets collected from roosts of various sizes. Pellets from family roosts (parents + flying young) were excluded.

No. kites in roost	Mean pellet weight	Standard deviation	No. of pellets
1	1,34	0,59	61
2	$1{,}40^{a}$	0,68	212
3-4	$1{,}31^{ab}$	0,64	243
5-8	$1{,}12^{b}$	0,66	259
⩾ 9	1,15	0,64	385
All non-communal	$1{,}37^{c}$	0,65	245
All communal	$1{,}20^{c}$	0,64	915

^{aa}N.S.; $^{bb}p < 0{,}005$; $^{cc}p < 0{,}005$

may have been inversely related.

DISCUSSION

The descriptions of calls here and in Chapter 4 p. 154 should be considered as preliminary only. The general similarity of many of the whistles and screams, and the variety of contexts in which calls were used, suggest that a detailed study is necessary to understand the calls fully. I found also that many calls were difficult to identify since they seemed ventriloquial and were almost inaudible at more than 50 m. However, some tentative comparisons can be made between the calls and displays of Blackshouldered Kites and the three other Elanus species.

Several whistles and screams have been described in various written forms for all three species, suggesting that the basic structure of most Elanus calls is the same. Hollands (1977) notes that the Letterwinged Kite utters a "high clear whistle" and a "harsh rasping jarr" and these may be equivalent to any of the whistles and screams of the Blackshouldered Kite. Calls listed by Brown & Amadon (1968) for the Letterwinged Kite include a "wee-er wee-er", which may be the same as a WHISTLE-SCREAM (Fig. 5.4 b,c), a "kar-kar-kar", a "kack-kack-kack" and a "chirp-chirp-chirp". The latter call, observed in males carrying prey, may be analagous to the TIP...TIP call (Chapter 4 — Fig. 4.2 c). A number of authors have described WHISTLE-SCREAMS in the Whitetailed Kite as, for example, "keerack" (Peyton 1915) or "eee-grack" (Watson 1940). Furthermore, a sonagram in Waian (1973) and tape recordings I have heard (from the Library of Natural Sounds, Laboratory of Ornithology, Cornell University), suggest that WHISTLE-SCREAMS are identical in Whitetailed and Blackshouldered Kites. These tape recordings indicate also that Whitetailed Kites have very similar BEGGING and LONG SCREAMS and TIP... TIP calls (Chapter 4 — Fig. 4.2). Watson (1940) describes the TIP...

TIP call in Whitetailed Kites as "chip-chip", and Brown & Amadon (1968) give the same description for a call of the Blackwinged Kite. A tape recorded whistle of the Whitetailed Kite was slightly higher pitched than most whistles of the Blackshouldered Kite, but was reminiscent of a LONG WHISTLE (Fig. 5.4 a). Waian (1973) presents sonagrams of two whistles given by Whitetailed Kites but, apart from a general similarity to LONG WHISTLES and INTENTION WHISTLES (Chapter 4 — Fig. 4.2 a), it is not clear whether the calls are comparable or not.

FLUTTER display flights (Chapter 4, p.148), or very similar displays have been observed in the three other species, while SHALLOW FLAPPING and TAIL WAGGING are known for the Whitetailed Kite (Brown & Amadon 1968; Hollands 1977; Waian 1973; Watson 1940; D. Manry pers. comm.). TAIL WAGGING, and no doubt TAIL FANNING, probably also occur in the Blackwinged and Letterwinged Kite since, curiously, this conspicuous display has seldom even been reported for the Blackshouldered Kite.

These brief comparisons and those of social and spatial behaviour in Chapter 3 (p.135), indicate that Elanus kites have rather similar patterns of behaviour. On present evidence, it seems that there are few, if any, marked differences between the allopatric Blackshouldered, Blackwinged and Whitetailed Kites.

Steyn's (1963) observations and those reported here suggest that TAIL WAGGING and FANNING were used in conspecific threat, FANNING probably indicating more intense threat. Both movements displayed white feathers that were usually concealed. Displaying kites also drooped their wings and this exposed the black "shoulder" feathering maximally (Fig. 5.3 e). The exposed black area possibly provided a contrasting background which helped emphasize the white signals of the tail.

Perched-hunting birds often TAIL WAGGED just before attempting to catch prey. In this "non-conflict" context kites were probably warning away potential intruders to the immediate areas in which they were searching. Such intruders included mates and fledglings, and hunting kites certainly displayed when these birds came close. Hunting kites probably benefited from keeping others away because the movements of intruders may have alarmed rodents moving into open areas where they were accessible for capture.

Throughout the study, kites gave the impression of being sensitive to even slight temperature extremes. Much of their behaviour, aside from feeding and breeding, was linked to cooling or warming themselves. On hot days they soared, perched inactive for long spells in shade, sleeked their plumage, exposed their legs and underwings to airflow, and panted. Their nest sites also probably protected incubating females and nestlings from direct sun during the heat of the day (Chapter 4, p. 197). To warm themselves, they fluffed their plumage and perched low down where they were least exposed to wind. In winter they sought roosting sites where there was a minimal flow of cold air. Although several authors (review in Mosher 1976) have examined thermodynamic relations in raptors and owls, the subject deserves much more study, particularly in hot areas. In addition, cooling or heating clearly involves costs which may vary according to temperature, wind speed, shade availability. It may therefore be instructive to look for optimum strategies for temperature regulation in the same way that, e.g. feeding tactics are now being studied (Krebs 1978).

Communal roosting by kites is well known. Brooke (1965) found roosts in reed beds and a stand of poplars numbering between five and 30 birds. Morgan-Davies (1965) counted about 80 kites roosting in one tree about 3 m high. Hustler (1979) recorded 60 to 80 birds on different nights gathered in a group of poplars in a reed bed. W.R. Tarboton (pers. comm.)

made counts of between 25 and 31 birds roosting in a bed of reeds. Finally, Morel & Poulet (1976) found about 500-600 birds roosting communally. Some of these accounts suggest that kites regularly roost in drainage lines. While several roosts in the Settlers area were in trees along dry watercourses, most trees in the area were along drainage lines anyway. Furthermore, there were many other roosts away from these lines.

Ward & Zahavi (1973) suggest that communal roosts serve as information centres for birds exploiting patchy food sources. The observations made here suggest that communal roosting by kites is consistent with their hypothesis. Kites exploit potentially patchy rodent populations which are known to "plague" or "crash" (Chapter 2). They are also highly mobile and may feed in aggregations at rich sources of food (Chapter 3). As expected from the "information" hypothesis, they usually roosted communally when not breeding (Fig. 5.7) and when food supplies were poorest (Table 5.2).

As food supplies decreased, the number of communally roosting birds probably increased (Table 5.2). Presumably each kite had to choose whether to incur the costs of flying to a distant roost (and to temporarily leave its territory) to enjoy the potential benefits of finding better feeding areas. It would be of interest to know on what basis they made this choice. Did they assess feeding conditions each late afternoon before roosting, or was the decision based on longer experience? The latter was more likely because a substantial proportion of heavy pellets (see S.D. values in Table 5.2) showed that some kites in large roosts had sometimes hunted very successfully.

Communal roosts were probably most effective if they drew birds, and therefore information, from a wide area. Certainly, those roosts with, say, 20 kites seemed potentially useful. However, the great number of small roosts appeared ineffective. They usually consisted of neighbouring residents drawn from between 3 and 10 km². The information potential from such small areas would be small, particularly as the areas were already defended territories. Data in Table 5.2 suggest that kites in the smallest communal roosts (3-4 birds) did not suffer from substantial food shortages. It may therefore be possible that these small roosts had some other function, possibly as protection against nocturnal predators (Lack 1968), or to help birds find potential mates.

SUMMARY

Most kites were inactive during the early morning and midday hours; the remaining time was largely spent hunting.

Conspecific intruders to territories were actively repulsed by residents who TAIL WAGGED and TAIL FANNED, made pursuits, stoops and SHALLOW-FLAPPING displays, displacement preened, and uttered various calls.

Kites usually avoided larger birds, but attacked them if they approached nests or fledglings.

Resident kites roosted communally or solitarily. Those that roosted communally had to fly greater distances to roosts, and had a poorer daily food intake than kites that roosted alone on their territories.

Chapter 6

MOULT, PLUMAGES AND MEASUREMENTS

INTRODUCTION

While much attention has been paid to the population dynamics and breeding of raptors, little is known of their morphological characteristics. In particular, plumage patterns and structural designs are little understood. The few published accounts on these subjects (e.g. Cade 1955; Nieboer 1973; Wattel 1973) are based mainly on museum material and therefore are limited by the low information content of most specimens. The classical studies of Stresemann & Stresemann (1960, 1966) contain most of the available information on moult, but they, too, confined their study to primary and tail moult in museum specimens. Although there are several studies of comparative anatomy (Jollie 1976-77 and references therein), variation in a few species only has been studied (Mueller et al. 1976; Temple 1972).

Some of the basic morphology of kites is described in this chapter. The results are confined to aspects that could be studied on live birds, so no attempt has been made to document internal anatomy. Specific attention has been paid to age and sexual variation. The timing of moult and sequences of moult in the remiges and rectrices are described. Brief comments, which supplement already published accounts (Brown & Amadon 1968; Clancey 1964; Cramp & Simmons 1980; Swann 1945; Van Someren 1956), are made. The measurements of 21 structural variables recorded on 96 kites are analysed to describe differences between males and females and adults and subadults. The measurements are also used to predict the sexes of 43 colour marked kites in the Settlers study area.

METHODS

Results presented here were obtained from kites trapped (Chapter 1, p. 9) during the 1977-78 Settlers study and several preceding years.

Some information was also kindly supplied by H.C. Biggs (44 moult records and 94 weights), J.A. Ledger (25 moult records), F. von Maltitz (53 moult records and weights), A.C. Kemp (eight weights), and M.B. Schmitt (14 moult records and weights). H.P. Mendelsohn helped catch most of the kites examined before 1977-78.

Primaries were numbered 1-10, and secondaries 1-13 from the distal wing inwards. Most kites had between 14 and 16 secondaries, but analyses were limited to the outermost 13 because it was usually difficult to identify the other secondaries. The rectrices were numbered 1-6 from the inner tail outwards. Each remex and rectrix was given a score of between 0 and 5 depending on whether it was old (0), growing (1, 2, 3 or 4), or new (5). These scores were used to compare the stages of growth in different feathers and therefore to determine moult sequences. The sequences were identified by comparing moult counts for the feathers. The moult count of a given feather was the total number of times it moulted (i.e. had a greater moult score) before other feathers. Those feathers with high moult counts obviously moulted earlier than those with lower counts. The great number of comparisons involved in calculating moult counts were performed with a computer programme written by D. Schultz. The programme compared the moult score (0-5) of each feather with that of each other feather. If the score was greater than another score, the moult count was increased by one; if it was equal or smaller, the moult count remained unchanged.

During 1977 and 1978 measurements (Fig. 6.1) were taken from trapped birds using methods similar to those of Biggs et al. (1978). The variables were as follows (abbreviation and smallest measured unit in parentheses):

1) Bill length (Bill L 0,1 mm) - from the tip of the upper mandible to the distal dorsal margin of the cere
2) Bill width (Bill W 0,1 mm) - distance between the two lower distal margins of the cere, i.e. where the cere meets the cutting edges of the bill

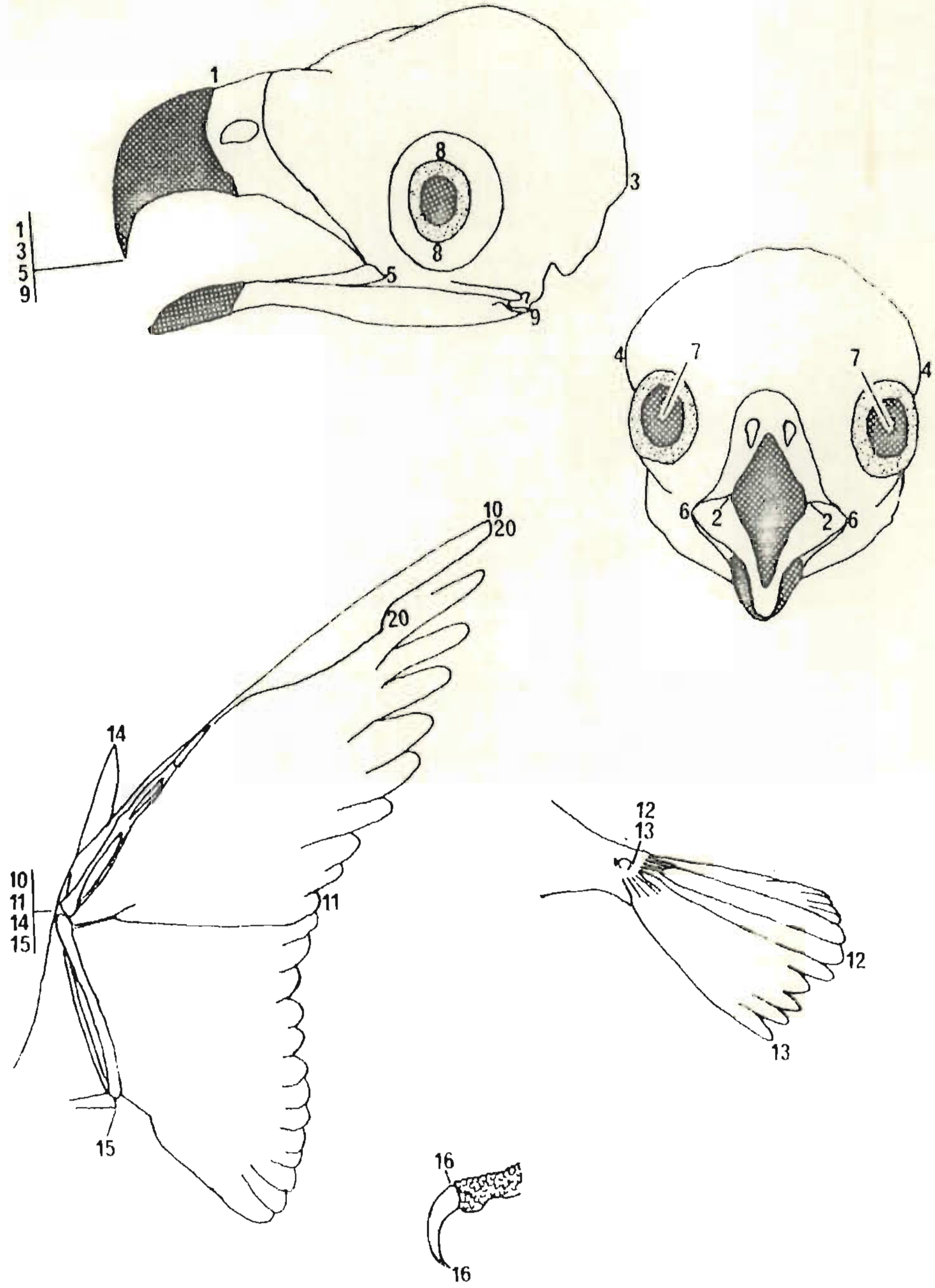


FIGURE 6.1 Structures measured on kites. Numbers refer to **the measurements** listed in the text. Adapted from Biggs _et_ _al_. (1978).

3) Skull length (Skull L 0,1 mm) - the greatest distance from the tip of the upper mandible to the back of the skull

4) Skull width (Skull W 0,1 mm) - distance between the two widest points of the skull behind the eyes

5) Gape Length (Gape L 0,1 mm) - from the tip of the upper mandible to the corner of the mouth

6) Gape Width (Gape W 0,1 mm) - distance between the left and right corners of the mouth. Measured with the mouth closed

7) Eye spacing (Eye S 0,1 mm) - distance between the centres of the eyes, measured with the calipers as close to the eye surface as possible

8) Eye diameter (Eye D 0,1 mm) - diameter of the coloured area of the eye (iris)

9) Jaw length (Jaw L 0,1 mm) - taken from the tip of the upper mandible to the point of articulation between the upper and lower jaw, the calipers being hooked behind the ridge marking this point

10) Wing length (Wing L 1 mm) - from the front of the folded wrist to the tip of the longest primary (P2); the wing flattened

11) Secondary length (Sec L 1 mm) - taken from the front of the folded wrist to the tip of the first secondary (S1) with the feathers flattened

12) Tail centre length (Tail C L 1 mm) - from the posterior edge of the uropygial gland to the tip of the longest central rectrix

13) Tail outer length (Tail O L) same as (12), but to the tip of one of the outermost rectrices

14) Alular length (Alular L 1 mm) - from the front of the folded wrist to the tip of the longest alular feather

15) Ulnar length (Ulnar L 1 mm) - from the front of the folded wrist to the distal margin of the process at the ulno-humeral joint. This process is actually on the posterior surface of the humerus

16-19) Claw lengths (Claw I, II, III & IV 0,1 mm) - taken from the tip of the claw to the dorsal surface of the claw where it meets the skin of the toe. The measurement is therefore the chord of the claw. The four measurements are for the four claws (I - hind, II - inner, III - middle, IV - outer)

20) Primary emargination (Primary E 1 mm) - the length of vane "missing" as emargination on P1 (the outermost remex)

21) Wing area (1 cm^2) - measured by opening the wing so that the anterior marg formed as straight a line as possible, and tracing the outline of the wing on paper. The outline was traced up to the posterior and anterior points where the wing joins the body. The traced outline was then superimposed on a grid scale (cm^2) and the enclosed area recorded

22) Weight (1 g) - measured on Pesola spring or triple-beam balance. Some analyses include data from birds caught before the 1977-78 study.

Measurements for certain linear variables were missing for some birds. Some measurements were not recorded early in the 1977-78 study and measurements affected by moult or substantial abrasion (e.g. Wing L and Alular L) were omitted. No attempt was made to take into account the weight of crop contents.

The SPSS package programme (Nie et al. 1975) was used to analyse the measurements statistically. Analyses included the calculation of means, standard deviations and sample sizes, and correlation matrices. In addition, a step-wise discriminant analysis on the same programme was used to predict the sexes of birds that could not be identified as males or females on behavioural grounds (see Chapter 4). The analysis used Wilks lambda as the criterion for selecting the most discriminating variables, and took into account correlations between the variables. This meant that the predictions were not biased in favour of suites of measurements that may have reflected the size of the same structure (e.g. Tail C L and Tail O L).

Kites were grouped according to three age categories: 1st plumage, 2nd plumage, and adult. The term subadult was collectively used to describe birds in 1st and 2nd plumage.

RESULTS

Moult

Although some moult activity was observed in all months, the first few adult kites started moulting during July/August, and the first adults with completed moults were caught 8-9 months later (Figs 6.2 & 6.3). However, most kites started moulting in September and completed their moult in March/April. Only during November-February were all adults moulting, suggesting that this was the period of most intense moult.

Primary moult usually started 1-2 months before secondary and rectrix moult (Fig. 6.3). While all birds had started replacing their primaries by November, some kites only started their rectrix moult in January and secondary moult in February. In spite of these differences in starting times, the moults of the tracts were completed at similar times in most birds (Fig. 6.3). Other differences and variations in the relative timing of moulting remiges and rectrices are considered below.

Adults and subadults generally moulted at similar times (Fig. 6.2). However, some subadults that were not moulting were caught throughout the year. Most of these non-moulting birds, particularly those examined between November and June, were in fresh plumage after having left their nests only 2-4 months previously. Some subadults also started moulting between December and February. These late-starters had probably left their nests later than subadults that started moulting in September.

Few subadults were examined for moult between February and June because, on completing their moult, they resembled adults and were classed as such. Little can therefore be said of when young birds completed their moult. However, except for late starters finishing their moult, there were

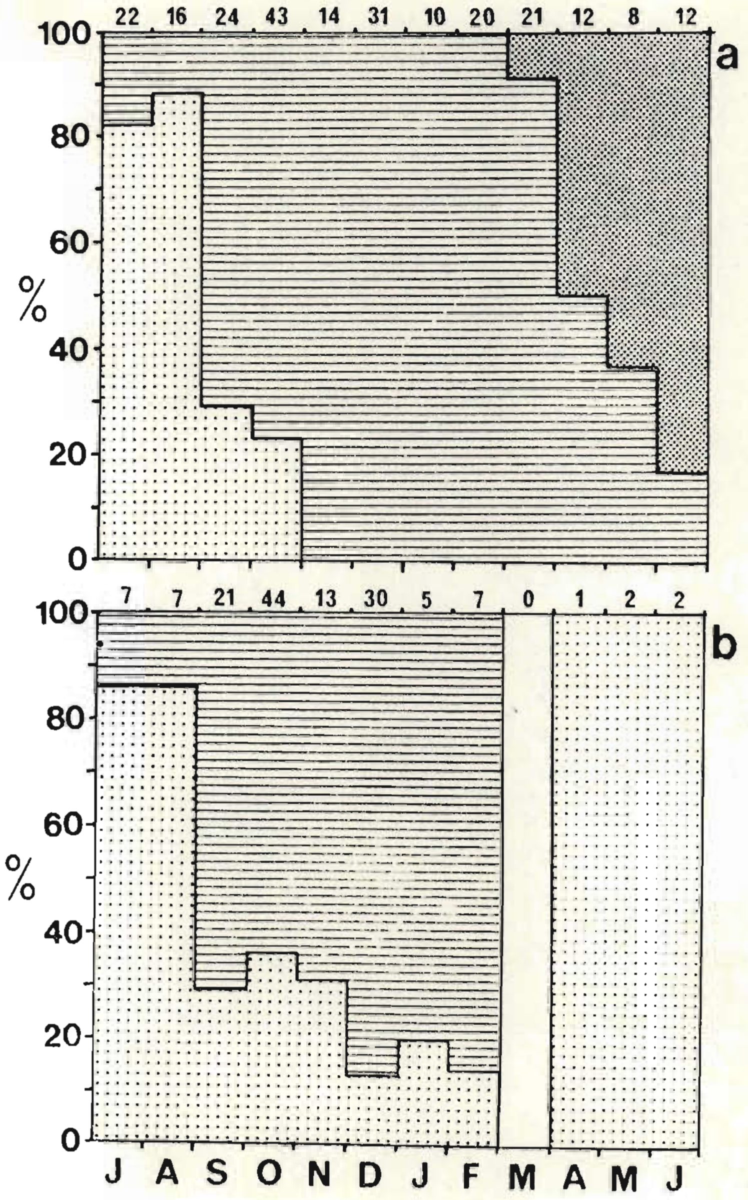


FIGURE 6.2 Percentages of adults (a) and subadults (b) not moulting (open stippling), moulting (lined area), and with completed moults (dense stippling). Numbers of kites examined each month are shown above each column.

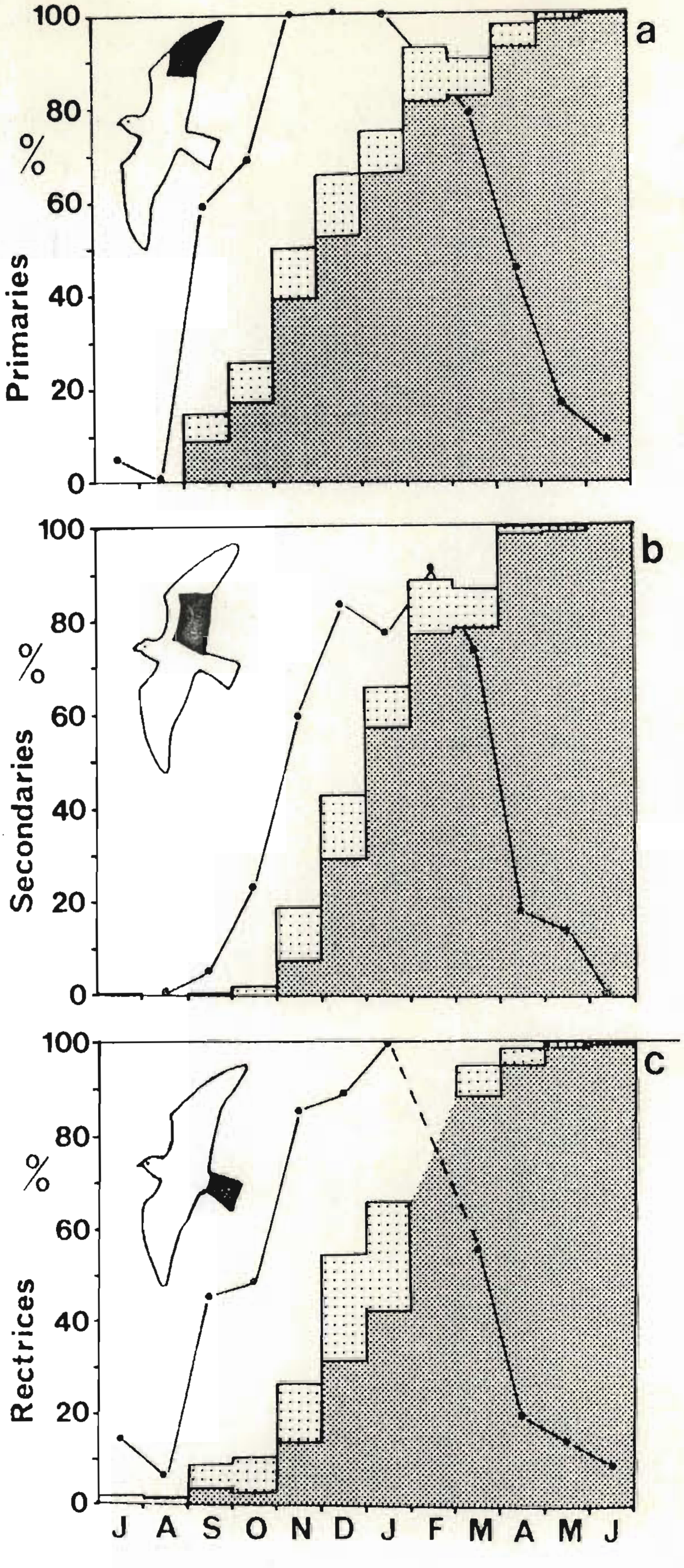


FIGURE 6.3 Average percentages of the primaries, secondaries and rectrices unmoulted (unshaded), moulting (open stippling) and renewed (dense stippling). The solid line shows the percentage of kites kites actively moulting. The data are for adult kites only.

probably no significant differences between adults and subadults in the timing of the latter stages of moult. Three young captive kites (Fig. 6.6) started moulting in October and acquired full adult plumages during May. The relative timing of the moult of the remiges and rectrices of subadults was similar to that of adults (see below).

Body feathers were replaced in all months, but the most intense moult activity, when most kites were moulting all feather tracts, was during October-February. Extensive tracts on the breast, belly, flanks, mantle and rump started before and finished moulting after smaller tracts. The alula was usually moulted late, between January and March. Primary coverts were replaced individually with their respective primaries, but all the secondary coverts appeared to be dropped and grown simultaneously. No differences between adults and subadults were noted in the pattern of body moult. However, some subadults moulted their body feathers only and not their remiges and rectrices (see p. 244), and some others started moulting later between December and February, 2-3 months after the majority of kites.

Moult sequences in the remiges and rectrices were analysed using moult counts for each feather (see METHODS, p. 231). Feathers that moulted first had the highest counts while those that moulted later had lower counts. The counts were affected by the distribution of samples during the moult. Thus, feathers that moulted early had disproportionately high counts because samples of kites caught during September-December were large (Fig. 6.2). In contrast, there were only small differences in counts between those feathers that usually moulted last because of the small samples during January-April. The counts nevertheless show the usual moult sequences and indicate the variation in sequences.

The results of the moult counts are shown in Figure 6.4 and 6.5, and Table 6.1. The remex and rectrix moult of adults and subadults followed a similar sequence (Fig. 6.4; Appendix 6.1). The primaries were moulted

TABLE 6.1 Matrix showing the number of times that each primary, secondary and rectrix moulted before other feathers in the same and other tracts. The data were obtained from 242 kites inspected for moult in the three tracts simultaneously. The 'total' moult count for each feather is plotted in Figure 6.5.

Feathers that moulted later		Feathers that moulted first																												
		Primaries										Secondaries													Rectrices					
		1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	6	5	4	3	2	1
Primaries	1	0	20	30	44	61	79	96	114	131	135	54	42	30	33	63	53	36	30	25	27	45	52	56	41	28	41	54	67	95
	2	0	0	21	35	53	70	87	105	122	126	45	32	20	24	53	44	26	19	15	18	36	44	46	33	24	32	46	60	87
	3	0	0	0	20	38	55	72	90	107	111	31	18	6	12	39	29	11	6	4	6	22	32	35	21	6	18	34	47	75
	4	0	0	0	0	31	48	65	83	100	104	24	6	4	9	34	20	4	4	3	4	14	26	30	16	3	14	26	39	66
	5	0	0	0	0	0	35	52	70	87	91	8	4	4	7	24	8	2	2	1	3	7	14	20	2	1	7	14	27	54
	6	0	0	0	0	0	0	37	55	72	76	4	3	3	3	10	4	1	1	0	2	3	5	15	0	0	4	4	15	43
	7	0	0	0	0	0	0	0	38	54	59	0	2	1	1	5	1	1	1	0	1	1	2	7	0	0	3	3	7	26
	8	0	0	0	0	0	0	0	0	35	39	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2	1	1	19
	9	0	0	0	0	0	0	0	0	0	22	0	1	1	0	1	1	1	0	0	0	0	0	1	0	1	2	1	1	10
	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	7
Secondaries	11	0	0	0	3	15	34	52	69	86	90	0	1	0	5	22	7	0	1	1	1	5	15	19	6	1	8	14	27	55
	2	0	0	2	14	32	49	66	82	99	103	24	0	3	8	33	22	3	4	3	1	13	28	30	18	5	15	27	40	68
	3	1	4	9	24	40	56	74	91	108	112	32	18	0	11	41	29	14	8	6	7	24	34	38	23	11	20	35	48	76
	4	0	4	8	21	36	51	70	87	104	108	30	17	8	0	37	26	13	8	3	7	19	30	34	21	8	18	32	45	70
	5	0	1	3	8	13	25	43	60	78	82	9	6	4	5	0	6	3	3	2	2	7	9	17	5	3	11	11	23	48
	6	0	1	2	7	20	39	56	74	91	95	15	4	3	6	23	0	1	2	1	1	6	18	23	9	0	9	19	34	59
	7	0	0	2	16	25	51	68	85	102	106	25	10	4	9	35	24	0	3	3	2	13	28	30	20	4	14	29	43	69
	8	0	1	7	20	38	54	71	88	105	109	29	17	6	9	38	27	12	0	1	6	21	30	33	20	8	19	33	45	72
	9	0	3	9	22	40	56	73	91	108	112	32	20	11	12	40	30	15	7	0	8	23	32	37	22	9	20	35	49	74
	10	1	3	9	25	41	59	76	93	110	114	35	22	9	14	43	32	16	8	7	0	25	35	37	26	12	23	38	50	77
	11	0	1	3	14	29	44	62	79	96	100	21	9	6	9	30	19	3	5	4	1	0	23	24	18	4	13	27	37	63
	12	2	5	7	12	22	36	56	75	91	96	17	10	9	12	25	12	7	7	5	8	10	0	22	10	5	15	22	30	55
	13	0	2	8	14	23	36	51	68	86	90	19	11	8	10	22	17	8	8	7	8	9	11	0	11	7	14	20	29	53
Rectrices	6	2	4	6	14	34	50	68	86	102	107	28	14	9	11	35	25	11	8	5	9	17	24	31	0	5	13	26	36	66
	5	1	2	10	24	42	58	75	93	110	114	34	21	11	15	42	32	15	10	7	10	25	34	36	23	0	20	36	49	75
	4	3	5	8	19	37	53	71	88	105	110	30	19	11	13	39	29	13	11	8	9	22	31	33	19	4	0	30	46	68
	3	2	5	6	10	21	38	56	74	92	95	19	9	8	11	29	17	8	8	6	8	14	20	25	5	5	12	0	31	59
	2	3	5	6	13	20	35	52	73	92	96	19	11	6	9	25	16	10	6	5	8	16	21	21	9	7	10	21	0	59
	1	4	4	8	10	18	26	41	61	71	79	15	10	9	10	21	13	11	7	5	9	12	14	16	9	6	9	13	18	0
Total		19	70	164	389	729	1137	1590	2072	2544	2671	599	337	194	268	810	543	245	177	127	166	409	612	717	387	167	387	652	945	1648

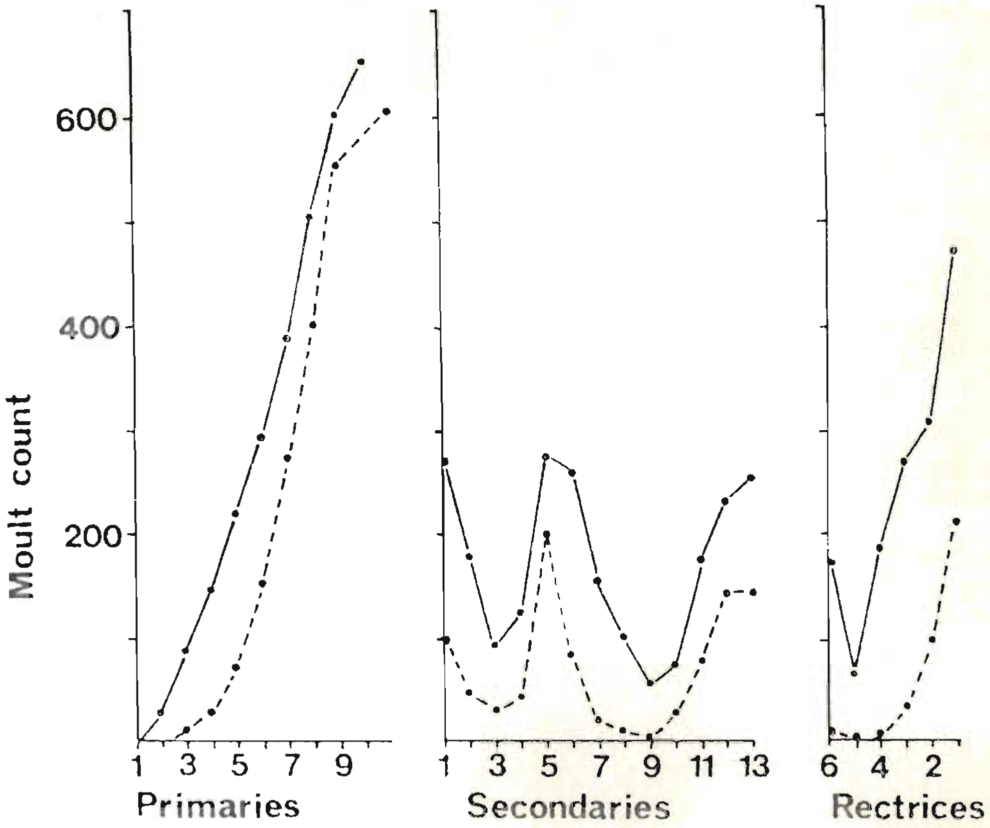


FIGURE 6.4 Moult counts of the number of times that feathers moulted before other feathers in the same tracts; adults (——), subadults (---). The individual counts were shown in Appendix 6.1.

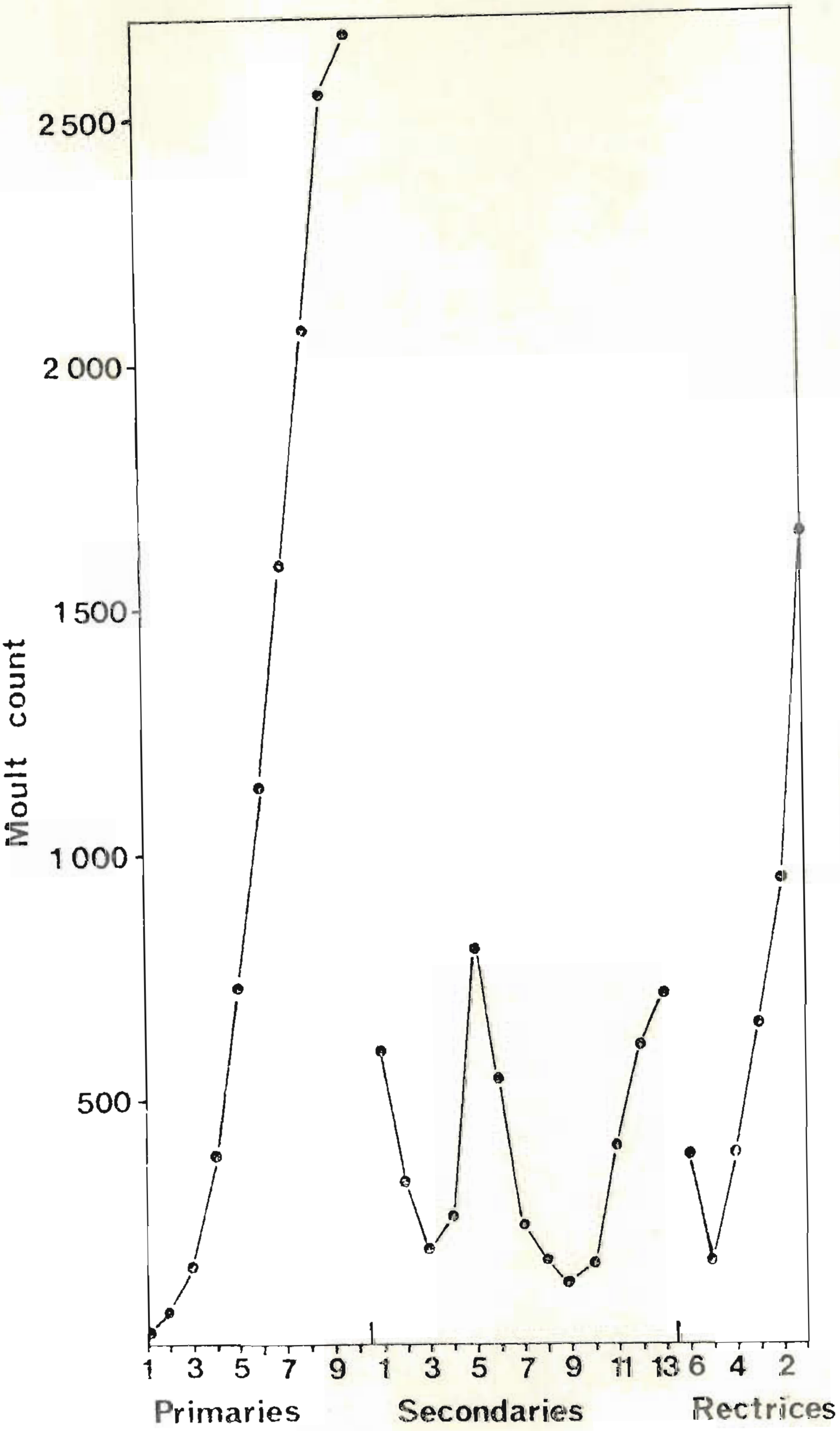


FIGURE 6.5 Moult counts for all kites of the number of times that each feather moulted before all other feathers both in the same and other two tracts. The actual counts are shown in Table 6.1.

in one wave, starting at the innermost P10 and ending with the outermost P1. There was no variation in this sequence (Table 6.1). The secondaries generally moulted in waves from three moult centres at S1, S5 and S13, with the following average sequence : S5-13-12-1-6-11-2-4-7-3-8-10-9. There was, however, substantial variation, both in the position of the moult centres and the sequence of moult (Table 6.1 & 6.2; Appendix 6.1). The centre at S1 varied least, with S1 usually moulting before S2 and S3. The centre at S5 was more variable since S4 and 6 sometimes moulted before S5. If S4 did not moult before S5, it normally moulted after S3. The innermost centre at S13 was seldom clearly defined because S12 often moulted before S13. In addition, the variable number of innermost secondaries in this region (see p. 231) meant that it was difficult to compare feathers in different birds. Table 6.1 also shows much variation in the overall sequence of moult, with secondaries that usually moulted last (S3, 8, 9, 10) sometimes moulting before those that usually moulted first (S1, 5, 12, 13).

There was a similar high degree of variation in the sequence of rectrix moult (Table 6.1 & 6.2), although there was a clear sequence on average: R1-2-3-4 or 6-5 (Fig. 6.4 & 6.5).

Comparisons in Figure 6.5 show that kites took longer to moult ten primaries and six rectrices than the 13 secondaries. Although there was much variation (Table 6.1), rectrix and secondary moult only started after three and five primaries respectively had moulted. The data in Figure 6.5 also indicate that only a few feathers were moulted simultaneously during the early and late stages of the moult. Many more feathers, in contrast, moulted simultaneously during the middle of the moult.

Fourteen of the 373 kites examined for moult had arrested their moult or showed signs of having replaced, out of sequence, feathers that were probably damaged accidentally (Table 6.2). Arrested moult was only evident when the condition of a bird's remiges and rectrices contrasted with that of other kites caught in the same month. Other cases of arrested and

TABLE 6.2 Moult stages of remiges and rectrices of kites showing examples of variation in normal sequences, arrested moult and feathers replaced out of sequence (underlined).

Date	Primaries (1 → → 10)	Secondaries (1 → → → 13)	Rectrices (1 → 6)
Normal sequence			
17 Sep	0000000355	0000000000000	000000
10 Oct	0000015555	0000150000000	000015
10 Oct	0000155555	0005000000555	000014
25 Nov	0001555555	3000553000355	055101
1 Dec	0002555555	5200531000145	205515
26 Dec	0035555555	5554045530355	511555
26 Dec	0000035555	0000000000000	000000
22 Jan	0025555555	5555555555550	004005
12 Jan	0001555555	0000000000000	401551
10 Feb	1455555555	5515555555555	555555
13 Mar	0355555555	5350153550353	552055
15 Mar	3555555555	5555555555555	555555
Arrested moult			
11 Jul	0000555555	5000550000555	555505
29 Aug	0000555555	0000500000005	500555
26 Sep	5550000555	0000000000000	000000
26 Sep	0155555555	5500555101550	000000
21 Sep	0055555555	5555555555550	555555
5 May	0000055555	5555555551555	555555
23 May	0005555555	5055500555500	005505
29 Apr	2355555555	5555555555555	000500
29 Apr	3555555555	5525555555555	150105
Replacement moult			
18 Jul	0000000000	0000000000000	000100
3 Oct	0000000000	0000000100000	000000
10 Dec	0355555535	5550555201000	355003
22 Feb	0205555555	5550555500555	------
18 Feb	2455555515	5555530555525	------

replacement moult were probably not recognised, particularly during October-March when most kites were moulting rapidly and common moult stages were not clearly defined. The condition of feathers (Table 6.2) suggested that some kites stopped moulting their primaries, secondaries and rectrices simultaneously, while others appeared to arrest moult in one or two tracts only.

Plumages

The plumages of kites have been described by a number of authors, e.g. Brown & Amadon (1968), Clancey (1964), Cramp & Simmons (1980), Swann (1945) and Van Someren (1956). The present section serves only to point out several aspects either missed or erroneously described in the literature.

1st plumage kites have a brown wash to their breast feathers. Each feather has a black shaft and a pale russet vane. The brown colour soon starts to fade so that birds 4-6 months old appear almost white at a distance The black shafts, however, remain visible at close range.

Of 34 nestlings examined during the Settlers study, 33 showed the normal white edging to feathers of the mantle, scapulars, upper wing coverts and remiges. The remaining kite differed in having the same feathers edged with russet (Fig. 6.6). This gave the bird's dorsal surface a dark brown-grey cast. The bird later moulted into normal adult plumage. A.C. Kemp (pers. comm.) has observed a similar nestling lacking white on the dorsal surface.

The outermost five pairs of rectrices of 1st plumage kites have subterminal grey spots (Fig. 6.7). These spots may be the only subadult features present when kites develop a 2nd plumage (see below). The presence of the spots may be associated with TAIL FANNING (Chapter 5 — Fig 5.3) since they may be visible only during this display.

1st plumage kites either moulted directly into adult plumage or first assumed an intermediate 2nd plumage. This 2nd plumage developed in kites that moulted and acquired adult body feathers, but retained their 1st

FIGURE 6.6 Back and front views of three captive kites in the same order (left to right) showing the 'dark-backed' individual in the centre.

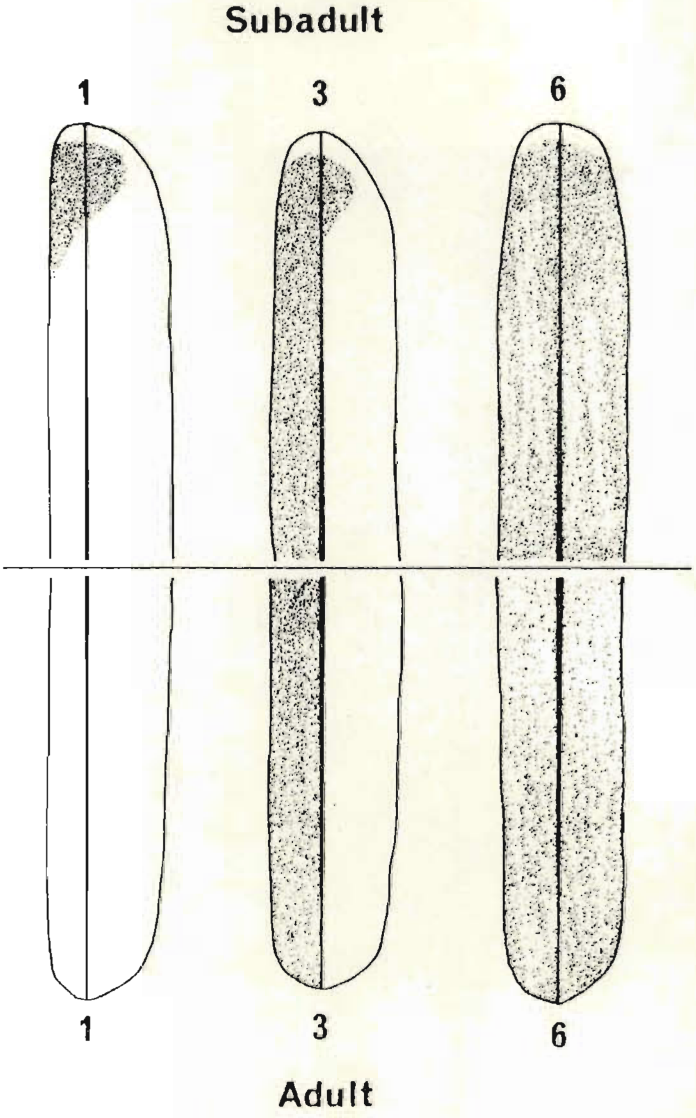


FIGURE 6.7 A comparison of the distribution of grey and white on the outermost (R1), intermediate (R3) and central (R6) rectrices of adults and subadults.

plumage remiges, rectrices, greater coverts and alular feathers. Those young, in contrast, that moulted directly into adult plumage renewed feathers from all tracts during the same moult. The partial moult into a 2nd plumage probably occurred only in young birds that left the nest in summer. Kites that fledged at other times moulted directly into adult plumage during their first summer. This was the case with three captive kites that left the nest in May-June; by the following May they had assumed full adult dress. 2nd plumage kites probably acquired their first complete adult plumage during their second summer, <u>i.e</u>. at an age of more than one year.

The proportions of adults and subadults in trapped samples changed markedly during the year (Fig. 6.8). The number of subadults increased after July, probably as a result of breeding during autumn and spring (Chapte 4, p. 173). The sharp decrease in numbers of subadults after December was probably because many young kites then acquired adult plumage after moulting during summer (Fig. 6.2).

Adult males were usually paler above than females. In particular, males had more white on the forehead and above the eyes, less black on the upper wings and ventral surfaces of the primaries, and a paler grey on the whole upper side (Fig. 6.9). These differences were not consistent in all birds, some males being as dark as some females. However, the sexes could usually be identified if a pair were examined together in the hand. Male Whitetailed Kites are similarly paler above than females (Hawbecker 1942).

On leaving the nest, young kites have dark grey-brown irides. Within three to four weeks the irises become yellow and then over the next year change to orange and ultimately to a deep red colour. However, several adults examined at Settlers showed orange-red irides. Previous ringing showed that two of these adults were at least 3-4 years old. Three young

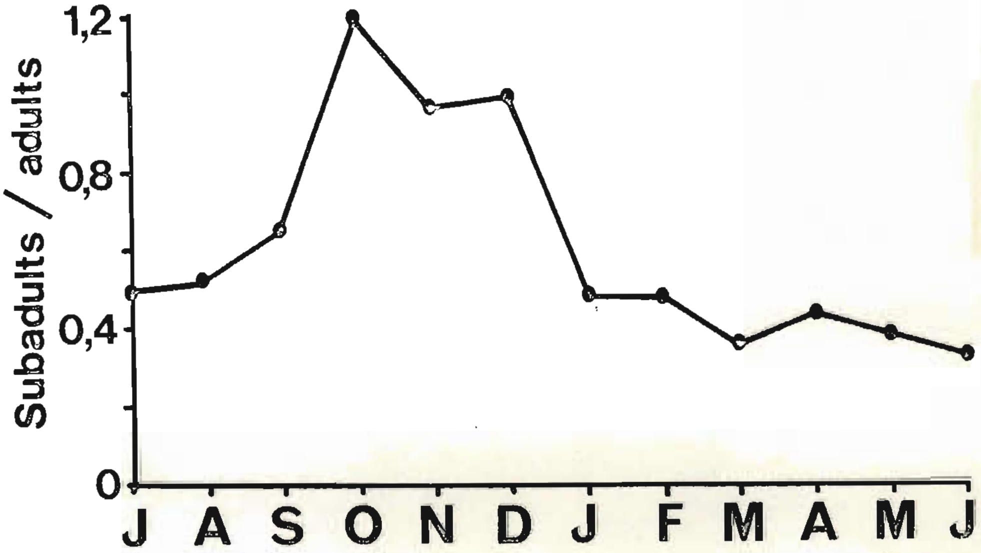


FIGURE 6.8 Monthly changes in the proportion of adults and subadults in trapped samples. A total of 492 adults and 324 subadults were trapped.

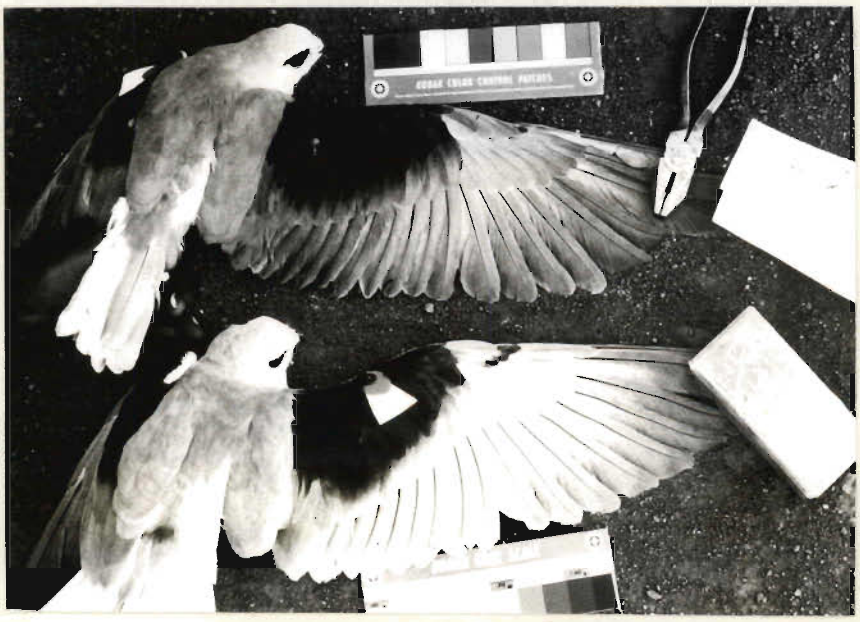


FIGURE 6.9 A pair of kites showing the paler uppersides of the lower male. The contrast between male and female is exaggerated because the print was made from a colour transparency.

captive kites, in contrast, all showed deep red irides by the time they were a year old. These observations suggest that eye colour is not a reliable age character.

The vanes of kite remiges have a velvet or hairy appearance, due to greatly elongated barbules, particularly on the primaries. The distal portions of the barbules extend as filaments 1-3 mm beyond the surface of the vane. Slightly elongated barbules are present on other flight and contour feathers. An examination of other African birds of prey shows that most species have similar structures, but only in those preying largely on small mammals are they as well developed as in kites. This is especially evident in the Bat Hawk _Macheiramphus alcinus_ and owls (except Pel's Fishing Owl _Scotopelia peli_). Elongations of the barbules are virtually absent in carrion and fish-eating birds of prey. Presumably, kites and other small mammal predators often rely on a silent approach in catching prey. The 'hairy' vanes probably reduce the noise produced by feathers moving rapidly through the air.

Measurements

Table 6.3 lists statistics describing the weights of various groups of kites. Adults were slightly, but significantly, heavier than all subadults. Females were about 9,1% heavier than males. The mean weights of males and females identified on behavioural criteria were close ($p > 0,6$) to those from larger samples that included kites whose sex had been predicted by discriminant analysis (see below). (Weight was not used as a discriminating factor.) Nomads were about 6,5% lighter than all other kites, the great majority of which were residents. The weights of kites in different mating classes did not differ significantly.

Although adults showed smaller changes in weight during the year than subadults (Fig. 6.10), a significant positive correlation ($r_{12} = +0,54$; $p < 0,05$) suggests that weights increased and decreased at similar times in the

TABLE 6.3 Weights of kites. Subadults included all flying birds not yet in full adult plumage. Nomads, unpaired, paired or breeding birds were identified by criteria described in Chapter 3. Sexes were determined from behaviour or discriminant analysis of linear measurements (see text). About 95% of the weights were measured on kites trapped in the Transvaal. The remaining weights were obtained elsewhere in southern Africa.

Category	Mean	S.D.	Sample size
All kites	$244{,}2^{c}$	19,5	816
Adults	$247{,}0^{a}$	19,0	492
Subadults	$240{,}0^{a}$	19,7	324
Males - positive	$237{,}0^{b}$	15,9	28
Females - positive	$258{,}5^{b}$	20,6	27
Males - positive & predicted	235,2	17,5	60
Females - positive & predicted	256,4	18,5	38
Nomads	$228{,}4^{c}$	24,0	14
Males - unpaired	$233{,}3^{d}$	17,1	18
- paired	$242{,}0^{d}$	18,1	11
- breeding	$234{,}6^{d}$	15,2	17
Females - unpaired	$247{,}3^{e}$	11,9	4
- paired	$259{,}3^{e}$	17,9	19
- breeding	$265{,}8^{e}$	24,7	16

$^{aa}p < 0{,}005$; $^{bb}p < 0{,}005$; $^{cc}p < 0{,}005$; ^{dd}N.S.; ^{ee}N.S.

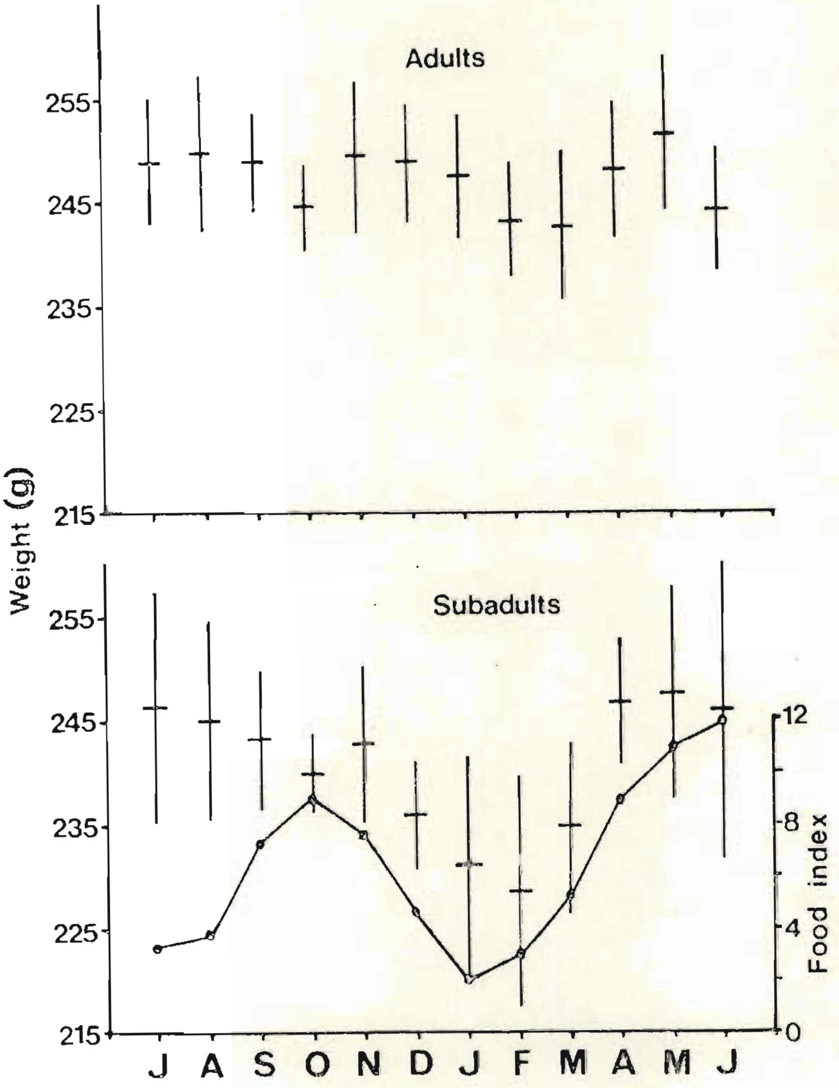


FIGURE 6.10 Monthly changes in the weights of 492 adults and 324 subadults. The horizontal lines are means and the vertical lines show 2(SE$\bar{x}$) above and below the means. The index of food supply is adapted from Chapter 2 (Fig. 2.8c) and is for the year July 1977 — June 1978.

two groups. Changes in the weights of subadults were positively correlated with changes in food supply (Fig. 6.10) (Spearman's Rank r_{12} = +0,60; $p <$ 0,025). There was, however, no significant correlation between adult weights and food supply (Spearman's Rank r_{12} = +0,13; NS).

Kites in 1st, 2nd and adult plumage differed in several measurements and proportions (Table 6.4). Comparing the two subadult groups, 2nd plumage kites had shorter, broader wings (see Wing L/Sec L) and slightly longer claws than 1st plumage birds. Subadults had wider heads (Eye S, Skull W, Gape W), shorter wings and longer tails than adults. Proportional differences mainly involved these structures and weight differences (Table 6.3).

Males and females also differed significantly in several measurements and proportions (Table 6.5). Females were larger than males in Bill L (4,3% larger than males) and W (2,7%), Skull L (2,2%), Gape L (2,9%) and W (2,3%), Jaw L (1,6%). Sec L (3,0%), Ulnar L (1,8%), and Wing Area (4,4%). Males had slightly longer tails than females (Tail O L - 1,9% greater than females). Differences in Skull L /W and Eye S /Jaw L indicate that males had broader heads than females. The ratio of Wing L to Sec L suggests that females had shorter, broader wings than males. Females also had a greater loading on the whole wing and the alula (see Wing Area/Weight and Alular L /Weight). Finally, differences in Wing L /Tail C L and Wing Area/Tail C L suggested that males derived relatively more lift from their tails than females.

The sexes of 43 kites (Table 6.6) were predicted using a step-wise discriminant analysis (see METHODS, p. 234). Seventeen sexed birds were excluded from the analysis because measurements of several of their structures were missing. Weights and measurements of Primary E (too few data) were also omitted from the analysis.

The discriminating variables selected were: Bill L and W, Skull L, Gape

TABLE 6.4 Measurements and proportions of kites in different age groups. Data are presented as: mean ± standard deviation (sample size). Measurements are in mm, except for wing area (cm^2). Weight data are given in Table 6.3. Significant differences (t-test) between 1st and 2nd plumage birds, and between 2nd plumage and adult kites, and between adults and all young birds[1] are shown. Significance values are + $p < 0{,}05$; ++ $p < 0{,}025$; +++ $p < 0{,}01$.

Variable	1st Plumage	diff	2nd plumage	diff	diff[1]	Adult
Bill L	16,38 ± 0,46 (9)		16,70 ± 0,82 (10)		+	16,79 ± 0,68 (77)
Bill W	11,64 ± 0,65 (9)		11,86 ± 0,56 (10)			11,82 ± 0,52 (76)
Bill L/W	1,410 ± 0,089 (9)		1,412 ± 0,110 (10)			1,438 ± 0,070 (76)
Skull L	53,94 ± 1,12 (9)		53,53 ± 1,98 (10)			53,96 ± 1,24 (77)
Skull W	32,40 ± 0,45 (9)		31,96 ± 0,61 (9)	+++	+	32,54 ± 0,65 (74)
Skull L/W	1,665 ± 0,035 (9)		1,677 ± 0,050 (9)			1,661 ± 0,042 (74)
Gape L	27,66 ± 1,15 (9)		27,66 ± 0,75 (9)			27,62 ± 0,94 (75)
Gape W	27,49 ± 0,91 (9)		26,69 ± 0,68 (9)		++	26,51 ± 0,85 (73)
Gape L/W	1,006 ± 0,038 (9)		1,037 ± 0,042 (9)			1,043 ± 0,037 (73)
Eye S	37,84 ± 0,34 (9)		37,69 ± 0,47 (9)	+++	+++	38,43 ± 0,63 (64)
Eye D	8,71 ± 0,25 (9)		8,67 ± 0,15 (6)			8,75 ± 0,24 (61)
Eye D/S	0,230 ± 0,005 (9)		0,230 ± 0,005 (6)			0,228 ± 0,006 (59)
Jaw L	40,09 ± 0,84 (9)		40,13 ± 1,05 (9)			40,00 ± 1,24 (73)
Eye S/Jaw L	0,944 ± 0,023 (9)		0,943 ± 0,028 (8)		+	0,960 ± 0,030 (61)
Primary E	37,00 ± 3,39 (5)		39,01 ± 1,41 (4)			38,47 ± 2,50 (32)

TABLE 6.4 continued

Variable	1st plumage	diff	2nd plumage	diff	diff^1	Adult
Wing L	262,8 ± 7,74 (9)		261,7 ± 7,28 (8)	+++	+++	267,9 ± 6,54 (70)
Sec L	141,9 ± 6,35 (9)		146,7 ± 4,79 (7)			146,7 ± 5,65 (74)
Wing L/Sec L	1,853 ± 0,048 (9)	++	1,785 ± 0,052 (7)	+		1,828 ± 0,059 (70)
Tail C L	118,8 ± 5,04 (9)		118,6 ± 4,53 (9)		+	116,6 ± 3,73 (76)
Tail O L	123,9 ± 3,98 (9)		123,1 ± 3,67 (10)		++	120,8 ± 4,44 (76)
Wing L/ Tail C L	2,214 ± 0,069 (9)		2,208 ± 0,072 (8)	+++	+++	2,294 ± 0,066 (70)
Alular L	83,89 ± 3,55 (9)		84,33 ± 4,80 (9)			84,76 ± 3,35 (71)
Alular L/ weight	0,368 ± 0,035 (9)		0,359 ± 0,021 (9)		++	0,347 ± 0,026 (71)
Alular L/ Wing L	0,319 ± 0,013 (9)		0,328 ± 0,011 (7)	++	+	0,317 ± 0,012 (67)
Ulnar L	87,22 ± 2,22 (9)		87,60 ± 2,72 (10)			88,06 ± 2,78 (77)
Wing L/ Ulnar L	3,014 ± 0,095 (9)		2,963 ± 0,086 (8)	++		3,043 ± 0,106 (70)
Claw I	16,26 ± 0,43 (9)	+	16,80 ± 0,53 (9)			16,83 ± 0,61 (76)
Claw II	15,92 ± 0,49 (9)		16,31 ± 0,32 (9)			16,29 ± 0,64 (76)
Claw III	14,32 ± 0,42 (9)		14,57 ± 0,57 (9)			14,30 ± 0,70 (76)
Claw IV	12,43 ± 0,45 (9)		12,71 ± 0,52 (9)			12,50 ± 0,60 (76)
Wing Area	437,9 ± 29,70 (9)		443,7 ± 22,15 (10)		+	454,7 ± 23,42 (76)
Wing Area/ Tail C L	3,684 ± 0,146 (9)		3,763 ± 0,141 (9)	++	+++	3,902 ± 0,181 (76)
Wing Area/ weight	1,918 ± 0,191 (9)		1,920 ± 0,116 (10)			1,867 ± 0,136 (76)

TABLE 6.5 Measurements and proportions of males and females. Data are presented as: mean ± standard deviation (sample size). Measurements are in mm, except for Wing Area (cm^2). Proportional data and that for Primary E include kites whose sex was predicted by discriminant analysis. Weights are given in Table 6.3. Significant differences (t-test) are shown by + $p < 0{,}05$; ++ $p < 0{,}025$; +++ $p < 0{,}01$.

Variable	Males	diff	Females
Bill L	16,60 ± 0,55 (26)	+++	17,32 ± 0,57 (27)
Bill W	11,68 ± 0,51 (25)	++	12,00 ± 0,54 (27)
Bill L/W	1,425 ± 0,078 (56)		1,443 ± 0,074 (39)
Skull L	53,41 ± 1,41 (26)	+++	54,58 ± 1,12 (27)
Skull W	32,30 ± 0,52 (24)		32,53 ± 0,76 (27)
Skull L/W	1,651 ± 0,041 (54)	+++	1,680 ± 0,037 (38)
Gape L	27,35 ± 0,82 (25)	+++	28,13 ± 0,84 (27)
Gape W	26,38 ± 0,76 (23)	+++	26,98 ± 0,73 (27)
Gape L/W	1,035 ± 0,043 (53)		1,045 ± 0,033 (38)
Eye S	38,39 ± 0,66 (20)		38,32 ± 0,56 (24)
Eye D	8,76 ± 0,28 (17)		8,76 ± 0,19 (24)
Eye D/S	0,228 ± 0,007 (40)		0,228 ± 0,005 (34)
Jaw L	39,74 ± 1,06 (24)	+	40,37 ± 1,18 (26)
Eye S/Jaw L	0,964 ± 0,029 (45)	+++	0,945 ± 0,028 (33)
Primary E	38,05 ± 2,54 (20)		38,62 ± 2,56 (21)
Wing L	268,7 ± 6,39 (23)		267,9 ± 6,33 (24)
Sec L	145,0 ± 3,85 (25)	+++	149,4 ± 5,90 (25)
Wing L/Sec L	1,846 ± 0,054 (51)	+++	1,800 ± 0,055 (35)
Tail C L	117,6 ± 3,78 (26)		115,9 ± 3,80 (27)
Tail O L	121,8 ± 4,06 (26)	+	119,5 ± 4,25 (27)

continued on p. 257

TABLE 6.5 continued

Variable	Males	diff	Females
Wing L/ Tail C L	2,263 ± 0,076 (52)	+	2,298 ± 0,065 (35)
Alular L	84,04 ± 3,84 (24)		85,03 ± 3,29 (26)
Alular L/ Weight	0,361 ± 0,021 (52)	+++	0,335 ± 0,029 (37)
Alular L/ Wing L	0,318 ± 0,011 (48)		0,319 ± 0,014 (35)
Ulnar L	87,00 ± 2,94 (26)	++	88,56 ± 2,55 (27)
Wing L/ Ulnar L	3,045 ± 0,106 (52)		3,014 ± 0,103 (35)
Claw I	16,88 ± 0,52 (25)		16,94 ± 0,69 (27)
Claw II	16,38 ± 0,53 (25)		16,23 ± 0,66 (27)
Claw III	14,29 ± 0,65 (25)		14,45 ± 0,73 (27)
Claw IV	12,52 ± 0,68 (25)		12,53 ± 0,69 (27)
Wing Area	444,4 ± 23,59 (26)	+++	464,0 ± 20,58 (27)
Wing Area/ Tail C L	3,779 ± 0,160 (56)	+++	3,998 ± 0,144 (38)
Wing Area/ Weight	1,910 ± 0,131 (57)	+++	1,828 ± 0,141 (38)

TABLE 6.6 Observed (Obs. sex) and predicted (Pred. sex) sexes of 96 kites. Probabilities (Prob.) are that the predicted sexes are correct, given the present data and method of analysis. Dashes (-) indicate that sexes were not predicted because of incomplete data (n=17) or not previously known (n=43). Birds were listed in numerical order, resident males first, resident females second, and nomads and those caught outside the study area third.

Bird	Obs. sex	Pred. sex	Prob.	Bird	Obs. sex	Pred. sex	Prob.	Bird	Obs. sex	Pred. sex	Prob.
1	♂	-	-	84	-	♂	0,999	98	♀	♀	1,000
2	♂	-	-	87	-	♂	0,992	102	♀	♀	1,000
4	♂	-	-	89	-	♂	1,000	109	♀	-	-
5	♂	-	-	91	♂	-	-	8	-	♂	0,986
7	♂	-	-	99	-	♂	0,998	9	-	♂	0,994
10	♂	-	-	12	♀	-	-	11	-	♂	0,966
13	-	♂	0,995	14	♀	-		16	♂	-	-
15	♂	-	-	24	-	♀	1,000	17	-	♂	0,999
19	♂	-	-	25	♀	♀	1,000	22	-	♂	0,867
20	♂	-	-	28	♀	-	-	26	-	♂	0,998
23	-	♂	0,999	29	♀	(♂)	0,959	37	-	♂	0,726
27	-	♂	0,998	31	-	♀	0,999	38	♂	♂	0,998
30	♂	♂	0,994	32	-	(♂)	0,986	40	-	♂	0,995
34	♂	♂	0,850	36	♀	♀	0,894	43	♂	♂	0,938
39	♂	♂	0,999	45	♀	♀	1,000	47	-	♂	0,998
41	-	♂	1,000	60	♀	♀	0,999	48	-	♂	0,993
44	♂	♂	0,991	62	♀	♀	1,000	77	-	♂	0,996
46	-	♂	0,999	64	♀	♀	1,000	78	-	♂	0,988
49	♂	♂	0,995	66	♀	♀	1,000	79	-	♂	0,999
50	♂	♂	0,983	67	♀	♀	1,000	82	-	♂	0,997
51	♂	♂	0,999	68	♀	♀	1,000	95	-	♂	0,999
52	-	♂	0,608	69	♀	♀	1,000	97	-	♂	0,855
53	-	♂	0,999	70	♀	♀	1,000	3	-	♀	0,783
55	♂	♂	0,845	72	♀	♀	1,000	6	-	♀	1,000
56	-	♂	0,636	74	♀	♀	1,000	18	♀	-	-
59	♂	♂	0,998	76	♀	♀	1,000	21	-	♀	1,000
61	-	♂	0,994	80	♀	♀	1,000	33	-	♀	1,000
63	♂	♂	0,999	85	♀	-	-	35	-	♀	1,000
71	♂	♂	0,999	86	-	♀	1,000	54	-	♀	1,000
73	-	♂	0,998	88	♀	♀	1,000	58	-	♀	1,000
75	♂	♂	0,998	90	♀	♀	1,000	101	-	♀	1,000
83	♂	♂	0,980	94	♀	♀	1,000	110	-	♀	0,990

W, Eye S and D, Jaw L, Sec L, Tail C L, Alular L, Ulnar L, Claw III and IV, and Wing Area. The remaining variables, Skull W, Gape L, Wing L, Tail O L, and Claw I and II were therefore not used to discriminate between males and females. Thirty-one kites were classified as males and 12 as females. The probability that the prediction was correct, given the present data, was usually high (Table 6.6). A measure of the accuracy of the analysis was provided by predictions of the sexes of those kites already identified as males or females on behavioural grounds. Of these 36 kites, 35 (97%) were correctly classified.

The 43 unsexed kites in Table 6.6 included partners in pairs. In the first of these (♂56, ♀24), one bird was classified as male and the other as female. However, in the second pair (No. 27 & 32), both kites were identified as males. As a result, No. 32 has been taken as the female of the pair because a) the probability associated with her classification was lower than that of No. 27 (Table 6.6), and b) her behaviour in leaving No. 27 to care for their flying young (Chapter 4 — Table 4.5) suggested that she was female.

The discriminant analysis calculated a discriminant score for each kite and, depending on its sex, compared this score with group centroid values for either males or females. The two group centroids were the discriminant scores of typical (= average) males or females. The distance between an individual score and a group centroid was expressed as the probability of obtaining a score as far away from the centroid as the case in question. Low probabilities were associated with scores far from the centroid while nearby scores were linked with high probabilities. These "distance" probabilities differ from those given in Table 6.6. The occupancy of males and females (Chapter 3) was compared with these probabilities (Fig. 6.11) in an attempt to discover whether their morphological properties were related to their performance. There was a significant positive correlation between

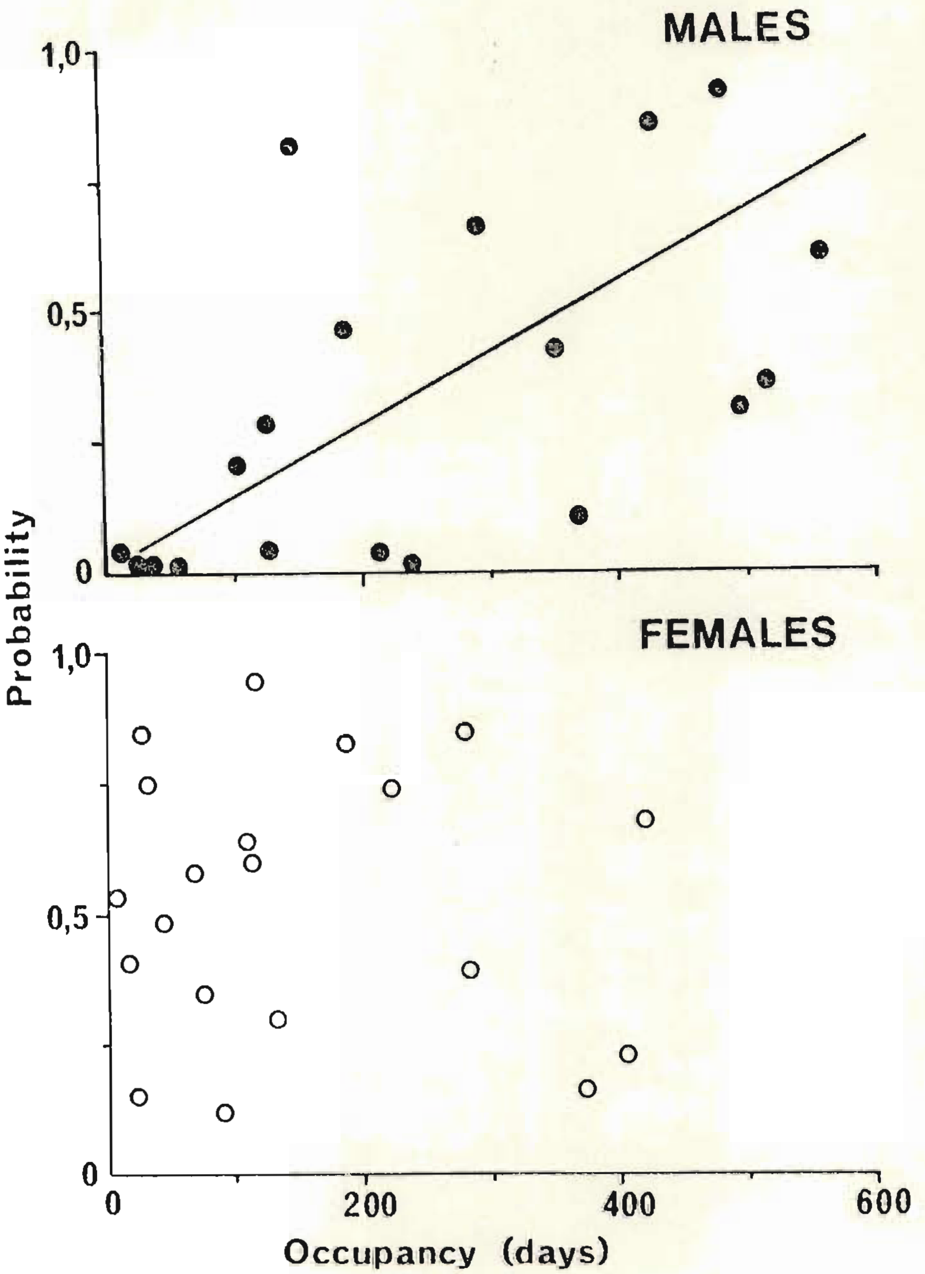


FIGURE 6.11 Scattergram showing the occupancy of adult males and females (from Chapter 3 - Appendix 3.1) and the probability of obtaining birds as far removed from group centroid values as the ones in question (see text).

occupancy and "distance" probability for males (Spearman's Rank $r_{20} = +0,65$; $p < 0,005$), but not for females (Spearman's Rank $r_{21} = +0,10$; NS). This suggests that males remaining resident for long periods were more "average" or "typical" morphologically than other males. Similar tests were used to search for possible relationships between breeding performance (Chapter 4) and "distance" probability, and between occupancy and breeding performance and univariate measurements (as in Table 6.4). However, none of these correlations revealed significant relationships between morphological variables and performance.

DISCUSSION

Moult

The descending sequence of primary moult found in adult and subadult kites (Fig. 6.4) is common to many accipitrids. All juveniles and the adults of several genera show the descending sequence (Stresemann & Stresemann 1960, 1966). Among adults, the descending sequence occurs in small accipitrids, e.g. Accipiter, Circus and Milvus, while larger species, e.g. Buteo and Aquila (Broekhuysen & Siegfried 1970; Brooke et al. 1972) show a jumbled moult which may result from several overlapping waves of moult.

The three moult centres in the secondaries of kites are similar to those of most accipitrids (Miller 1941), although few species have been studied. Miller (1941) also found a high degree of variation in the position of the two proximal centres at S5 and S13.

The pattern of tail moult in kites, however, differs from that established for most accipitrids. Most species show two moult centres, at the innermost and outermost rectrices, from which moult proceeds inwards and outwards in the sequence: R1-6-4-2-3-5 or R6-1-4-5-3-2 (Stresemann & Stresemann 1966). The moult sequence in kites, R1-2-3-4-6-5 or R1-2-3-6-4-5, while also showing moult centres at R1 and R6, differs mainly in the outermost rectrix R6 moulting later than in other species.

Some of the variation in rectrix and secondary moult sequences may have been due to arrested and replacement moult in one year affecting sequences in following years. If a kite stopped moulting or renewed a feather out of normal sequence, it may have resumed moult in a different position the next time it moulted. However, if this was the case, young kites would have shown less variability than adults. This was not the case, as shown by moult counts in Appendix 6.1.

Although there was some variation in when kites moulted, the great majority moulted between September and April. This seasonality contrasts with the flexible timing of breeding (Chapter 4 — Fig. 4.6). It is perhaps significant that the most intense period of moult, during November-February, was in the hottest months of the year (Chapter 1 — Fig. 1.5). Presumably the loss of feathers during these warm periods was less critical since kites did not have to retain as much body heat.

Measurements

The index of food supply shown in Figure 6.10 was based on data from one area during one year. The weights of kites, in contrast, were obtained from birds trapped in many areas over several years. However, this may not detract from the significance of the positive correlation between the weights of subadults and food supply, because seasonal changes in feeding conditions at Settlers were probably similar to those over much of southern Africa (Chapter 2, p. 75). The correlation may therefore show quite confidently that the body condition of young kites was closely dependent on food supply. Presumably, kites lost fat reserves when feeding conditions were poor and gained reserves when they improved.

Although not shown by data in Figure 6.10 similar changes in the condition of adults probably occurred. Samples of adults weights were biased by the methods used to catch kites and therefore did not reflect changes in condition as closely as those of non-breeding subadults. The great majority of weights were obtained from kites trapped along roads and most of these birds would have been hunting actively (Chapter 5, p. 207). However, the proportions of adult males and females hunting along roads probably changed during the year. During periods of good food supply, when kites were breeding (Chapter 4, p.173), many females were probably restricte to nest areas where they were not caught readily. The proportions of heavie females in trapped samples were therefore lower when feeding conditions were good and many kites were breeding.

Weight differences (Table 6.3) suggest that nomads and subadults were ir poorer condition than residents and adults respectively. Young kites were probably less experienced hunters than adults and, like nomads, they also had little access to dependable food sources on territories. However, the poorer condition of nomads may also have been due to food shortages that probably caused them to desert territories (Chapter 3 — Table 3.4 & p. 124).

Differences in size between adults and subadults (Table 6.4) are widespread in raptors but their significance is not easily explained (Amadon 1980). As in kites, subadults of most species have longer tails which may provide them with greater lift in flight. It is possible that young birds spend more time in flight than adults, moving greater distances in search of promising feeding areas. A more likely explanation, and one that might explain other structural differences, is that adults and young birds hunt in different ways. Similar differences in hunting behaviour probably occur between male and female raptors (Koplin 1973; Snyder & Wiley 1976) and even between colour morphs (Preston 1980), so age related differences in feeding ecology seem quite possible.

Size differences between males and females mainly involved weight, (Table 6.3), the shape of the head, and structures associated with feeding and flight (Table 6.4). The greatest difference was in weight, but this was expected because increases in volume are proportionately bigger than those for linear or area measurements. Females had larger bills and gapes, possibly suggesting that they fed faster than males by tearing up prey quickl and swallowing larger pieces. Although I found no differences in the size of prey caught by males and females (Chapter 2 — Table 2.14), females with higher wing loading may have struck prey with greater impact than males (Mueller et al. 1976) and therefore caught bigger prey. (Kites, and probably most raptors, immobilise their prey by impact (Harris 1978)). Against these arguments, however, males and females had similar claw lengths, suggesting that they usually carried prey of similar size. It thus seems probable that there were no marked differences in the size of prey caught by males and females.

I can offer no explanation for the differences in head shape between males and females, unless these, too, have bearing on feeding. The significance of the differences in the size and proportions of the wing and tail is also unclear. The longer tails and lower wing loading of males might indicate that, in the long run, they hover more than females, but the limited data in Chapter 2 (Table 2.14) do not show any such difference. The narrower wings (higher aspect ratio) of males suggest that they may fly faster than females, but again no information is available.

The measure of the degree to which kites were morphologically "average" depended on the variables and sample of kites used in the analysis. A different set of birds would have yielded other group centroid values, and other variables may not have given the significant correlation found in this study (Fig. 6.11). Nevertheless, the variables measured were chosen to try to reflect some of those structures that were important to the birds' overall performance. Many of the variables emphasised structures that were importar in hunting and this emphasis may explain why a significant correlation was found for males but not females. I suggested in Chapter 3 (p. 124) that much of the behaviour of males was concerned with occupying territories for as long as feeding conditions were suitable. The performance of males as territory occupants (and thus as breeders — Chapter 3, p. 110) therefore depended on their ability to feed themselves. While much of the variation in feeding success was due to environmental conditions (Chapter 2), at least some was due to the physical ability of males to catch prey. It is therefore possible that the significant correlation, between occupancy and the degree to which males were morphologically typical, partly reflected the physical properties of males in being successful hunters.

The behaviour of females, in contrast, suggested that their occupancy and breeding performance were not as dependent on their ability to catch prey. They moved around frequently in search of males holding territories with good breeding prospects, and their performance on these territories was probably related to the breeding potential of the areas and the males' success in feeding them and their young (Chapter 4). The physical properties of females that were important in hunting may therefore have had no significant influence on their social and breeding performance.

SUMMARY

Adult and subadult kites usually moulted between August/September and March/April. Primary moult started earlier and finished slightly later than secondary and rectrix moult.

Primaries moulted in an unvarying sequence from the inner wing outwards. There were three moult centres in the secondaries and two in the rectrices. However, the positions of these centres and the overall moult sequences varied greatly.

Young kites develop adult plumages at different ages. Some moult directly into adult plumage during their first summer moult season, while others first pass through an intermediate 2nd plumage. The development of these plumages depends on when young kites hatch relative to the summer moult season.

Females, adults and residents were heavier than males, subadults and nomads respectively. Seasonal changes in the weight of subadults were related to changing feeding conditions.

Subadults had wider heads, shorter wings and longer tails than adults. Females were larger than males in several structures of the head and wing; males had slightly longer tails.

A multivariate analysis suggested that the dimensions of males that occupied territories for long periods (Chapter 3) closely approached those of morphologically "average" males.

APPENDIX 6.1 Matrices showing the number of times that each primary, rectrix and secondary moulted before other feathers in the same tract. Moult counts for adults and subadults (in parenthesis) are separate. The three tracts were not always examined for moult in the 233 adults and 139 subadults inspected. Sample sizes were: adults - primaries (230), rectrices (198), secondaries (197); subadults - primaries (132), rectrices (124), secondaries (84). The 'total' moult count for each feather is plotted in Figure 6.4.

		Primaries moulting first									
		1	2	3	4	5	6	7	8	9	10
Primaries moulting later	1	0 (0)	29 (3)	50 (6)	62 (11)	78 (21)	92 (35)	103 (52)	117 (67)	123 (84)	132 (88)
	2	0 (0)	0 (0)	38 (5)	50 (10)	66 (20)	80 (34)	91 (51)	105 (66)	116 (83)	120 (87)
	3	0 (0)	0 (0)	0 (0)	30 (8)	46 (18)	60 (32)	71 (49)	85 (64)	96 (81)	100 (85)
	4	0 (0)	0 (0)	0 (0)	0 (0)	30 (14)	44 (28)	55 (45)	69 (60)	80 (77)	84 (81)
	5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	30 (24)	42 (41)	56 (56)	67 (73)	71 (77)
	6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	28 (35)	42 (50)	53 (67)	57 (71)
	7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	29 (37)	39 (54)	44 (58)
	8	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	25 (34)	29 (38)
	9	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	14 (19)
	10	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total		0 (0)	29 (0)	88 (11)	142 (29)	220 (73)	296 (153)	390 (273)	504 (400)	604 (553)	651 (604)

		Rectrices moulting first					
		6	5	4	3	2	1
Rectrices moulting later	6	0 (0)	6 (0)	14 (1)	26 (9)	27 (24)	42 (43)
	5	23 (3)	0 (0)	22 (2)	36 (9)	39 (24)	52 (43)
	4	17 (3)	6 (0)	0 (0)	28 (9)	36 (23)	44 (43)
	3	4 (1)	6 (0)	13 (0)	0 (0)	21 (19)	35 (41)
	2	9 (0)	8 (0)	11 (0)	20 (4)	0 (0)	37 (38)
	1	12 (1)	8 (0)	11 (0)	19 (2)	23 (6)	0 (0)
Total		65 (8)	34 (0)	71 (3)	129 (33)	146 (96)	210 (208)

continued on p. 268

Appendix 6.1 continued

		Secondaries moulting first												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Secondaries moulting later	1	0 (0)	1 (0)	0 (0)	3 (3)	9 (13)	4 (3)	0 (0)	2 (0)	1 (0)	0 (1)	1 (4)	5 (10)	8 (10)
	2	24 (8)	0 (0)	6 (1)	11 (3)	24 (16)	23 (7)	9 (0)	8 (0)	4 (0)	3 (1)	13 (5)	20 (13)	20 (12)
	3	30 (11)	23 (5)	0 (0)	13 (3)	30 (19)	28 (9)	18 (3)	10 (0)	9 (0)	7 (1)	23 (9)	28 (15)	29 (15)
	4	31 (13)	23 (8)	13 (6)	0 (0)	30 (20)	28 (11)	21 (5)	14 (4)	7 (1)	13 (5)	23 (9)	28 (15)	31 (14)
	5	9 (2)	6 (1)	4 (1)	3 (3)	0 (0)	8 (0)	5 (0)	6 (0)	3 (0)	2 (1)	4 (3)	7 (4)	11 (7)
	6	10 (6)	4 (1)	2 (2)	4 (4)	9 (15)	0 (0)	2 (0)	3 (0)	2 (0)	1 (1)	3 (4)	8 (11)	12 (11)
	7	20 (9)	11 (4)	4 (2)	9 (4)	22 (17)	20 (8)	0 (0)	5 (0)	4 (0)	0 (2)	10 (7)	19 (13)	19 (12)
	8	32 (12)	25 (7)	11 (5)	15 (4)	32 (20)	31 (11)	23 (3)	0 (0)	6 (0)	11 (5)	25 (10)	27 (16)	28 (15)
	9	36 (13)	30 (8)	19 (6)	19 (5)	35 (21)	35 (12)	27 (4)	15 (3)	0 (0)	16 (6)	27 (11)	29 (17)	32 (16)
	10	34 (13)	24 (8)	11 (3)	18 (5)	33 (21)	33 (11)	22 (4)	12 (1)	9 (0)	0 (0)	25 (10)	30 (16)	29 (15)
	11	18 (7)	9 (2)	6 (2)	8 (3)	18 (14)	19 (4)	6 (0)	9 (0)	5 (0)	3 (0)	0 (0)	17 (9)	17 (8)
	12	16 (4)	11 (2)	9 (2)	11 (4)	15 (12)	12 (3)	10 (1)	8 (1)	4 (1)	8 (2)	9 (2)	0 (0)	15 (7)
	13	18 (6)	12 (3)	9 (2)	11 (3)	16 (11)	17 (5)	11 (1)	8 (1)	6 (1)	8 (2)	10 (3)	11 (4)	0 (0)
Total		278 (104)	179 (49)	94 (32)	125 (44)	273 (199)	258 (84)	154 (21)	100 (10)	56 (3)	72 (27)	173 (77)	229 (143)	251 (142)

Chapter 7

GENERAL SUMMARY AND CONCLUSIONS

Blackshouldered Kites Elanus caeruleus were studied during 1977-1978 in a 6900-ha area near Settlers (24 57S; 28 33E) in the Springbok Flats, Transvaal. Most of the annual rainfall of 601 mm fell during the summer months. About 75% of the area was cultivated. Results from ringing and moult studies during 1970-1976 in a wider area of the Transvaal are incorporated into the present work.

The study aimed mainly to describe the basic biology of kites and to investigate the role of food supply in their behaviour and breeding. About 97% of prey found in pellets were small mammals. Three rodent species, Otomys angoniensis, Rhabdomys pumilio and Praomys natalensis, formed about 92% of the weight of their prey. Regular trapping of rodents at six trap-lines suggested that rodent densities changed substantially during the study. Measures of the food intake of kites showed changes that closely matched changes in rodent numbers.

Kites usually caught 1-3 prey items each day after highly unpredictable periods of hovering and perched-hunting. The proportions of hovering (about 30%) and perched-hunting (70%) and the duration of hunting each day varied greatly. Non-breeders probably hunted for average periods of about 2 h each day while breeding males hunted for about 4 h. The two hunting methods differed in several ways; when hovering, kites caught prey more rapidly than when perched-hunting, but hovering was more expensive energetically. Hovering was probably used to obtain prey as rapidly as possible, while perched-hunting was advantageous in that it helped to minimize energy costs. It was important for kites to use as little energy as possible each day because the unpredictability of prey capture meant that excessive energy spent in hunting could not be replaced with certainty.

Individual kites showed a high degree of variability in their social behaviour and dispersion. Residents were unpaired, paired or breeding birds; unpaired kites experienced the poorest and breeders the best feeding conditions. Males usually established territories and remained resident as long as their food supply allowed. Territories with good feeding conditions were at a premium and nomadic males probably spent long periods searching for suitable territories. Females seldom occupied territories alone, but usually settled with territorial males. Most females arrived to pair with males when most pairs were starting to breed. Females also deserted territories more readily than males and probably moved around in search of those males with territories holding the best breeding prospects. There were always more males than females in the study area and this could have allowed females to change territories often.

A great number of males and females were resident for short periods and, as a result, the average monthly turnover of residents was about 26%. These short-term residents and records of great concentrations of kites suggest that kites are often eruptive and nomadic, particularly when rodent densities vary erratically. Information concerning changes in food supply is probably exchanged at communal roosts; kites were found to roost communally when their feeding conditions were poor. Such itinerant behaviour contrasts with the site-tenacity of some individuals in the study area that remained resident for most or all of the census period.

Residents bred repeatedly and opportunistically at any time of the year. Some males made up to seven breeding attempts in 19 months, but most of these failed, particularly at early stages of the cycle. The average duration of breeding was: pre-laying (24 days), incubation (31 days), nestling period (35 days) and post-nestling period (82 days). Adult females deserted soon after the young left the nest. They then probably searched for unpaired males with which they could attempt breeding again. The flying young were fed by adult males for the remaining part of the post-nestling period. For adult males, each successful breeding cycle lasted on average 172 days. Some males started breeding again immediately after the young became independent and they therefore bred twice in one year. Females, with their shorter participation in each breeding cycle, could breed three times each year.

Breeding females seldom hunted. Males supplied them and the young with food. Several observations indicated that breeding attempts failed because of food shortages which kites experienced frequently. Females accumulated energy reserves during the pre-laying period which helped them to produce eggs and probably withstand food shortages later in the cycle. Other adaptations to future feeding conditions are indicated. Kites may stop breeding if poor feeding conditions early in the cycle indicate that great food demands are unlikely to be met later during the nestling period. They may also time breeding on the basis of the amount of breeding activity in their rodent prey, again as an indication of expected food availability.

It is suggested that breeding females do not hunt and remain largely inactive at the nest so that they can conserve energy reserves. Furthermore, the fact that females are larger than males enables them to store proportionately greater reserves. Males probably do not help store energy because the increased weight of reserves would hinder their flying ability in catching fast and agile prey.

Residents in the study area defended hunting and breeding territories against all intruders. The use of several displays during territorial conflicts appeared to depend on how easily residents could expel trespassers. The characteristic tail wagging of kites is probably an aggressive display which serves to warn other kites away. The most violent conflicts, sometimes involving physical contact, were between neighbouring residents; intruding nomads were repulsed more readily.

Kites showed several reactions to excessive heat and cold and a substantial part of the variation in their daily activity was probably linked to thermal conditions. They usually perched in the shade of trees during the hot midday period or, if they were hunting, they soared sporadically. Most nests were built in the SW sectors of trees where incubating females and nestlings were protected from the direct sun. In the early morning kites usually perched low above the ground where they were less exposed to cold winds. Similarly, they roosted within the foliage of trees during winter, where they were more protected from cold wind than on perches on the outermost branches of trees, their roost sites at other times.

Most kites moulted during summer and this seasonality contrasted with the variable timing of their breeding. Primary feathers were moulted in a single sequence from the inner wing outwards, but sequence of moult in the secondaries and rectrices was highly variable. A method was found for determining the average sequences in spite of this variability. Many other raptors are described as having irregular or jumbled moult sequences, and this method may help to identify the average sequences.

Several size differences were found between males and females and between adults and two age groups of subadults. Changes in the weights of subadults during the year, and probably in those of adults, corresponded to changes in food supply. Males that remained resident for long periods were probably morphologically more 'typical' than males that were short-term residents. The physical features of males may therefore in part determine their ability to catch prey and consequently to pair and breed successfully. The performance of females, however, may depend more on their ability to choose mates and territories which will provide them with the best feeding conditions.

In conclusion, I suggest that unpredicted fluctuations in feeding conditions play a central role in the biology of kites. These fluctuations occur at two levels, one on an hourly or daily basis and the other on a weekly or monthly scale. The capture of large and irregularly spaced prey is an unpredictable event and several aspects of hunting behaviour and daily activity are probably geared to meeting the general requirement of obtaining prey as rapidly and at the least possible energy expense. Many social, spatial and breeding strategies are probably adaptations to feeding conditions that fluctuate over longer periods. While kites often survive and occasionally breed in situations of moderate food supply, the 'slumps' and 'gluts' in prey numbers are the periods when selection is most severe. It is then that kites will either manage to survive or will se capitalize on a superabundant food supply that they leave great numbers of offspring.

REFERENCES

ALTMANN, J. 1974. Observational study of behaviour: sampling methods *Behaviour* 49: 227-267.

AMADON, D. 1975. Why are female birds of prey larger than males? *Raptor Res.* 9: 1-11.

AMADON, D. 1980. Varying proportions between young and old raptors. *Proc. 4th Pan-Afr. Orn. Congr*: 327-331. Johannesburg, South African Orn. Soc.

AMAT, J.A. 1979. Notas sobre la ecologia alimenticia del Elanio Azul (*Elanus caeruleus*). *Doñana Acta Vert.* 6: 124-128.

ANDERSSON, M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. *J. Anim. Ecol.* 49: 175-184.

ASCHOFF, J. & POHL, H. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29: 1541-1552.

BALGOOYEN, T.G. 1976. Behaviour and ecology of the American Kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. *Univ. of Calif. Publs.Zool.* 103: 83 pp.

BEECHAM, J.J. & KOCHERT, M.N. 1975. Breeding biology of the Golden Eagle in southwestern Idaho. *Wilson Bull.* 87: 506-513.

BENSON, C.W., BROOKE, R.K., DOWSETT, R.J. & IRWIN, M.P.S. 1971. The Birds of Zambia. London, Collins.

BERGER, D.D. & MUELLER, H.G. 1959. The bal-chatri; a trap for birds of prey. *Bird banding* 30: 18-26.

BERULDSEN, G.R. 1971. The Letterwinged Kite, *Elanus scriptus*. *Aust. Bird Watcher* 4: 46-52.

BIGGS, H.C., BIGGS, R. & KEMP, A.C. 1978. Measurement of raptors. *Proc. Symp. African Predatory Birds*: 77-82. Pretoria, Northern Transvaal Orn. Soc.

BIRD, D.M. and HO, S.K. 1976. Nutritive values of whole-animal diets for captive birds of prey. *Raptor Res.* 10: 45-49.

BIRKHEAD, M.E. 1981. The social behaviour of the Dunnock *Prunella modularis*. *Ibis* 123: 75-84.

BODENHEIMER, F.S. & SULMAN, F. 1946. The estrous cycle of *Microtus guentheri* and its ecological implications. *Ecology* 27: 255-256.

BROEKHUYSEN, G.J. & SIEGFRIED, W.R. 1971. Age and moult in the Steppe Buzzard in southern Africa. *Ostrich* suppl. 8: 223-237.

BROEKHUYSEN, M. & BROEKHUYSEN, G. 1974. Blackshouldered Kite (*Elanus caeruleus*) builds a nest on a telegraph pole. *Bokmakierie* 26: 36.

BROOKE, R.K. 1965. Roosting of the Blackshouldered Kite *Elanus caeruleus* (Desfontaines). *Ostrich* 46: 43.

BROOKE, R.K., GROBLER, J.H. & IRWIN, M.P.S. 1972. A study of the migratory eagles *Aquila nipalensis* and *A. pomarina* (*Aves*: *Accipitridae*) in southern Africa with comparative notes on other large raptors. *Occ. Pap. natn. Mus. Rhod.* 1972 B5: 61-114.

BROOKS, P.M. 1974. The ecology of the Fourstriped Field Mouse, *Rhabdomys pumilio* (Sparrman, 1784), with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria. D.Sc. thesis, University of Pretoria.

BROWN, L.H. 1980. The African Fish Eagle. Cape Town, Purnell.

BROWN, L.H. & AMADON, D. 1968. Eagles, hawks and falcons of the World. Vol. 1 & 2. Feltham, Country Life Books.

BROWN, L.H. and DAVEY, P.R.A. 1978. Natural longevity, as determined by plumage variation, in Ayre's Eagle *Hieraaetus dubius*. *Bokmakierie* 30: 27-31.

BROWN, L.H. & WATSON, A. 1964. The Golden Eagle in relation to its food supply. *Ibis* 106: 78-100.

BRYANT, D.M. & WESTERTERP, K.R. 1980. The energy budget of the House Martin (*Delichon urbica*). *Ardea* 68: 91-102.

CADE, T.J. 1955. Variation of the Common Roughlegged Hawk in North America. *Condor* 57: 313-346.

CADE, T.J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. *Univ. Calif. Publs. Zool.* 63: 151-290.

CADE, T.J. 1980. Book review: "Population ecology of raptors". *J. Wildl. Manage.* 44: 969-972.

CAIRNS, J. 1940. Birds of Penang and Province Wellesley. *Malayan Nat. J.* 1: 118-127.

CAVE, A.J. 1968. The breeding of the Kestrel, *Falco tinnunculus* L., in the reclaimed area Oostelijk Flevoland. *Netherlands J. Zool.* 18: 313-407.

CESKA, V. 1980. Untersuchungen zu Nahrungsverbrauch, Nahrungsnutzung und Energie-haushalt bei Eulen. *J. Orn.* 121: 186-199.

CHIDUMAYO, E.N. 1980. Population ecology of *Tatera leucogaster* (Rodentia) in southern Zambia. *J. Zool., Lond.* 190: 325-336.

CHOATE, T.S. 1972. Behavioural studies of some Rhodesian rodents. *Zool. afr.* 7: 103-118.

CLANCEY, P.A. 1964. The birds of Natal and Zululand. Edinburgh, Oliver & Boyd.

CODY, M.L. 1966. A general theory of clutch size. *Evolution* 20: 174-184.

COETZEE, C.G. 1965. The breeding season of the Multimammate Mouse *Praomys* (*Mastomys*) *natalensis* (A. Smith) in the Transvaal highveld. *Zool*. *afr*. 1 29-39.

COETZEE, C.G. 1967. The breeding season and population structure of the Multimammate Mouse *Praomys* (*Mastomys*) *natalensis* (A. Smith, 1834) in the Transvaal highveld. M.Sc. thesis, University of Pretoria.

✓ COETZEE, C.G. 1972. The identification of southern African small mammal remains in owl pellets. *Cimbebasia* (A) 2: 53-64.

COLLAR, N.J. 1978. Nesting of the Blackshouldered Kite in Portugal. *Brit*. *Birds* 71: 398-412.

CRAMP, S. & SIMMONS, K.E.L. (eds) 1980. The Birds of the Western Palearctic Vol. II. Oxford, Oxford University Press.

CUMMINS, K.C. & WUYCHECK, J.C. 1971. Caloric equivalents for investigations in ecological energetics. *Int*. *Ver*. *Theor*. *Angew*. *Limnol*. *Verh*. 18: 1-158.

CURTIS, B.A. & PERRIN, M.R. 1979. Food preferences of the Vlei Rat (*Otomys irroratus* Brants, 1827) and the Fourstriped Mouse (*Rhabdomys pumilio* Sparrman, 1784). *S*. *Afr*. *J*. *Zool*. 14: 224-229.

DAVID, J.H.M. 1980. Demography and population dynamics of the Striped Field Mouse *Rhabdomys pumilio* in alien *Acacia* vegetation on the Cape flats, Cape Province, South Africa. Ph. D. thesis, University of Cape Town.

DAVIES, N.B. 1978. Parental meanness and offspring independence: an experimen with hand-reared Great Tits *Parus major*. *Ibis* 120: 509-514.

✓ DAVIES, N.B. 1980. The economics of territorial behaviour in birds. *Ardea* 68: 63-74.

DAVIS, R.M. 1973. The ecology and life history of the Vlei Rat *Otomys irroratus* (Brants, 1827) on the Van Riebeeck Nature Reserve, Pretoria. D. Sc. thesis, University of Pretoria.

DEAN, W.R.J. 1971. Breeding data for the birds of Natal and Zululand. *Durban Mus*. *Novit*. 9: 59-91.

DEAN, W.R.J. 1973a. Analysis of a collection of Barn Owl *Tyto alba* pellets from Warmbaths, Transvaal. *Zool*. *afr*. 8: 75-81.

DEAN, W.R.J. 1973b. Age distribution of *Praomys natalensis* prey in *Tyto alba* pellets. *Zool*. *afr*. 8: 140.

DE GRAAF, G. 1981. The Rodents of southern Africa. Pretoria, Butterworths.

DE MOOR, P.P. 1969. Seasonal variation in local distribution, age classes and population density of the gerbil Tatera brantsi on the South African highveld. J. Zool., Lond. 157: 399-411.

DESAI, J.H. & MALHOTRA, A.K. 1979. Breeding biology of the Pariah Kite Milvus migrans at Delhi Zoological Park. Ibis 121: 320-325.

DE VRIES, T. 1975. The breeding biology of the Galapagos Hawk Buteo galapagoensis. Gerfaut 65: 29-57.

DE WIT, C. 1972. An ecological study of a small mammal community with emphasis on the status of Praomys (Mastomys) natalensis. M.Sc. thesis, University of Pretoria.

DIPPENAAR, N.J. 1974. Bait preferences of Rhabdomys pumilio. Zool. afr. 9: 90-92.

DIXON, J.B., DIXON, R.E. & DIXON, J.E. 1957. Natural history of the Whitetailed Kite in San Diego County, California. Condor 59: 156-165.

DOWNHOWER, J.F. 1976. Darwin's finches and the evolution of sexual dimorphism in size. Nature 263: 558-563.

DRENT, R.H. & DAAN, S. 1980. The prudent parent; energetic adjustments in avian breeding. Ardea 68: 225-252.

EBERSOLE, J.P. 1980. Food density and territory size: an alternative model and a test on the reef fish Eupomacentrus leucostictus. Am. Nat. 115: 492-509.

EISENMANN, E. 1971. Range expansion and population increase in North and Middle America of the Whitetailed Kite (Elanus leucurus). Am. Birds 25: 529-536.

EMLEN, S.T. 1978. Co-operative breeding in birds. In KREBS, J.R. & DAVIES, N.B. (eds) Behavioural ecology; an evolutionary approach. Oxford, Blackwell Scientific Publs.

ENDERSON, J.H. 1960. A population study of the Sparrow Hawk in east- and central Illinois. Wilson Bull. 72: 222-231.

ETTINGER, A.O. & KING, J.R. 1980. Time and energy budgets of the Willow Flycatcher (Empidonax traillii) during the breeding season. Auk 97: 533-546.

FAABORG, J., DE VRIES, T., PATTERSON, C.B. & GRIFFIN, C.R. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galapagos Hawk (Buteo galapagoensis). Auk 97: 581-590.

FIELD, A.C. 1975. Seasonal changes in reproduction, diet and body composition of two equatorial rodents. E. Afr. Wildl. J. 13: 221-235.

FORBES-WATSON, A.D. 1977. Maximum carrying potential of a Blackshouldered Kite *Elanus caeruleus*. *Scopus* 1: 44.

GALPIN, E.E. 1926. Botanical survey of the Springbok Flats, Transvaal. Memoir No. 12. Botanical Survey of South Africa. Cape Town, Cape Times

GALUSHIN, V.M. 1974. Synchronous fluctuations in populations of some raptors and their prey. *Ibis* 116: 127-134.

GIBB, J.A. 1960. Populations of tits and goldcrests and their food supply in pine plantations. *Ibis* 102: 163-208.

GOSLOW, G.E. 1971. The attack and strike of some North American raptors. *Auk* 88: 815-827.

GRAUL, W.D., DERRICKSON, S.R. & MOCK, D.W. 1977. The evolution of avian polyandry. *Am. Nat.* 111: 812-816.

GREEN, R. 1976. Breeding behaviour of Ospreys *Pandion haliaetus* in Scotland. *Ibis* 118: 475-490.

HALLETT, J.M. 1979. Chromosome polymorphism in *Praomys* (*Mastomys*) *natalensis* in southern Africa. *S. Afr. J. Sci.* 75: 413-415.

HAMERSTROM, F. 1969 . A harrier population study in HICKEY, J.J. (ed.). Peregrine Falcon Populations. Madison, Univ. Wisconsin Press.

HANNEY, P. 1965. The Muridae of Malaŵi (Africa: Nyasaland). *J. Zool., Lond.* 146: 577-633.

HANTGE, E. 1980. Untersuchungen über den Jagderfolg mehrerer europäischer Greifvögel. *J. Orn.* 121: 200-207.

HARRIS, T. 1978. Prey immobilization by the Blackshouldered Kite *Elanus caeruleus* (Desfontaines) B. Sc. Hons. thesis, University of Rhodesia.

HAWBECKER, A.C. 1940. The nesting of the Whitetailed Kite in southern Santa Cruz County, California. *Condor* 42: 106-111.

HAWBECKER, A.C. 1942. A life history study of the Whitetailed Kite. *Condor* 44: 267-276.

HAYWARD, J.L. & MACFARLANE, N. 1971. Bird predators and a mouse plague. *Aust. Bird Watcher* 4: 62-66.

HIRONS, G.J.M. 1976. A population study of the Tawny Owl (*Strix aluco* L.) and its main prey species in woodland. Ph. D. thesis. University of Oxford.

HIXON, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* 115: 510-530.

HOBBS, J.N. 1971. A plague of mice at Warren. *Aust. Bird Watcher* 4: 43-46.

HOLLANDS, D.G.W. 1977. Field observations on the Letterwinged Kite, Eastern Simpson Desert, 1974-1976. *Aust. Bird Watcher* 7: 73-80.

HOLLANDS, D.G.W. 1979. The Letterwinged Kite irruption of 1976-1977. *Aust. Bird Watcher* 8: 1-18.

HOUSTON, D.C. 1976. Breeding of the Whitebacked and Rüppell's Griffon Vultures. Gyps africanus and G. rueppelli. Ibis 118: 14-40.

HOWELL, A.H. 1932. Florida Bird Life. New York, Coward-McCann.

HUSAIN, K.Z. 1959. Notes on the taxonomy and zoogeography of the genus Elanus. Condor 61: 153-154.

HUSTLER, K. 1979. Roost orientation of the Blackshouldered Kite Elanus caeruleus. B.Sc. thesis, University of the Witwatersrand.

JACOBSEN, N.H.G. 1977. An annotated checklist of the amphibians, reptiles and mammals of the Nylsvlei Nature Reserve. S. Afr. Nat. Sci. Prog. Rep. 21: 1-65.

JENNI, D.A. 1974. Evolution of polyandry in birds. Am. Zool. 14: 129-144.

JOHNSON, S.J. 1973. Post-fledging activity of the Redtailed Hawk. Raptor Res. 7: 43-48.

JOLLIE, M. 1976-1977. A contribution to the morphology and phylogeny of the Falconiformes. Evol. Theory 1: 285-298; 2: 115-300; 3: 1-141.

JONES, P.J. & WARD, P. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Redbilled Quelea Quelea quelea. Ibis 118: 547-574.

KEMP, A.C. 1977. Some marking methods used on a variety of southern African raptors. Safring News 6: 38-43.

KENDEIGH, S.C. 1952. Parental care and its evolution among birds. Illinois Biol. Monog. 22: 1-356.

KENDEIGH, S.C. 1973. Discussion in KING, J.R. Energetics of reproduction in birds. In PAYNTER, R.A. Jnr. (ed.). Breeding biology of birds. Nuttall Ornithol. Club Publ. No. 15. Cambridge, Massachusetts.

KENDEIGH, S.C., DOL'VIK, V.R. & GAVRILOV, V.M. 1977. Avian Energetics. In PINOWSKI, J. & KENDEIGH, S.C. (eds) Granivorous birds in ecosystems. Cambridge, Cambridge Univ. Press.

KLAPSTE, J. 1979. Field notes on Letterwinged Kites at Werribee, Victoria. Aust. Bird Watcher 8: 19-26.

KOPLIN, J.R. 1973. Differential habitat use by sexes of American Kestrels wintering in northern California. Raptor Res. 7: 39-42.

KOPLIN, J.R., COLLOPY, M.W., BAMMANN, A.R. & LEVENSON, H. 1980. Energetics of two wintering raptors. Auk 97: 795-806.

KREBS, J.R. 1978. Optimal foraging; decision rules for predators. In KREBS, J.R. & DAVIES, N.B. (eds) Behavioural Ecology; an evolutionary approach. Oxford, Blackwell Sci. Publs.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LENDRUM, A.J. 1979. The Augur Buzzard in the Matopos, Rhodesia. *Ostrich* 50: 203-214.

LEVENSON, H. 1979. Time and activity budgets of Ospreys nesting in northern California. *Condor* 81: 364-369.

LOCKIE, J.D. 1966. Territory in small carnivores. *Symp. Zool. Soc. Lond.* 18: 143-165.

LUNDBERG, A. 1979. Residency, migration and a compromise; adaptations to nest-site scarcity and food specialization in three Fennoscandian Owl species. *Oecologia* 41: 273-281.

LUNDEVALL, C.F. & ROSENBERG, E. 1955. Some aspects of the behaviour and breeding biology of the Pallid Harrier (*Circus macrourus*). *Proc. Int. Orn. Congr.* 11: 599-603.

MACARTHUR, R.H. & PIANKA, R.E. 1966. On the optimal use of a patchy environment. *Am. Nat.* 100: 603-609.

MACDONALD, M.A. 1980. Breeding of the Black Kite in southern Ghana. *Ostrich* 51: 118-120.

MACLEAN, G.L. 1970. The Pygmy Falcon *Polihierax semitorquatus* *Koedoe* 13: 1-21.

MACLEAN, G.L. 1973. Arid-zone adaptations in southern African birds. *Cimbebasia* (A) 13: 163-176.

MADDEN, S.T. 1977. Notes on two nests of the Blackshouldered Kite. *Ostrich* 48: 115-116.

MADER, W.J. 1975. Biology of the Harris' Hawk in southern Arizona. *Living Bird* 14: 59-85.

MALHERBE, A.P. 1963. Notes on birds of prey and some others at Boshoek north of Rustenburg during a rodent plague. *Ostrich* 34: 95-96.

MARCSTRöM, V. & KENWARD, R. 1981. Sexual and seasonal variation in condition and survival of Swedish Goshawks *Accipiter gentilis*. *Ibis* 123: 311-327.

MARTI, C.D. & HOGUE, J.G. 1979. Selection of prey by size in Screech Owls. *Auk* 96: 319-327.

MEBS, Th. 1964. Zur Biologie und Populationsdynamik des Mäuserbussards (*Buteo buteo*). *J. Orn.* 105: 247-306.

MEESTER, J. 1963. A systematic revision of the shrew genus *Crocidura* in southern Africa. *Transv. Mus. Mem.* 13: 1-127.

MEESTER, J. 1970. Collecting small mammals. *Spectrum* 8: 403-408.

MENDELSOHN, J.M. 1968. Nest-site preferences of the Whitebrowed Sparrow-Weaver in the central Transvaal. *Ostrich* 39: 263.

MENDELSOHN, J.M. 1979. A note on hunting in Lesser and Eastern Redfooted Kestrels. *Ostrich* 50: 121-122.

MESERVE, P.L. 1977. Food habits of a Whitetailed Kite population in central Chile. *Condor* 79: 263-265.

MILLER, A.H. 1941. The significance of molt centres among the secondary remiges in the Falconiformes. *Condor* 43: 113-115.

MOORE, R.T. & BARR, A. 1941. Habits of the Whitetailed Kite. *Auk* 58: 453-462.

MOREL, G-J. & POULET, A-R. 1976. Un important dortoir d'*Elanus caeruleus*, Accipitridae, au Sénégal. *Oiseau et R.F.O.* 46: 429-430.

MORGAN-DAVIES, A.M. 1965. On the roosting habits of the Blackwinged Kite *E. caeruleus*, Desfontaines. *Bull. Brit. Orn. Cl.* 85: 110-111.

MORITZ, D. & VAUK, G. 1976. Der Zug des Sperbers (*Accipiter nisus*) auf Helgoland. *J. Orn.* 117: 317-328.

MOSHER, J.A. 1976. Raptor energetics: a review. *Raptor Research* 10: 97-107.

MOSS, D. 1979. Growth of nestling Sparrowhawks (*Accipiter nisus*) *J. Zool., Lond.* 187: 297-314.

MUELLER, H.C. 1974. Food caching behaviour in the American Kestrel (*Falco sparverius*). *Z. Tierpsychol.* 34: 105-114.

MUELLER, H.C., BERGER, D.D. & ALLEZ, G. 1976. Age and sex variation in the size of Goshawks. *Bird banding* 47: 310-318.

MURTON, R.K. & WESTWOOD, N.J. 1977. Avian breeding cycles. Oxford, Oxford University Press.

NEWTON, I. 1972. Finches. London, Collins.

NEWTON, I. 1973. Studies of Sparrowhawks. *Brit. Birds* 66: 271-278.

NEWTON, I. 1978. Feeding and development of Sparrowhawks *Accipiter nisus* nestlings. *J. Zool., Lond.* 184: 465-487.

NEWTON, I. 1979. Population ecology of raptors. Berkhamsted, T. & A.D. Poyser.

NEWTON, I. & MARQUISS, M. 1976. Occupancy and success of Sparrowhawk nesting territories. *Raptor Res.* 10: 65-71.

NEWTON, I., MARQUISS, M., WEIR, D.N. & MOSS, D. 1977. Spacing of Sparrowhawk nesting territories. *J. Anim. Ecol.* 46: 425-441.

NEWTON, I., MARQUISS, M. & MOSS, D. 1979. Habitat, female age, organo-chlorine compounds and breeding of European Sparrowhawks. *J. Appl. Ecol.* 16: 777-793.

NIE, N.H., HULL, C.H., JENKINS, J.G., STEINBRENNER, K. & BENT, D.H. 1975. Statistical package for the social sciences. New York. McGraw-Hill.

NIEBOER, E. 1973. Geographical and ecological differentiation in the genus *Circus*. Thesis, Free University, Amsterdam.

NOLAN, V. 1978. The ecology and behaviour of the Prairie Warbler *Dendroica discolor*. *Orn. Monog.* No. 26. Am. Ornith. Union.

✓NORBERG, R.A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. J. Anim. Ecol. 46: 511-529.

PARKER, S.A. 1971. Critical notes on the status of some central Australian birds. Emu 71: 99-102.

PARKES, K.C. 1958. Specific relationships in the genus Elanus. Condor 60: 139-140.

PERRIN, M.R. 1980. The breeding strategies of two coexisting rodents, Rhabdomys pumilio and Otomys irroratus; with a brief review of some pertinent life history ideas. Acta Oecologica Oecol. Gener. 1: 383-410.

PERRINS, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

PEYTON, L. 1915. Nesting of the Whitetailed Kite at Sespe, Ventura County, California. Condor 17: 230-232.

PHELAN, F.J.S. 1977. Food caching in the Screech Owl. Condor 79: 127.

PIANKA, E.R. 1970. On r and K selection. Am. Nat. 104: 592-597.

PICKWELL, G. 1930. The Whitetailed Kite. Condor 32: 221-239.

PICOZZI, N. 1971. Wing tags for raptors. The Ring 68-69: 169-170.

PRESTON, C.R. 1980. Differential perch site selection by color morphs of the Redtailed Hawk (Buteo jamaicensis). Auk 97: 782-789.

✓✓PULLIAM, H.R. 1980. Do Chipping Sparrows forage optimally? Ardea 68: 75-82.

✓✓PYKE, G.H., PULLIAM, H.R. & CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137-154.

RALLS, K. 1976. Mammals in which females are larger than males. Q. Rev. Biol. 51: 245-276.

RAUCH, B. & LANDMAN, J.C.K. 1974. Voëls van Suid-Afrika 9. Blouvalkie. Landbouweekblad 20: 74-75.

RAUTENBACH, I.L. 1978. The Mammals of the Transvaal. Ph.D. thesis. University of Natal, Pietermaritzburg.

REAL, L.A. 1980. Fitness, uncertainty, and the role of diversification in evolution and behaviour. Am. Nat. 115: 623-638.

REYNOLDS, H.G. 1960. Life history notes on Merriams Kangaroo rat in southern Arizona. J. Mammal 41: 48-58.

✓✓RICKLEFS, R.E. 1968. Patterns of growth in birds. Ibis 110: 419-451.

RIDLEY, M. 1978. Paternal care. Anim. Behav. 26: 904-302.

ROTHSCHILD, M., FORD, B. & HUGHES, M. 1970. Maturation of the male rabbit flea (Spilopsyllus cuniculi) and the oriental rat flea (Xenopsylla cheopis: some effects of mammalian hormones on development and impregnation. Trans. Zool. Soc. Lond. 32: 105-188.

ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. *Ibis* 108: 313-347.

SCHANTZ, T. VON. & NILSSON, I.N. 1981. The reversed size dimorphism in birds of prey; a new hypothesis. *Oikos* 36: 129-132.

SCHLATTER, R.P., TORO, B., YÁÑEZ, J.L. & JAKSIĆ, F.M. 1980. Prey of the Whitetailed Kite in central Chile and its relation to the hunting habitat. *Auk* 97: 186-190.

// SCHOENER, T.W. 1971. Theory of feeding strategies. *A. Rev. Ecol. Syst.* 2: 369-404.

SCHULZE, B.R. 1974. Climate of South Africa. Weather Bureau, Dept. of Transport, South Africa. *WB 28*: 330 pp.

SERVENTY, D.L. 1971. The biology of desert birds. In FARNER, D.S. & KING, J.R. (eds) Avian Biology, Vol. I. New York, Academic Press.

SIEGFRIED, W.R. 1965. On the food of the Blackshouldered Kite. *Ostrich* 36: 224.

SKEAD, D.M. 1974. Roadside counts of Blackshouldered Kite in the central Transvaal. *Ostrich* 45: 5-8.

SKUTCH, A.F. 1957. The incubation patterns of birds. *Ibis* 99: 69-93.

SLATER, P. 1971. A field guide to Australian birds: non-passerines. Edinburgh, Oliver & Boyd.

SMEENK, C. & SMEENK-ENSERINK, N. 1975. Observations on the Pale Chanting Goshawk *Melierax poliopterus*, with comparative notes on the Gabar Goshawk *Micronisus gabar*. *Ardea* 63: 93-115.

SMITHERS, R.H.N. 1971. The mammals of Botswana. *Mem. natn. Mus. Rhod.* 4: 1-340.

SNOW, D.W. (ed.) 1978. An atlas of speciation in African non-passerine birds. London, Brit. Mus. (Nat. Hist.).

SNYDER, N.F.R. 1974. Can the Cooper's Hawk survive? *Natl. Geog. Mag.* 145: 433-442.

SNYDER, N.F.R. & WILEY, J.W. 1976. Sexual size dimorphism in hawks and owls of North America. *Orn. Monogr.* No. 20: Am. Ornith. Union.

SOUTH AFRICAN WEATHER BUREAU. 1954. Climate of South Africa, Part 1, Climate Statistics. WB 19, Pretoria, Government Printer.

SOUTH AFRICAN WEATHER BUREAU. n.d. Climate of South Africa, Part 2, Rainfall Statistics. WB 20. Pretoria, Government Printer.

SOUTHERN, H.N. & LOWE, V.P.W. 1968. The pattern of distribution of tawny owl territories. *J. Anim. Ecol.* 37: 75-97.

STENDELL, R.C. 1972. The occurrence, food habits and nesting strategy of Whitetailed Kites in relation to a fluctuating vole population. Ph.D. thesis, University of California, Berkeley.

STEYN, P. 1963. The wagtail kite. *Bokmakierie* 15: 9-10.

STINSON, C.H. 1978. The influence of environmental conditions on aspects of the time budget of breeding Ospreys. *Oecologia* 36: 127-140.

STRESEMANN, E. & AMADON, D. 1979. Falconiformes. In MAYR, E. & COTTRELL, G.L. (eds) Checklist of the birds of the World. Cambridge, Massachusetts, Mus. of Comp. Zool.

STRESEMANN, E. & STRESEMANN, V. 1966. Die Mauser der Vögel. *J. Orn.* 107: 1-445.

STRESEMANN, V. & STRESEMANN, E. 1960. Die Handschwingen-Mauser der Tagraubvögel. *J. Orn.* 101: 373-403.

SUETENS, W. & VAN GROENENDAEL, P. 1977. Nidification de L'Elanion Blac (*Elanus caeruleus*) en Espagne. *Gerfaut* 67: 54-72.

SWANN, H.K. 1945. A monograph of the birds of prey. Vol. II. London, Wheldon and Wesley.

TARBOTON, W.R. 1977. Food consumption and pellet production in the Blackshouldered Kite. *Zool. Afr.* 12: 252-255.

TARBOTON, W.R. 1978a. Hunting and the energy budget of the Blackshouldered Kite. *Condor* 80: 88-91.

TARBOTON, W.R. 1978b. A survey of birds of prey in the Transvaal. Progress Report, Transvaal Provincial Admin. 101 pp.

TAYLOR, K.D. & GREEN, M.G. 1976. The influence of rainfall and diet on reproduction in four African rodent species. *J. Zool., Lond.* 180: 367-389.

TAYLOR, P. & GORDON, D.H. 1978. Sibling species of *Praomys* (*Mastomys*) *natalensis*: identification, distribution and sympatric population ecology. *S. Afr. J. Sci.* 74: 143.

TEMPLE, S.A. 1972. Sex and age characteristics of North American Merlins. *Bird Banding* 43: 191-196.

THIOLLAY, J.M. 1980. Stratégies d'exploitation par les rapaces d'un écosystème Néotropicale. *Alauda* 48: 221-253.

TINBERGEN, L. 1940. Beobachtungen über die Arbeitsteilung des Turmfalker (*Falco tinnunculus*) während der Fortpflanzungszeit. *Ardea* 29: 63-98.

TRIVERS, R.L. 1972. Parental investment and sexual selection. In CAMPBELL, B. (ed.) Sexual selection and the descent of man. London, Heinemann.

TULLOCK, G. 1979. On the adaptive significance of territoriality: comment. *Am. Nat.* 113: 773-775.

TYSON, P.D. & DYER, T.G.J. 1978. The predicted above-normal rainfall of the Seventies and the likelihood of droughts in the Eighties. *S. Afr. J. Sci.* 74: 372-377.

VAN DER MERWE, F.J. 1975. Waarnemings oor die Blouvalk. *Bokmakierie* 27: 56-59.

VAN DER MERWE, F. & HEUNIS, F. 1980. Nest building in the Blackshouldered Kite. *Ostrich* 51: 113-114.

VAN DER MERWE, G. & KEOGH, H. 1970. Comprehensive report on the rodent population explosion in the Republic 1966 to 1969. Unpublished report, S.A. Inst. for Medical Research, Johannesburg.

VAN DER RIET, H.M. 1974. Aangepaste boerderystelsels vir die Springbokvlakte. D. Inst. Agrar.thesis, University of Pretoria.

VAN SOMEREN, V.G.L. 1956. Days with birds. *Fieldiana:Zoology* 38: 1-520.

VERNER, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111: 769-775.

VILLAGE, A. 1979. The ecology of the Kestrel (*Falco tinnunculus*) in relation to vole abundance at Eskdalemuir, south Scotland. Ph.D. thesis, Edinburgh University.

WAIAN, L.B. 1973. The behavioural ecology of the North American Whitetailed Kite (*Elanus leucurus majusculus*) of the Santa Barbara coastal plain. Ph.D. thesis. University of California, Santa Barbara.

WAKELEY, J.S. 1978a. Activity budgets, energy expenditures, and energy intakes of nesting Ferruginous Hawks. *Auk* 95: 667-676.

WAKELEY, J.S. 1978b. Factors affecting the use of hunting sites by Ferruginous Hawks. *Condor* 80: 316-326.

WAKELEY, J.S. 1978c. Hunting methods and factors affecting their use by Ferruginous Hawks. *Condor* 80: 327-333.

WARD, P. & ZAHAVI, A. 1973. The importance of certain assemblages of birds as "information centres" for food finding. *Ibis* 115: 517-534.

WARNER, J.S. & RUDD, R.L. 1975. Hunting by the Whitetailed Kite (*Elanus leucurus*) *Condor* 77: 226-230.

WATSON, F.G. 1940. A behaviour study of the Whitetailed Kite. *Condor* 42: 295-304.

WATTEL, J. 1973. Geographical differentiation in the genus *Accipiter*. Publ. Nuttall Orn. Club No. 13. Cambridge, Massachusetts.

WEBSTER, H.M. 1944. A survey of the Prairie Falcon in Colorado. *Auk* 61: 609-616.

WEIR, D. & PICOZZI, N. 1975. Aspects of social behaviour in the Buzzard. *Brit. Birds* 68: 125-141.

WILSON, V.J. 1970. Notes on the breeding and feeding habits of a pair of barn owls, *Tyto alba* (Scopoli), in Rhodesia. *Arnoldia* (Rhod.) 4: 1-8.

WILSON, V.J. 1975. Mammals of the Wankie National Park, Rhodesia. *Mem. natn. Mus. Rhod.* 5: 1-147.