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THE FEEDING ECOLOGY OF THE BLACKSHOULDERED KITE *ELANUS CAERULEUS* (AVES: ACCIPITRIDAE)

by

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INTRODUCTION

Intensive studies of raptor feeding ecology are seldom practical. Most species either catch prey rarely (*e.g.* large eagles) or hunt within closed habitats (*e.g.* accipiters). 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 *Elanus leucurus*, Tarboton (1977; 1978 a) of Blackshouldered Kites *E. caeruleus*, 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 relationships between Blackshouldered Kites and their prey, I aimed in this paper to investigate some of these poorly understood subjects. Basic descriptions are first given of hunting behaviour and performance and the prey caught by kites. These variables are then compared for different habitats, seasons and groups of kites. Results from a study of small mammal prey populations in the area (Mendelsohn in press) are compared with data on the feeding success of the study species. 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 relationships between time, energy and hunting behaviour.

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STUDY AREA

Blackshouldered Kites were studied in a 6900-ha area at Settlers (28°33'E, 24°57'S) in the Springbok Flats. The topography was flat with a 60-m drop over 12 km from north to south. The study area consisted of black turf soil (64%) or red clay (36%). Cultivation accounted for 72% of the area, with six predominant crops: wheat (38%), sunflowers (33%), maize (9%), millet (9%), sorghum (7%), and manna (5%). Wheat was usually planted in February and March and harvested between July and September. Other crops were planted between September and November and harvested between April and August.

Other major habitats in the area were woodland (17%), grassland (5%), road and field verges (5%) and farmyards (1%). The distinction between grasslands and woodlands 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. These varied in width between 3 and 20 m; using an average width of 10 m, there was about 370 ha of verge in the study area. Farmhouses, and thus 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.

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 study area. Power lines averaged 9-11 m while telephone lines varied between 5 and 8 m in height.

The study area was in Springbok Flats Turf Thornveld (Acocks 1975). 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 woodii*, *Ischaemum glaucostachyum*, *Bothriochloa insculpta*, *Sorghum 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, and *Themeda triandra*, *Hyparrhenia hirta*, *Bothriochloa insculpta*, *Eragrostis* spp., *Heteropogon contortus*, *Fingerhuthia africana* and *Panicum coloratum* were the commonest grasses.

The mean annual rainfall at Settlers was 601 mm, of which about 90% fell between October and April. Much of the rain fell in localised thunderstorms, often resulting in marked differences in rainfall between areas. Winter temperatures seldom reached 0°C, but frost occurred on about 20% of the days in June and July. Maximum temperatures in summer often rose to 35-38°C.

The geography of the whole Springbok Flats area is described in detail by Van der Riet (1974).

METHODS

Feeding ecology was studied by observing hunting performance and by analysing pellets. Small mammal populations in the area were also monitored (Mendelsohn in press) to provide comparative data on food availability.

Hunting behaviour and performance was recorded during observation periods ($n = 648$), each of which lasted a maximum of 30 minutes. The periods were shorter if birds under observation were lost to view or stopped hunting. The variables, most of which follow Tarboton (1978a), noted during hunting observations were:

- (1) date, time (see below), locality and habitat
- (2) individual identity, and, therefore, sex and mating class, of kite. (Identities were indicated by coloured patagial tags, and sex by breeding behaviour or a discriminant analysis of body measurements (Mendelsohn 1981). There were three mating classes: *unpaired* (a singleton holding a territory), *paired* (paired territorial birds not breeding), and *breeding* (breeding territorial adult))
- (3) 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)
- (4) the number of perch changes
- (5) duration of hovering bouts (a bout ended when a kite landed or started soaring)
- (6) the number of hovers in each bout (a hover occurred when a kite hovered above one position and ended when the bird moved elsewhere or started a descent towards prey)
- (7) duration of each hover
- (8) number of descents towards prey during each hovering bout
- (9) 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)
- (10) wind speed (estimated at ground level and scored 0-5; 0 indicating no wind and 5 a wind stronger than about 16 m/s)
- (11) 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.

I also recorded all sightings of kites in the study area. Variables noted included the time and the activity of the bird when first sighted. Time was the number of hours and minutes after sunrise. For most analyses the times were pooled into three periods: morning, midday or afternoon. The lengths of these periods were calculated weekly by dividing the daylight period into four quarters. The "morning" period was taken as the first quarter in addition to any activity observed before sunrise, the second and third quarters formed the "midday" period, while the "afternoon" was the final quarter and any activity noted after sunset.

The activities, relevant to this paper, recorded during sightings were: perched (hunting, not hunting, or feeding) or flying (hovering, not hunting, or carrying prey).

Pellets were collected below roost trees and other favoured perches. All pellets were dried to constant weight and weighed to the nearest 0.1g 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; *Lemmiscomys 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 (Mendelsohn 1981). The hunting activity of five individuals during dawn-to-dusk watches is shown in Figure 1. On four days no hunting occurred during the middle of the day. Morning hunting normally stopped after prey had been caught and the birds 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 individual. 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 birds 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 Table 4) for the population, and the five

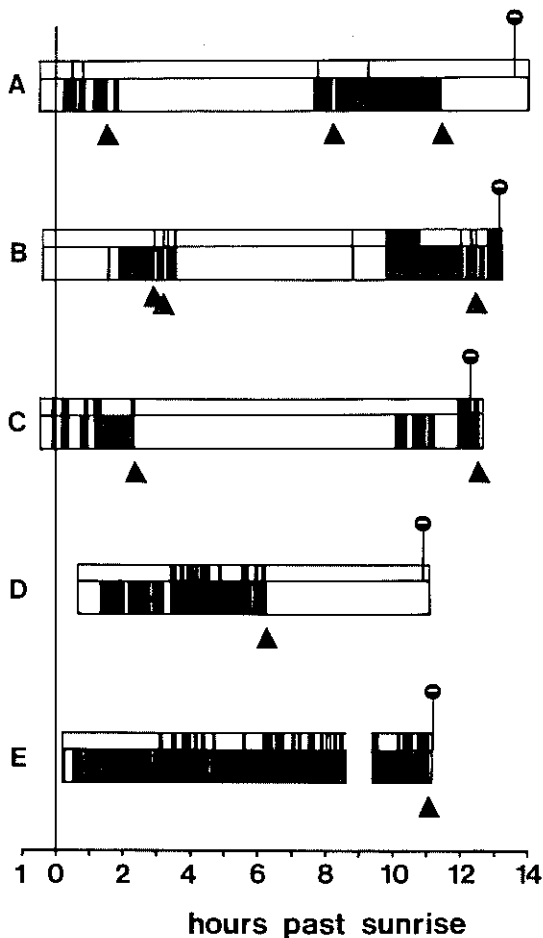


FIGURE 1

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. (D) and (E) from W. R. Tarboton (pers. comm.).

birds 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*).

Table 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 observations also favour perched-hunting because sitting kites were more readily spotted and watched than hovering ones. Data for full-day watches are unbiased but the samples 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. 1).

TABLE 1. Observed proportions of hovering and perched-hunting. Two full-day watches from Tarboton (1978a) are included with data from Figure 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. 1)	1477	27,1
TOTAL	16375 (272,9 h)	26,3

TABLE 2. Indices showing the frequency of hovering and perched-hunting at different times of the day.

Data source	Time of day		
	Morning	Midday	Afternoon
% hovering of all kites sighted (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} $p < 0,05$.

Kites hovered least often in the morning and most often in the afternoon (Table 2). 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 suggest slightly more hovering at midday than in the morning, a trend also found by Tarboton (1978a).

Hovering usually started after a period of perched-hunting or soaring. After leaving a perch, height to a hovering position was gained 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 those ending when soaring started. At Settlers bouts ending when soaring started lasted an average 3,3 min ($n = 85$). Those resulting in a kill lasted 4,8 min ($n = 49$), while others which were unsuccessful lasted 4,1 min ($n = 386$). Morning bouts lasted 3,7 min ($n = 113$), those at midday 3,2 min ($n = 161$), and in the afternoon 5,7 min ($n = 112$). Afternoon bouts were significantly longer than the others ($\chi^2 = 24,8$; $p < 0,01$). Wind conditions apparently did not affect the duration of hovering; in wind rated 0-1 they 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 hovering position or started a descent towards prey. Excluding hovers ending with descents, each 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 they 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; $n = 125$) ($\chi^2 = 17,7$; $p < 0,05$). Hovers low over the ground (rated 1-2; 9,85 s; $n = 235$) were shorter than higher ones (rated 3-5; 13,8 s; $n = 209$) ($\chi^2 = 31,8$; $p < 0,001$). 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; $n = 237$) ($\chi^2 = 42,3$; $p < 0,001$).

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 dive; during a slow descent they were held far apart, and during a rapid drop close together. Some were uninterrupted with the kites reaching the

ground after a single long dive. In others, birds checked several times by pausing to hover; one spent 7 min hovering during a descent. Most descents (65,4%) did not end in strikes or final dives towards prey, presumably because the latter 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 3. 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 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 general for raptors (Goslow 1971).

TABLE 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).

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 ^c (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 ^c (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.

Perched-hunting individuals spent most of the time scanning the ground, only glancing up and around at 5-20-s intervals. Hunting perches characteristically provided a clear view of the ground below and appeared to be specifically selected. Resting and feeding stances were usually more robust than hunting perches. Thus, they hunted from telephone wires and insulators, but perched on telephone poles while resting. In order of frequency, birds hunted from telephone lines (5-8 m above ground), electricity lines (9-11 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. Kites also showed individual preferences. While some birds 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 from 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 km 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 ($\chi^2_2 = 13,6$; $p < 0,01$); in the morning it was 6,4 min, at midday 6,8 min, and in the afternoon 8,6 min.

Perched-hunters often "tail wagged" (Mendelsohn 1981; Steyn 1963), especially while watching prey intently and after making a strike, regardless of success. This display probably served to repel other kites from the immediate area in which the individual was hunting, since their flight may have alerted rodents which had moved into positions where they were exposed to capture.

Three perched-hunting birds made clucking and grated calls unlike any of their usual whistles and screams (Mendelsohn 1981). W. R. Tarboton (pers. comm.) heard the same call from a perched-hunting individual. Some of these calls were made from perches, but most were made during perch changes and strikes. In each case hunting seemed to be particularly intense. There were no others 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 those over greater distances and at the end of such flights individuals often hovered and then either dived or flew back to perch. One successful strike was over 130 m across a ploughed 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 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 performances from hovering, only the proportion of full- and half-strikes differed significantly (Table 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 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 birds; 90 (70,9%) were full-strikes and 24 (26,7%) of these were successful. These proportions, too, differ from those in Table 3 (full-strikes/all strikes, $z = 3,8$; $p < 0,001$; kills/full-strikes, $z = 2,5$; $p < 0,01$).

Hunting performance

Table 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) suggests that although most prey was obtained quite rapidly, hunting birds often had to wait long periods before catching prey.

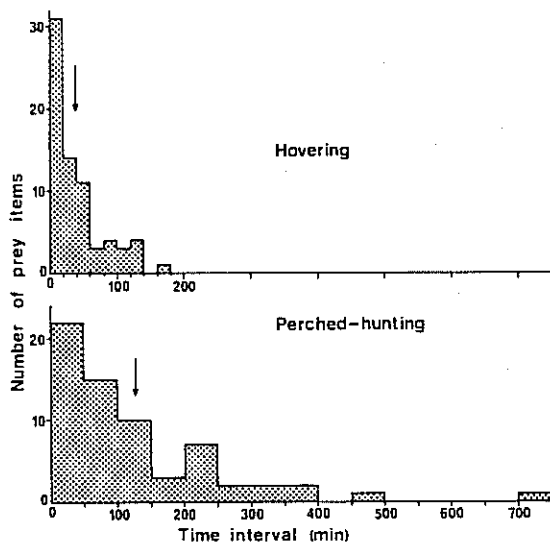


FIGURE 2

Frequencies of time intervals spent hunting between successive kills. The intervals were those that I recorded between observing consecutive kills. They therefore approximate to the time periods that kites had to spend hunting before capturing prey. Mean rates of prey capture (arrows) from Table 4.

TABLE 4. Aspects of hunting success for hovering and perched-hunting kites at different times of the day.

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 ⁱ (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 ⁱ (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; ⁱⁱ+++; ^{jj}+++; ^{kk}+++;
+p<0,1; +++p<0,01; ++++p<0,001

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 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; Davis 1973).

Tarboton (1978 a) recorded 1250 min of hovering with the following rates 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 ($\chi^2=3,02$; $p<0,1$), 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 46,6 min/full-strike. Only the rate of kills differed from Settlers data ($\chi^2=6,24$; $p<0,025$) and this, too, was due to a difference in strike success. The hunting performance of kites in Tarboton's study and mine therefore differed mainly in strike performances; the birds 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 ploughed fields. Fourteen (6,8%) very large rodents (13 *Otomys*, 1 *Praomys*) were not carried away and feeding started at the capture sites in dense cover. In each case I flushed the bird 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). They later returned to their prey, fed on them some more, and carried them to a perch. The birds could have carried these rodents away initially but by eating part of them first, reduced them to a more manageable size (see below). I observed an individual 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 branches (> 3-4 cm diameter) were used for feeding. One breeding female regularly fed on the ground in a bare ploughed field in spite of other feeding perches 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 rejected because kites were unable to swallow or tear them into smaller pieces. The body parts that would not have been eaten were removed from 25 rodents to get an indication of weight loss (Table 5). These data show substantial percentage weight losses which increase in proportion to rodent weight.

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 bird. 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 posteriorly from the neck. Some fur was plucked from large rodents, but this was only after a substantial meal had already been eaten. 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 juveniles 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.

Feeding birds 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 (Mendelsohn 1981).

TABLE 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	<i>Praomys</i>	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	<i>Otomys</i>	36,5	28,5 (i)	21,9
	<i>Praomys</i>	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	<i>Otomys</i>	60,5	38,0 (ih)	37,2
	<i>Rhabdomys</i>	62,0	46,5 (ie)	25,0
			(Mean reduction = 31,1%)	
71 - 160	<i>Otomys</i>	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%)	

Pellets, prey composition and size

Pellets consisted largely of hair, a few fragments of the large limb and jaw bones, and teeth. Some contained no bones or teeth; these had

probably 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 examples followed this pattern although I often fed them several meals at different times of the day. Pellets from captives held remains from the previous day's feeding only. Most, therefore, probably reflected feeding success on the previous day, but several observations suggested variability in their production. On five occasions I saw wild kites regurgitate 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 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.

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

TABLE 6. Prey composition in terms of frequency and weight. Species weights are given in Table 7. Shrew species are shown in Table 8.

Prey species	No. identified by:		Total	%	% weight of total diet
	Hair (%)	Skull			
<i>Otomys angoniensis</i>	386 (41)	554	940	27,6	43,4
<i>Rhabdomys pumilio</i>	270 (27)	734	1004	29,5	25,6
<i>Praomys natalensis</i>	288 (28)	726	1014	29,8	23,3
<i>Lemniscomys griselda</i>	21 (23)	70	91	2,7	3,4
<i>Dendromus melanotis</i>	0 (0)	11	11	0,3	0,1
<i>Saccostomus campestris</i>	2 (29)	5	7	0,2	0,2
<i>Steatomys pratensis</i>	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

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.

TABLE 7. Average weights of prey species (from Mendelsohn (in press)) and the weights consumed after discarding heads, guts and embryos. Discarded percentages were estimated from Table 5.

Prey species	Average weight (g)	Sample size	% discarded	Average weight eaten (g)	^a Mean weight in one prey item
<i>Otomys angoniensis</i>	83,2	128	40	49,9	13,77
<i>Rhabdomys pumilio</i>	34,4	240	20	27,5	8,11
<i>Praomys natalensis</i>	31,0	503	20	24,8	7,39
<i>Lemniscomys griselda</i>	54,0 ^b	-	25	40,5	1,09
<i>Dendromus melanotis</i>	8,2 ^b	-	0	8,2	0,02
<i>Saccostomus campestris</i>	49,0 ^b	-	25	36,7	0,07
<i>Steatomys pratensis</i>	23,0 ^b	-	15	19,5	0,04
Shrews	10,3 ^c	-	0	10,3	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 6)

b — estimated from Rautenbach (1978)

c — estimated average for different species (Table 8)

d — general estimate

Prey composition is shown in Table 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. 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 Fantailed Cisticola *Cisticola juncidis* was seen being caught. Most pellets with reptile scales also held insect remains, indicating lizard prey. An intact 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 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.).

TABLE 8. The frequencies and weights of shrews identified in kite pellets.

Species	Frequency	Weight (g) and source
<i>Crocidura hirta</i>	82	13,6 - Mendelsohn (in press)
<i>Crocidura cyanea</i>	37	9,0 - Rautenbach (1978)
<i>Crocidura bicolor</i>	6	4,0 - Rautenbach (1978)
<i>Suncus infinitesimus</i>	23	2,0 - Rautenbach (1978)
Unidentified	31	-
TOTAL and Average weight	179	10,3

Average weights for prey species (Table 7) have been corrected using wastage factors estimated from Table 5. Table 7 lists the calculated mean contribution of each species per prey animal. Adding these contributions yield a value of 31,6 g for an average food item.

A further measure of prey size comes from estimates of each item seen caught. Estimates were based on observations of how long captive kites took to eat certain sized prey, and on the prey size relative to the size of the kite. Perched-hunters caught significantly larger prey than hovering birds (Table 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 *Habitats and hunting*). The data in Table 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, 19,7% lower than the previous estimate.

Habitats and hunting

Kites hovered mainly over areas with sparse cover (Fig 3). This was obvious at dusk when hovering increased over harvested wheat and bare ploughed fields, probably in response to the onset of nocturnal rodent 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 fields during the wet summers when there were no crevices.

TABLE 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 ($\chi^2 = 10,8$; $p < 0,01$).

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

Perched-hunting occurred predominantly over areas with dense grass cover (Fig. 3). Road verges, in particular, attracted hunting birds 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. 3). 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.

Trapping showed that prey species composition and abundance differed on black turf and red soil areas (Mendelsohn in press). Table 10 compares several aspects of hunting success on the two soils, but these data do not reveal consistent differences. A greater number of descents and half-strikes on red clay suggests that prey was spotted more frequently on red than on black substrates. Apart from more frequent descents, the data in Table 10 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 (Mendelsohn in press). This species probably favoured the dense grass cover on black turf.

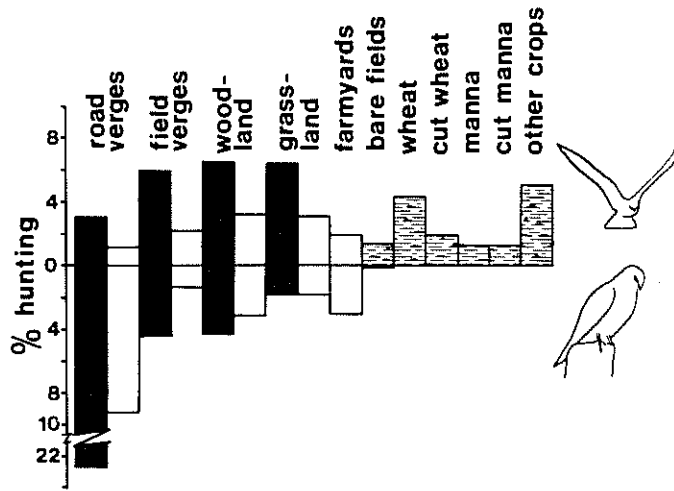


FIGURE 3

Percentage frequencies with which kites were observed hovering and perched-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.

TABLE 10. A comparison of hunting performance of kites over black turf and red clay.

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)	42,61 (176)	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)	$p < 0,001$

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

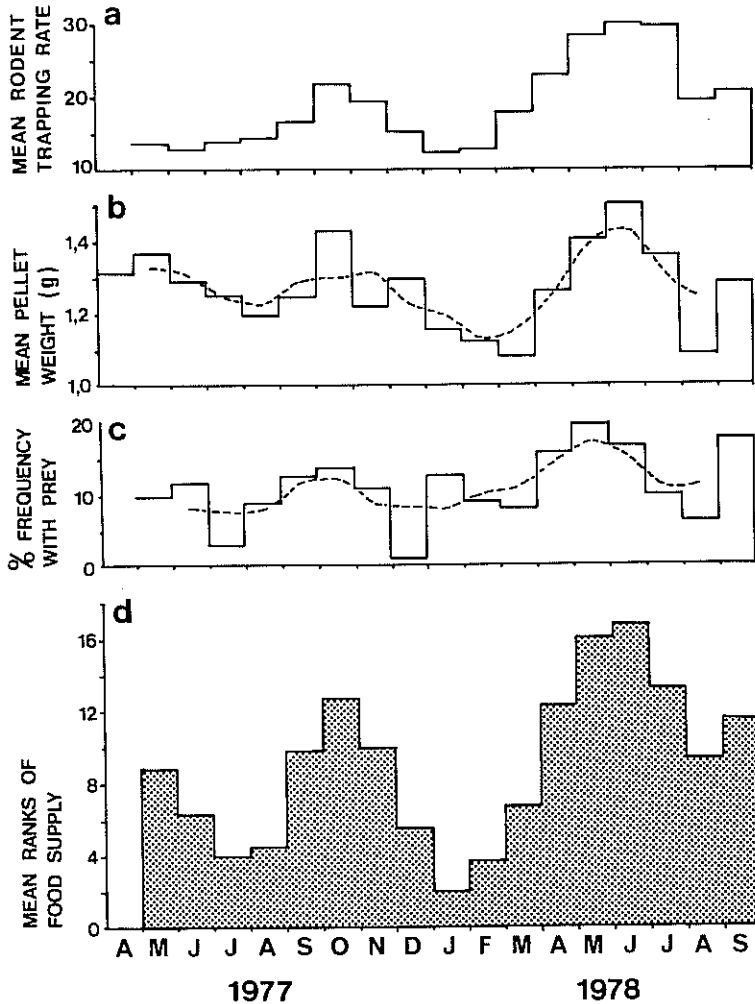


FIGURE 4

Seasonal changes in the food supply of kites. (a) Mean percentage trapping success for rodents (total $n = 1065$) at six trap-lines (from Mendelsohn in press); (b) mean pellet weights (total $n = 1990$); (c) percentage of kite sightings in which birds were perched or flying with prey (total $n = 144$), ((no. seen with prey/no. seen hunting)(100)); (d) mean ranked values for data in (a) and three-point moving averages (broken lines) in (b) and (c).

Seasonal food changes

Changes in rodent trapping rates suggested that prey densities varied substantially during the study (Mendelsohn in press). A curve showing average trapping success (Fig. 4 a) compares well with other measures (Fig. 4 b & c) indicating seasonal changes in food supply. There were good correlations between these indices 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 $r_{17} = +0,47$; $p < 0,05$). Figure 4d shows a mean index of food supply each month, calculated by averaging rank values for the three measures of food supply.

The proportion of hovering and perched hunting also varied seasonally. Two independent indices of hovering activity (Fig. 5 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

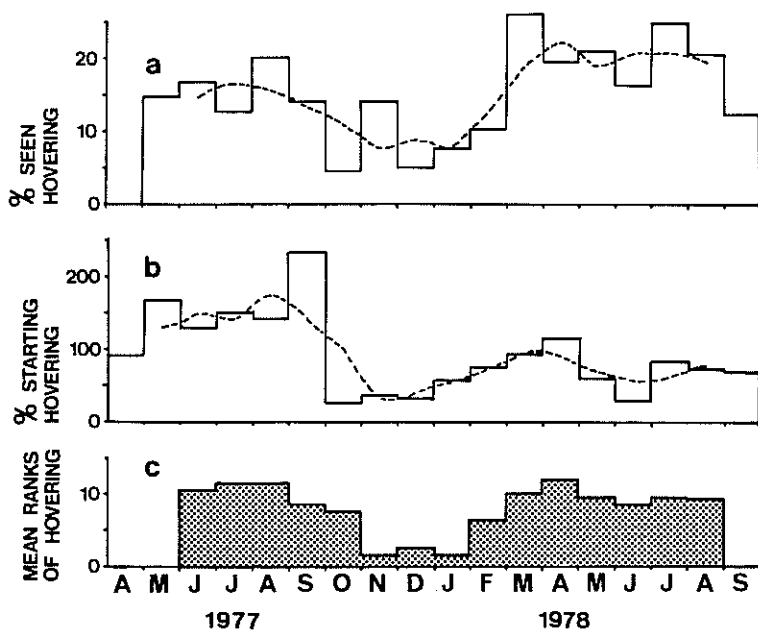


FIGURE 5

Seasonal changes in proportions of hovering and perched-hunting. (a) Percentage frequency of kites seen hovering (total $n = 198$), ((no. seen hovering/total no. seen hunting)(100)); (b) percentage frequency of perched-hunting birds to start hovering (total $n = 179$) during hunting observations ((no. starting to hover/total no. observed perched-hunting)(100)); (c) mean ranked values for three point moving averages (broken lines) in (a) and (b).

show that least hovering occurred in summer. This trend is highly significant if the data are combined into summer and non-summer periods (Table 11). The monthly values in Figure 5a & b have been ranked and the ranks averaged to give a mean curve (Fig. 5c). There was little variation in the percentage time spent hovering during autumn, winter and spring.

Overall, hovering gave an average prey capture rate 3,2 times greater than perched-hunting (Table 4). During summer this difference in capture rate was only 1,8 times (Table 11), suggesting that hovering was less frequent because of lower returns, this, in turn, perhaps being related to the denser grass cover.

TABLE 11. Differences in the proportion of hovering and hunting success in summer (October 1977-February 1978) and non-summer months (April-September 1977 and 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)	NS
Minutes/all strike (no. all strikes)	8,42 (273)	10,48 (54)	NS
Perched-hunting:			
Minutes/kill (no. kills)	140,62 (42)	104,56 (25)	NS
Minutes/all strike (no. all strikes)	24,92 (237)	24,20 (108)	NS

Average prey size did not vary significantly from month to month (Fig. 6) despite a possibly greater number of small prey during rodent breeding seasons (Mendelsohn in press). The lack of agreement between the two measures in Figure 6 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. 7) 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.

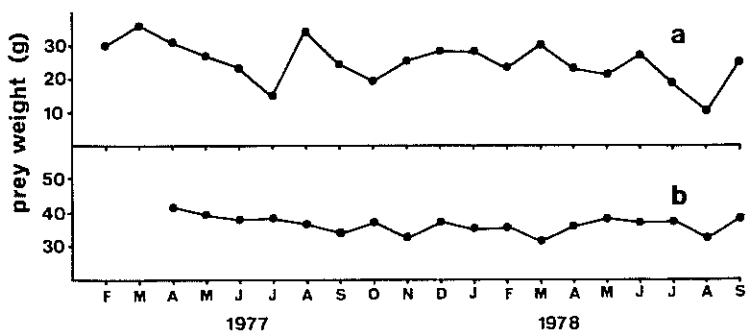


FIGURE 6

Seasonal changes in prey weight. (a) Mean weight of prey seen caught (total $n=203$); (b) mean weight of prey items in pellets (weight of prey represented in pellet/no. of prey animals in pellet).

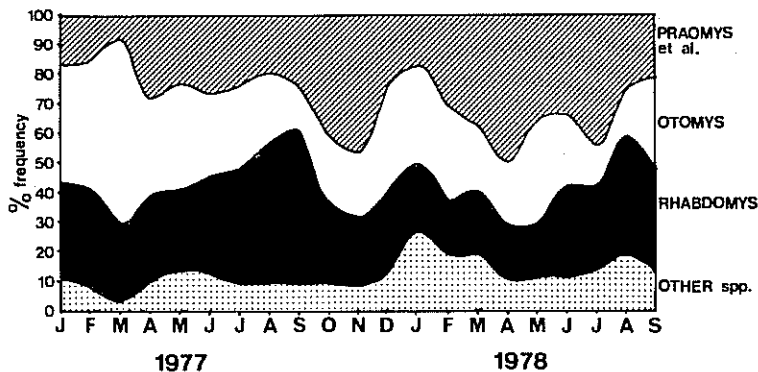


FIGURE 7.

Seasonal changes in the species composition in pellets ($n=3408$ prey items). *Praomys et al.* includes other nocturnal rodents: *Saccostomus*, *Dendromus* and *Steatomys* (see Table 6).

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 (Mendelsohn in press (Fig. 2)) and pellets (Fig. 7) (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* numbers (Mendelsohn in press).

Hunting differences between mating classes

Some aspects of the feeding ecology of unpaired, paired and breeding birds are compared in Table 12. Data for breeders were mainly those of males over the whole breeding cycle; breeding females seldom hunted (Mendelsohn 1981). The proportions of hovering and perched-hunting suggest that breeders and unpaired kites hovered more than paired birds. Hunting data indicate that unpaired individuals had the lowest and breeders the highest measure of success. However, this conclusion is supported by only two significant differences (Table 12). Breeding birds also made significantly more successful full-strikes from perches than unpaired birds.

The difference in pellet weight between breeders and non-breeders was highly significant (Table 12). Using Tarboton's (1977) regression equation (food weight = (pellet weight - 0,056)/0,025), and a 20% wastage correction factor (estimated from Table 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-breeders. This difference may have actually been greater because some breeders' pellets were included in the sample from non-breeding birds. Most non-breeders' pellets came from communal roosts (Mendelsohn 1981), 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 12). 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 12). In spite of the dietary differences, the pellet weights of paired and unpaired birds were similar (\bar{x} paired = 1,39 g; S.D. = 0,68; n = 192 & \bar{x} unpaired = 1,40 g; S.D. = 0,57; n = 127). The pellets on which these data are based were collected from solitary-roosting kites. Perhaps their weights would have differed if samples had also been collected from communal roosts, since communally-roosting birds produced pellets with lower weights than solitary ones (Mendelsohn 1981).

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 breed-

ing birds, breeders produced heavier pellets (Table 12), suggesting that they caught larger prey. Secondly, the mammals 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 rodents of similar size (Table 12).

TABLE 12. The hunting performance and prey of unpaired, paired and breeding kites.

Variables	Unpaired	Paired	Breeding
% hovering of all kites seen hunting (no. hunting)	11,2 ^a (294)	9,2 (502)	19,4 ^b (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 ^{mn} (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 \pm S.D. (n)	1,20 ^r \pm 0,58 (1231)		1,42 ^r \pm 0,69 (759)
PREY COMPOSITION:			
% <i>Praomys natalensis</i>	54,7 ^s	29,4 ^s	31,6
% <i>Otomys angoniensis</i>	16,8	28,0	27,8
% <i>Rhabdomys pumilio</i>	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

Sexual differences in hunting success

Kites usually deserted territories when food supply was lowest, and females deserted more frequently than males. (Mendelsohn 1981). This difference in behaviour might have been due to separate feeding strategies, with females more sensitive to food shortages. However, comparisons in Table 13 suggest that there were no important sexual differences in hunting behaviour and success. 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 (Mendelsohn 1981), and since paired kites caught more diurnal prey than unpaired birds (Table 12), females were probably only resident when diurnal prey was abundant. Most unpaired individuals, in

TABLE 13. The hunting performance of paired males and females.

Variables	Males	Females	Difference
% hovering of all kites seen hunting (no. seen hunting)	8,0 (238)	10,9 (256)	NS
% perched-hunting birds to start hovering (no. perched-hunting)	36,5 (96)	37,5 (112)	NS
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)	NS
Minutes/all strike (no. all strikes)	9,3 (55)	7,5 (81)	NS
Minutes/kill (no. kills)	34,0 (15)	40,6 (15)	NS
Minutes/hovering bout (no. bouts)	4,7 (53)	4,0 (78)	NS
Seconds/hover (no. hovers)	12,0 (90)	10,6 (89)	NS
No. hovers/descent (no. descents)	7,4 (103)	6,5 (172)	NS
PERCHED-HUNTING:			
% full-strikes of all strikes (no. all strikes)	47,1 (68)	48,7 (78)	NS
% successful full-strikes (no. full-strikes)	43,2 (44)	44,1 (59)	NS
Minutes/all strike (no. all strikes)	24,8 (68)	26,0 (78)	NS
Minutes/kill (no. kills)	139,7 (12)	126,7 (16)	NS
Minutes/perch change (no. perch change)	6,5 (259)	7,5 (271)	$p < 0,1$
Mean weight of prey seen caught (no. prey items)	23,8 (37)	21,9 (43)	NS

contrast, were males (Mendelsohn 1981), 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-breeders at Settlers. The daily food intake of 36,6 g 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 for the weight of food usually discarded.

Table 14 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 *Hunting behaviour*), and prey sizes and capture rates in Table 15. Inactive periods during the day were obtained by subtracting the total time spent in other activities from an average 13,6-h daylength period (Mendelsohn 1981).

Three models (Koplin *et al.* 1980; Tarboton 1978 a; Wakeley 1978 a,c) were used to convert the activity budget into an energy budget for non-breeding kites (Table 14). The models are explained in Appendix 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 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 14 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 but only 5% of the time was spent in flying.

TABLE 14. Activity and energy budgets for non-breeding kites at Settlers. The three models used to estimate energy expenditure from the activity data are explained in Appendix 1.

Activity	Activity h/24 h	Daily energy expenditure (kcal)		
		Tarboton (1978 a)	Wakeley (1978 a,c)	Koplin <i>et al.</i> (1980)
PERCHED:				
Inactive - night	10,40			
Inactive - day	7,49	22,8	1,0BM _t	13,6 (1-p)(SM _{nc})
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	38,7 NFA(EM _{dt} - (1-p)(SM _{nc}))
Subtotal	22,81	33,8	51,1	52,3
FLYING:				
Soaring	0,35	7,7	17,2BM _t	
Directional	0,26	5,7	17,2BM _t	17,8 FA(BM _n)(p)(13,7)
Hovering	0,58	12,7	17,2BM _t	
Subtotal	1,19	26,1	9,1	17,8
GRAND TOTAL	24,00	59,9	67,9	70,1

However, as shown by the activities of five birds during dawn-to-dusk watches, all these periods varied greatly in response to changes in daylength and fluctuations in hunting success (see DISCUSSION).

TABLE 15. Food intake, energy intake and expenditure values for hovering and perched-hunting by non-breeding and breeding kites. Data for non-breeders from Table 12 and 14, data for breeding males from Table 12 and Mendelsohn (1981). Prey weights (g) estimated from prey seen caught.

	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

Table 15 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 birds, 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 individuals 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 15).

DISCUSSION

Daily hunting time

Using observed capture rates, prey sizes and proportions of 30% hovering and 70% perched-hunting, I estimated that non-breeders 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 birds during dawn-to-dusk watches (Fig. 1), was probably due to their poor capture rates. 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 observed mainly individuals encountered along roads (W.R. Tarboton pers. comm.). Most of the birds encountered would have been hunting, while inactive ones perched in the shade of trees would have been missed. Nevertheless, lower capture rates than those at Settlers suggest that Tarboton's birds did have to hunt for a greater part of the day.

Irrespective of the discrepancies between the above estimates, it is clear that daily hunting time varied greatly. This is shown by the activities of the five birds in Figure 1. Presumably, variable intervals between successive prey captures (Fig. 2) meant that they often hunted for variable periods each day. The ability to vary daily hunting periods probably enabled them to compensate for substantial changes in prey densities (Mendelsohn in press). The daily energy requirements of non-breeders probably remained relatively constant, and to meet these requirements they 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. 1; Table 14). This was true also of breeding males (Mendelsohn 1981) 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 16). The non-breeding raptors in Table 16 all appear to forage 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, so that foraging could be separated from other activity. Other species in which hunting activity is not as obvious may either show similar patterns of short foraging periods, or they may search 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).

TABLE 16. 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 <i>Elanus leucurus</i>	N	—	5-9	—	—	Warner & Rudd 1975 Koplin <i>et al.</i> 1980
Blackshouldered Kite <i>E. caerulescens</i>	N	1-2	54	52 & 278	13	Tarboton 1978a (see text)
Goshawk <i>Accipiter gentilis</i>	N	0,5	25	—	—	This study Hantge 1980
Sparrowhawk <i>A. nisus</i>	N	2	25	—	—	Hantge 1980
Peregrine <i>Falco peregrinus</i>	N	0,5	15-25	—	—	Hantge 1980
Rock Kestrel <i>F. tinnunculus</i>	N	—	15-25	—	—	Hantge 1980
Osprey <i>Pandion haliaetus</i>	B	1-7	25-35	85	—	Green 1976
Ferruginous Hawk <i>Buteo regalis</i>	B	2-7	8-26	10-117	43-75	Levenson 1979
Whitetailed Kite	B	—	33	—	44	Stinson 1978
Blackshouldered Kite	B	8-9	45-53	45-60	37	Wakeley 1978a
	B	—	12-15	—	—	Warner & Rudd 1975
	B	3-10	30	35 & 75	37	This study

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).

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). Birds taking small prey items therefore have a high rate of energy intake and expenditure.

Large species, in contrast, can meet their energy requirements by consuming a few big 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 16, in contrast probably attempt mainly to minimize their daily hunting time (but see below).

Hunting methods

In recent years biologists have attempted to predict patterns of behaviour which enable animals to meet their requirements optimally.

The predictions involve both identification of the required goals and those decision criteria used by animals in choosing one of several possible courses of action. Such optimality theory has been used in studying 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 1), in the rate at which energy was obtained and spent, and in their energetic efficiencies (Table 15). 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 they usually spent a small proportion of the day hunting. However, if time was the only factor that determined hunting activity, kites would have hovered only since that was the quickest method of obtaining food (Table 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, they 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 15, this was not feasible because perched-hunting was more efficient than hovering.

These predictions may be too simple in suggesting that either hovering or perched-hunting (not both) was optimal. 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. 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 their options. Hovering obviously enlarged the potential hunting area, since many cultivated areas were devoid of perches. It was probably also useful for birds 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 they 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 15 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 breeders if the ratio, $30\%/70\%$, is adjusted by an unknown amount to account for the slightly greater time they spent hovering (Table 12). 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 food items obtained by each method. In 2864 min (25,2%) of hovering and 8520 min (74,8%) of perched-hunting (Table 1) I observed 72 kills by hovering and 67 by perch-hunting birds (Table 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.

These comparisons again consider single factors only 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 11), and kites hovered more in the afternoon (Table 2) when a higher rate of descents (Table 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 they could then hover and soar alternatively at lower temperatures high above the ground. Greater demands for food may have caused unpaired and breeding birds to hover more than paired birds (Table 12). 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 (Mendelsohn 1981). The demand for food may provide another explanation for the higher proportion of hovering in the afternoon: they 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 14 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, hunting methods (Table 11), and total time spent hunting (Fig. 1). 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.

Tarboton (1978 a) estimated the daily energy budget of non-breeding kites from pellet weights and activity budgets (as in Table 14). 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 14). His high figure for energy expenditure was due to the long hunting periods he observed (see *Daily hunting time*) and the high cost values he attached to flight activities (see Table 14). 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 breeders found near nests were heavier than those obtained from non-breeding birds (Table 12).

The average proportion of the DEB spent in perched activity for non-breeders at Settlers was estimated to be about 51 kcal (Table 14). 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 budgets are adjusted to take into account

the fact that the captive did not hunt. It therefore seems probable that perched birds that are not hunting use 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 14 vary greatly, and although Koplín *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,

$$\begin{aligned} \text{DEB} &= 1,079 W^{0.67} \text{ for } 30^{\circ}\text{C} \\ \text{and DEB} &= 8,059 W^{0.50} \text{ for } 0^{\circ}\text{C} \end{aligned}$$

given 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 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

Kites generally seem to be specialist small mammal predators, as shown in this study (Table 6) and elsewhere (Amat 1979; Siegfried 1965; Tarboton 1978 a). Other *Elanus* species show similar preferences (Hobbbs 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 they 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. 4a), 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 which has caught a very large item or can catch several prey items quickly. The prey discarded by satiated birds can, therefore, only be seen as having been wasted.

SUMMARY

The feeding ecology of Blackshouldered 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.

Two estimates of average prey weight were 31,6 g and 26,4 g. Perched-hunting kites caught larger prey than hovering birds.

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 birds 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.

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

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.

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.

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APPENDIX 1

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

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

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

where W is the bird's weight (g); $w = 244,2$ g for non-breeding kites of both sexes (Mendelsohn 1981).

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 14 were drawn from his two papers which differ only in the costs for perched-hunting (2,5 or 3,5 BM_d) and flapping flight (11,5 or 12,5 BM_d). I chose the higher cost of perched-hunting because of the many short flights during perch changes and strikes. The lower cost of 11,5 BM_d for 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 14, however, I have used his costs to estimate energy expenditures separately for hovering and directional flight.

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

$$DEB = NFA(EM_{dt} - (1-p)(SM_{nr})) + FA((BM_n)(p)(FC)) + (1-p)(SM_{nr})$$

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: average daylength at Settlers was 13,6 h (Mendelsohn 1981),

FC is the flight cost, taken as 13,7 by Koplín *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),

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

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,

$$SM_{nt} = 1,810W^{0,5944} - (nt)(0,0457W^{0,5866}),$$

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

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