HUNTING BEHAVIOUR OF BLACKSHOULDERED KITES IN THE AMERICAS, EUROPE, AFRICA AND AUSTRALIA

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SUMMARY

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We review studies of hunting behaviour and food habits of Blackshouldered Kites *Elanus caeruleus* in Chile, California, Spain, Morocco, the Ivory Coast, South Africa and Australia. The general sequence, timing of events and patterns of behaviour during hunting were similar throughout the world. Hovering and perch-hunting were the only methods used to search for prey. In California, kites only hovered, while up to 75 % of hunting time was spent perched in some areas in South Africa; the proportions of hovering and perch-hunting were apparently intermediate elsewhere. Kites usually hunted for 1–4 h/day, depending on hunting methods, food availability and requirements for breeding. In most areas, 40–50 % of strikes onto the ground yielded prey. Although prey was often caught after short periods of hunting, hunting success was unpredictable. When hovering, kites caught prey about twice as quickly in North and South America as in Africa. Hovering yielded prey 3–4 times more rapidly than perch-hunting in South Africa; however, prey caught from perches were larger than those obtained by hovering. In most areas 1–3 prey items, each weighing 20–40 g, were eaten daily. Grasslands, low shrub, open woodlands and cultivated areas were favoured for hunting. Analyses of over 19 000 prey items showed that rodents usually comprised over 95 % of the diet, and in most areas these consisted of 1–3 species. Birds, lizards and insects were also important components of the diet in Spain and Morocco. Wing loading in different populations is similar, but kites in Chile, California and Australia have relatively longer tails, and longer, narrower wings than those in South Africa, perhaps in relation to their respective use of hovering and perch-hunting. A number of questions requiring further study are considered.

INTRODUCTION

Blackshouldered Kites *Elanus caeruleus* are small diurnal raptors, widely distributed in South and North America, Europe, Africa, Asia and Australia. Although often divided into three species, *leucurus* in South and North America, *caeruleus* in Europe, Asia and Africa, and *notatus* in Australia, we consider that the populations constitute one cosmopolitan species *E. caeruleus* (see Parkes 1958; Husain 1959). Blackshouldered Kites typically hunt in open country where their activities are conspicuous and can be recorded over long periods, often for full days. Pellets regurgitated by kites can be analysed and weighed to identify the species and weight of prey consumed the previous day (Tarboton 1977). Many studies have reported on various aspects of their hunting behaviour and diet in Chile, California, Spain, Morocco, the Ivory Coast, South Africa and Australia. We review these studies to identify important variables in foraging behaviour, summarise the available data, and to compare hunting behaviour and food preferences in the widely separated populations. The comparisons also provide indications of the uniformity and variability of different components of foraging in a cosmopolitan species. The following aspects are considered in particular: amount of time spent hunting each day, use of different hunting methods, hovering behaviour, rates at which strikes and kills are made, habitats used for hunting, and the composition and size of prey. Some morphological properties of kites in different populations are also considered in relation to hunting behaviour. Finally, we consider questions that have yet to be studied or those that require further investigation.

As with most raptors, male Blackshouldered Kites are smaller than their mates and during breeding hunt to provision for themselves, their mates and young. Breeding females very seldom hunt. The differences in sizes and roles have significant effects on the activity of males and females during breeding and perhaps at other times of the year (Mendelsohn 1986).

METHODS AND COMPARATIVE DATA

In many studies observers watched focal birds, recording periods spent in different activities and the incidence of prey capture. Other data were obtained by "instantaneous sampling", noting ac-
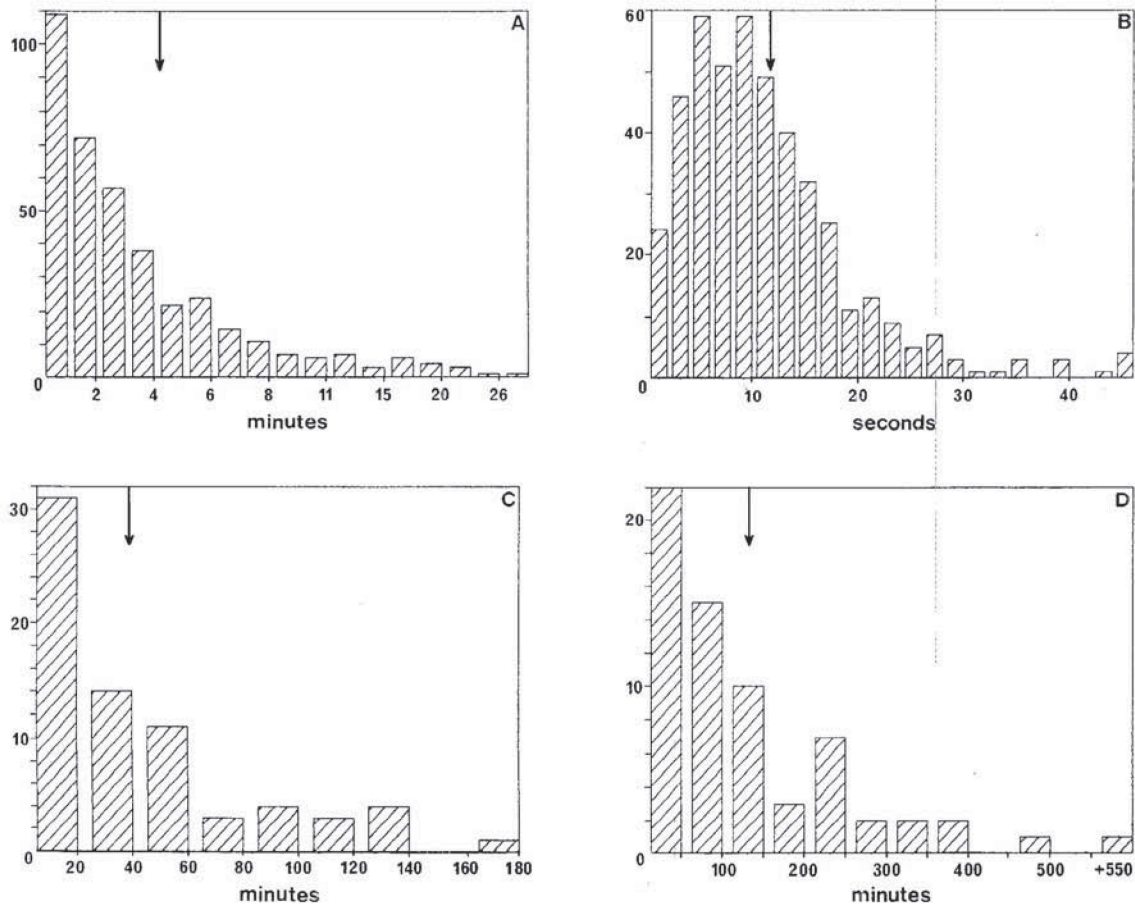
Figure 1

Frequency distributions of (A) the durations of hovering bouts (n = 386), (B) amounts of time kites hovered over each site (n = 446), and the lengths of time that kites hovered (C) or perch-hunted (D) before catching prey (n = 71 and 65). Arrows indicate means (data from Settlers, South Africa, after Mendelsohn 1982).

tivity when kites were first seen. Food habits were determined from the analysis of pellets. Each population showed a great degree of variation in hunting behaviour, some of which was attributable to factors reviewed below. Unfortunately, some studies failed to note these conditions, so many of the data are pooled for comparative purposes. Certain comparisons between the studies were also hampered by a lack of precision in descriptions of behaviour. Most studies also used only normal statistics to describe the duration of hunting activities. Since the distributions of these data may not be normal, as shown in one South African study (Fig. 1), we could not compare statistically activity data described using means and S.D.s only.

In Chile, at Polpaico (33 09 S; 70 57 W), Jaksić *et al.* (1987) recorded behaviour over 43,5 h throughout the year during which 13,8 h of hovering were observed. However, 31,4 h (72 %) of their observations were made in autumn and winter during the late afternoon and they reported no

data for other times of the day. Their results are thus pooled for most variables. Meserve (1977) analysed pellets collected throughout the year at the same locality, while Schlatter *et al.* (1980) compared prey caught in different habitats in Pudahuel (33 26 S; 70 47 W) and La Dehesa (33 21 S; 70 32 W), near Santiago.

In Solano and Yolo Counties, near Davis, California, Warner & Rudd (1975) studied hunting kites throughout the year, and recorded at least 56,2 h of hovering. Their results were partially analysed with respect to habitat, season, sex, and time of day. In Humboldt Co., California, Bamman (1975) described feeding and hunting behaviour and success in detail, and analysed aspects of these with respect to time of day and habitat on the basis of 441,5 of behaviour recorded during winter only. In compiling activity and energy budgets, Koplin *et al.* (1980) used the data compiled by Bamman (1975), but reported only the amount of time spent in different activities (one of which was hovering) and the average number of prey

caught. Waian (1973) provided incidental observations on hunting behaviour in Santa Barbara Co. Information on prey in California was derived from Hawbecker (1940), Bond (1942), Dixon *et al.* (1957), Waian & Stendell (1970), Stendell (1972), Waian (1973), Stendell & Myers (1973), Meserve (1977) and Wright (1978).

Amat (1979) provided data on hunting methods, habitat preferences and prey near Moraleja, western Spain, while Heredia (1983) analysed pellets and noted the hunting methods of kites in the Province of Salamanca, central Spain. Bergier (1982) collected data on hunting methods and prey at several sites in Morocco. Thiollay (1977, 1978) provided some information on hunting methods and prey in the Ivory Coast.

In South Africa, Tarboton (1978) monitored 72,1 h of hunting throughout the year and assigned the data to morning, midday or afternoon periods to compile daily activity and energy budgets. Observations for different sexes were pooled, although no breeding females were observed. Tarboton (1977) also estimated the daily food intake of kites using pellet weights to indicate the amount of prey eaten. His study area (24 29 S; 28 42 E) was about 35 km from that of Mendelsohn (1982) at Settlers (24 57 S; 28 33 E), who recorded about 190 h of hunting throughout the year. These data were partially analysed with respect to time of day, wind strength, sex, season, and habitat. Kites in southern Africa breed at any time of the year (Mendelsohn 1984), so in any population there are usually some birds breeding while others are either paired or unpaired non-breeding residents. This allowed comparisons to be made for birds in different breeding or social conditions. Mendelsohn (1982) also presented estimates of activity and energy budgets and food intake (based on pellet weights). Barnard (1986, 1987), working in montane grasslands in the foothills of the Drakensberg (29 08 S; 29 24 E), analysed the use of hovering in relation to topography, wind conditions and plant cover. Some additional data on activity were provided by Heunis (1975) for kites near Stellenbosch, Cape. Siegfried (1965) (near Stellenbosch), Tarboton (1978), Mendelsohn (1982) and Slotow (1987) (at Settlers) presented data on the prey of South African kites. Australian data on hunting behaviour and prey in coastal Victoria were provided by Baker-Gabb (1984a).

General patterns

All populations show broadly similar patterns of hunting behaviour, probably specifically characteristic of Blackshouldered Kites (Fig. 2). Two methods are used to search for prey; hovering, in which the bird searches the ground from a stationary position maintained by flapping its wings or hanging in the wind (Barnard 1986), and perch-hunting used to scan the ground from an elevated perch. Hovering should more properly be called "windhovering" since the bird maintains zero ground speed by flapping or gliding into the wind (Videler *et al.* 1983). A bout of hovering begins with the kite leaving its perch, flying to a position 5–30 m above ground level, and then successively hovering above a number of sites. After hovering at a site the kite may fly on to another site or, if prey is sighted, descend or dive to the ground (called a strike). Most strikes are unsuccessful, the kite hitting the ground and then immediately flying off. Kites also frequently abort dives just before reaching the ground (half-strike). Hunting is generally resumed nearby if the dive or strike is unsuccessful. Many bouts of hovering [often called hunts, e.g. by Bamman (1975), Warner & Rudd (1975) and Jaksić *et al.* (1987)] are unsuccessful and terminate once the bird returns to perch or begins soaring. If a kill is made, the prey is usually carried to a perch to be consumed. Perch-hunting kites intently scan the ground below, pausing to look around every 5–10 s. Forays at prey are similar to those made by hovering birds (with the same possible results). Intent scanning of the ground and frequent perch changes distinguish perch-hunting from other perched activities.

Searching methods

Although only hovering and perch-hunting have been described as regular methods of searching for prey, Baker-Gabb (1984a) described one instance of apparent hunting from a "high transect flight". The frequency of perch-hunting differed substantially between different areas (Table 1). Continuous observations provide the most reliable estimates of the amount of time spent perch-hunting and hovering. Tarboton (1978) and Mendelsohn (1982) found that perch-hunting was used for 71–75 % of the time during 273 h of hunt-

TABLE 1

NUMBER (%) OF PREY CAUGHT OR ATTACKED FROM DIFFERENT HUNTING METHODS IN CHILE, CALIFORNIA, SPAIN AND SOUTH AFRICA. AERIAL PURSUITS WERE INITIATED FROM HOVERING OF PERCH-HUNTING SEARCHING POSITIONS

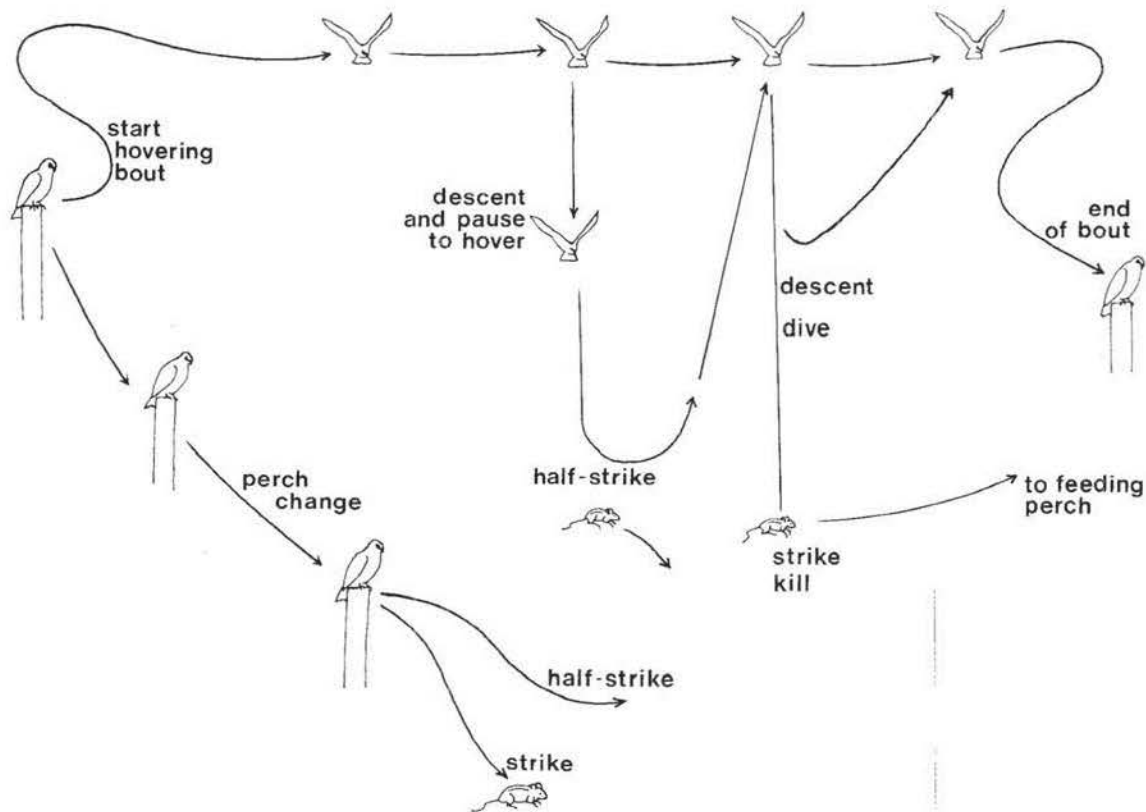| Country	Hovering	Perch-hunting	Aerial pursuit	Total	Source
Chile	24 (77)	4 (13)	3 (10)	31	Jaksić *et al.* (1987)
California	67 (100)	0 (0)	0	67	Warner & Rudd (1975)
California	191 (100)	0 (0)	0	191	Bamman (1975)
Spain	24 (57)	15 (36)	3 (7)	42	Amat (1979)
Spain	9 (90)	1 (10)	0	10	Heredia (1983)
S. Africa	24 (69)	11 (31)	0	35	Tarboton (1978)
S. Africa	72 (52)	67 (48)	0	139	Mendelsohn (1982)

FIGURE 2

General patterns and sequences of events during hunting and the terminology used to describe them.

ing in South Africa. In the Ivory Coast, Thiollay (1977) reported that kites hovered for 53 % and perch-hunted for 47 % of hunting time during more than 20 h of observation. A pair of kites in Morocco hovered for 40 % and perch-hunted for 60 % of the time (total time not recorded) (Bergier 1982). By comparison, perch-hunting was not distinguished or recorded during long periods of hunting in Chile and California (Bamman 1975; Warner & Rudd 1975; Jaksić *et al.* 1987), and other studies in California reported that all hunting is by hovering (e.g. Watson 1940; Hawbecker 1940, 1942; Moore & Barr 1941; Dixon *et al.* 1957). However, occasional prey may be caught from perches in both areas, since Jaksić *et al.* (1987) saw 4/31 prey items caught from perches, while Warner & Rudd (1975) mentioned perched birds scanning the ground and Waian (1973) observed perched kites attack mice used as bait.

Other estimates, based on instantaneous sampling, are biased in favour of the most visible activities. In the southwestern Cape, South Africa, Heunis (1975) saw 23 (12 %) hovering and 167 (88 %) perch-hunting kites. In coastal Victoria, Australia, Baker-Gabb (1984a) made 37 (90 %) sightings of hovering and 4 (10 %) of perch-hunting. Between 10 and 48 % of all prey captures recorded were made from perches (Table 1) in

Spain and South Africa, but these proportions only roughly reflect the amount of time spent hunting because the yields per hour of the two hunting methods differed.

In South Africa, the relative frequency of perch-hunting and hovering changed both during the day and seasonally. During five full-day watches of single focal birds the proportion of hovering varied between 3,5 and 37,3 %. Tarboton (1978) recorded hovering more frequently during midday than in the morning or afternoon. Mendelsohn (1982), by contrast, found that hovering occurred more frequently in the late afternoon than at other times of the day, when it was less effective. Similarly, kites hovered less frequently during summer than in other seasons when hovering provided higher yields (Mendelsohn 1982). Breeding males also spent more of their time hovering than did unpaired residents, again in association with the respective success rates of hovering.

The relative frequency of perch-hunting in South Africa is probably dependent on the availability of perches. Kites are frequently seen hunting from telephone and other utility wires and poles, especially along roads where they scan the verges below. These strips of dense grass cover provide a good food supply, seldom being grazed

or damaged by agricultural practices. Indeed, kites often hover over verges where perches are lacking. Open grasslands, with few suitable perches, are also often occupied by birds that must do most of their hunting by hovering. Barnard's (1986) study area contained few suitable hunting perches and she suggested that her birds spent less time hunting from perches than those of Tarboton (1978) and Mendelsohn (1982). No one, however, has yet investigated how the relative availability of perches might affect hunting behaviour and activity and energy budgets.

Timing of hunting

Bamman (1975) found that the frequency of hunting increased as the day progressed during winter in California; 8 % of all hunting was observed in the 1st quarter of the day, 21 % in the 2nd, 30 % in the 3rd and 41 % in the 4th quarter. This contrasts with patterns of activity reported elsewhere and during other seasons in California where most hunting occurred during the first 4 h after dawn and the last 4 h before dusk (Warner & Rudd 1975; Tarboton 1978; Mendelsohn 1982; Heredia 1983; Baker-Gabb 1984a; Jaksić et al. 1987). In South Africa, the first 1–2 h after dawn was usually spent preening on a low perch (<3 m above ground) in the sun (Tarboton 1978, Mendelsohn 1982). Morning periods of hunting generally ended once prey was caught and then kites spent the midday resting, usually on shaded perches. Hunting in the late afternoon ended when prey was caught or when it became dark. The duration of hunting in each period depended largely on when prey was caught (Bamman 1975; Mendelsohn 1982). If hunting was unsuccessful during the morning it continued through the midday period or, if a large prey item was caught in the early morning, there was often no further hunting that day. Descriptions of crepuscular hunting in Spain, South Africa and Australia probably refer to kites that had hunted unsuccessfully and attempted to exploit the onset of activity by nocturnal rodents (Mendelsohn 1982; Heredia 1983; Baker-Gabb 1984a). Although 25 °C was the modal temperature at which hovering occurred in Barnard's (1986) study, both Warner & Rudd (1975) and Mendelsohn (1982) noted that little hunting was done at temperatures above 25 °C. Hunting during the midday was far more frequent on cool than on hot days when it often stopped in the late morning regardless of whether they had fed or not. The low temperatures during Bamman's (1975) winter study probably explains the continued hunting during the middle of the day.

Although most hunting occurs during the first and last 4 h of the day, kites seldom hunt throughout these periods. In California, where all hunting was by hovering, kites spent less than 1 h/day hunting during winter, while breeding males in spring and summer hunted for less than 2,5 h (Table 2). In both seasons 80–90 % of the daylight hours thus remained for other activities. Because the yield of prey per hour by perch-hunting was much lower than hovering (see *Hunting success*), South African birds spent longer periods hunting than those in California. Even so, estimates indicate that non-breeders spent only about 2 h hunting daily, while breeding males hunted for about 4 h, leaving 85 and 70 % respectively of the day for other behaviour. Tarboton estimated that kites in his study area spent over 7 h hunting daily. This may be due to lower rates of prey capture in his study area (see below) and to the fact that he mainly followed birds encountered hunting along roads (pers. comm.); those perched inside trees were inconspicuous and monitored less frequently.

Hovering behaviour

Bouts of hovering (or "hunts") timed in Chile, California and South Africa averaged 6,5 (autumn only), 6,1 and 7,8 min in length respectively (Jaksić et al. 1987; Warner & Rudd 1975; Tarboton 1978). The lengths of bouts were highly variable (e.g. Fig. 1a) in all the studies (indicated by coefficients of variation of 0,81–1,07, although these data are probably not normally distributed). These studies measured the duration of hunting from when a kite first flew off to when it returned to perch, thus including flying time between hovering positions when the ground was not searched intently. Waian (1973) reported bouts lasting an average of 4,3 min in California, but he excluded all bouts that were unsuccessful. Bamman (1975) included bouts that ended when kites started soaring after periods of hovering in his sample of

TABLE 2
DURATION OF DAILY HUNTING IN CALIFORNIA AND SOUTH AFRICA

Daylength (h)	Hover (h)	Perch (h)	Total (h)	% Daylength	Season	Source
California						
11	0,98	0	0,98	9	winter	Koplin et al. (1980)
±11	0,55	0	0,55	5	winter	Warner & Rudd (1975)
13–16	1,6–2,4	0	1,6–2,4	12–15	breeding ♂♂	Warner & Rudd (1975)
South Africa						
13,6	0,58	1,35	1,93	15	non-breeding	Mendelsohn (1982)
13,6	1,22	2,86	4,08	30	breeding ♂♂	Mendelsohn (1982)
13,6	2,13	5,21	7,34	54	all	Tarboton (1978)

timed hunts. He recorded an average of 5,0 min/bout during winter, monthly averages for November–March ranging from 3,3 to 5,6 min. Using similar criteria, Mendelsohn (1982) reported an average of 4,2 min. Despite the use of different limits in timing hovering bouts, the similarity between the averages (4,2–7,8 min) is noteworthy, given the different degrees to which populations used hovering as a hunting method (Table 1) and difference in their flight-related morphology (see below).

The pattern of variation (Fig. 1a) suggests that "giving-up" times were usually short, but there is little information on factors affecting hovering bouts. Mendelsohn (1982) found that wind strength did not apparently affect the length of bouts but hovering bouts in the afternoon were longer than those during the morning or midday periods. However, Jaksić et al. (1987) found no significant differences between mornings and evenings in this respect (data for spring and summer).

Chilean kites hovered over an average 11,1 positions/hovering bout (Jaksić et al. 1987). In California, they hovered over an average of 16,2 positions/bout, spent an average of 8,1 s flying between each site and hovered for an average of 14,2 s at each site (Warner & Rudd 1975). It was not clear whether the 14,2 s spent hovering included time spent descending towards prey or was restricted to searching time alone. Bergier (1982) reported an average of 6,5 s spent hovering at each site in Morocco. In South Africa, Barnard (1986) measured an average of 9,5 s of hovering at each site and 15,5 s spent flying between each site. Mendelsohn (1982) reported an average of 11,6 s spent hovering at each position, excluding those hovers which ended in descents to prey. All studies reported much variation in the duration of hovering at each position, so it is surprising that averages in these studies ranged between 6,5 and 14,2 s only.

Although kites usually searched for short times (Fig. 1b) before moving on to other sites, a number of factors are reported as being related to the amount of time spent hovering. At lower wind speeds and at low heights above the ground, hovers were shorter than those in stronger winds and at greater heights (Mendelsohn 1982). However, kites avoided strong winds favoured for hovering by some other species (Barnard 1986). She showed that hovering was by "continuous flapping" during light and very strong winds, and that these hovers were shorter than those in moderate winds, in which "hanging" or "mixed" hovering was used. The latter modes of hovering were probably less expensive energetically than continuous flapping, which accounted for 79 % of hovering. In her montane study area, kites preferentially hovered on updrafts. Mendelsohn (1982) reported that hovers at midday were shorter than those in the morning and afternoon, but Barnard (1986) found no relationship between time and hovering mode.

Perch hunting

The only data on methods of perch hunting are those from South Africa, where hunting kites changed perches on average every 7,0 min (Mendelsohn 1982). This rate varied slightly with fewer moves in the afternoon than earlier. Tarboton (1978) reported that hunting birds "tail-cocked" or "tail-wagged" 14 % of the time, a display that probably served to warn other kites away from the hunting area (Bamman 1975; Mendelsohn 1981). The kinds of perches used for hunting varied according to their availability and to individual preferences. In Mendelsohn's study area, telephone lines (5–8 m above ground), electricity lines (9–11 m), trees (2–20 m) and fence posts (1,3 m) were used, in order of descending frequency. While many individuals used any available perch, others either consistently avoided using telephone and electricity lines or apparently learned to use them only several weeks or months after moving into the study area.

Prey capture

Aerial pursuit of flying birds and insects has been reported from Chile, Australia and Spain (Table 1). These attacks were made from searching positions while hovering or perching. Birds and insects were infrequent prey items (see below) and most birds were caught on the ground, so aerial pursuit was rarely used as a method of attack.

Hovering birds descended towards prey on the ground by holding their wings above them (Fig. 2), the speed of descent being adjusted by the angle at which the wings were held. Some descents were uninterrupted, turning into final dives to either hit the ground (strike) or to pull out just above the ground (half-strike). Other descents were interrupted one or more times as the kites paused to hover. In one study, kites hovered on average at 7,1 sites per descent, although this rate varied in relation to changes in prey availability (Mendelsohn 1982). Bamman (1975) observed 1 636 descents or responses to prey in California, of which 23,1 % terminated in strikes and 11,7 % in kills, while in South Africa 16,8 % of descents ended in strikes and 7,0 % in kills (Mendelsohn 1982). Bergier (1982) recorded that 14/36 (39 %) strikes were successful in Morocco, but the numbers made by hovering and perch-hunting birds were not reported. Combining the proportions of successful strikes in different areas (Table 3) with those of Bergier yields a total of 1 204 strikes, 536 (45 %) of which were successful. Success rates of hovering (46 %) and perch-hunting (40 %) were similar, as were many of the overall rates (39, 42, 46, 51 %) recorded in different studies.

In California, the proportion of successful strikes declined between November and February (Bamman 1975), probably reflecting a decreasing availability of prey. Males made more successful strikes while hovering than females (Mendelsohn 1982), although in Warner & Rudd's (1975) study this difference was not significant. Mendelsohn found that breeding males made more successful kills from hovering than unpaired residents.

Harris (1984) studied methods used by two captive kites to kill laboratory mice. He found that

TABLE 3

PROPORTIONS OF SUCCESSFUL AND UNSUCCESS-
FUL STRIKES IN CHILE, CALIFORNIA AND SOUTH AFRICA

Area	No. strikes	No. (%) successful	Source
Hovering			
Chile	61	24 (39)	Jaksić *et al.* (1987)
California	378	191 (51)	Bamman (1975)
California	108	67 (62)	Warner & Rudd (1975)
South Africa	90	24 (27)	Tarboton (1978)
South Africa	219	91 (42)	Mendelsohn (1982)
TOTAL	856	397 (46)	
Perch-hunting			
South Africa	66	11 (17)	Tarboton (1978)
South Africa	246	114 (46)	Mendelsohn (1982)
TOTAL	312	125 (40)	

impact was the most important factor leading to immobilisation, that prey was usually struck in the thoracic region, and that the birds tended to be left-footed.

Captured, wild prey was usually taken to a feeding perch immediately or, in the case of breeding males, to their mates or young. Of 205 animals seen being caught by Mendelsohn (1982), 188 were immediately carried off in flight (three tiny items were swallowed in flight), three were eaten on the ground in bare ploughed fields where they had been caught, and 14 very large rodents were firstly partially eaten on the ground at the site of capture. Eleven of these 14 rodents weighed an average of 115 g and were almost certainly too large for the kites to comfortably carry to a feeding perch. In California, prey (average 24,7 g) was consumed in 5–7 min (monthly means) (Bamman 1975; Koplin *et al.* 1980). Warner & Rudd (1975) recorded an average meal time of 6,2 min. Much larger prey was eaten over longer periods in South Africa, those weighing >60 g being fed upon sporadically over several hours. The guts, embryos and heads of large prey were usually discarded, so the weight of food ingested was often substantially lower (15–50 %) than that of the animal caught (Mendelsohn 1982). None of the studies reported any evidence of prey being cached; in fact, in South Africa, we often observed kites with distended crops drop substantial portions of rodents.

Hunting success

The variety of indices used to record hunting success makes it hard to compare performance in different areas. Success also depends on many factors that were seldom recorded, such as prey size and the energetic costs of hunting. Furthermore, success in any area was variable and unpredictable, so that while kites usually caught prey after short periods of hunting, they also often hunted for very long periods before being successful. This led to a highly skewed distribution of intervals between successive kills (Fig. 1c, d). In Chile, kills were made after hovering for an average of 34,6 min (n = 24 kills) (Jaksić *et al.* 1987). Wintering kites in California (Bamman 1975) spent an

average of 17,8 min kills hovering for each kill (n = 191); 28,4 % of all hovering bouts yielded prey. In Warner & Rudd's (1975) study, over the whole year, prey (n = 67) was caught in 39 % of all bouts. If each bout lasted an average of 6,1 min, their birds spent about 16 min hovering for each kill. In South Africa, Mendelsohn (1982) recorded 39,8 min/kill (72 kills) while Tarboton (1978) reported 52,1 min/kill (24 kills) as the success rate of all birds throughout the year. Combining the rates and periods sampled in Chile, California and Africa gives a total of 391 kills in 9 595 min (24,5 min/kill). Of these, 295 kills in 5 479 min (18,6 min/kill) were recorded in the New World and 96 kills in 4 116 min (42,9 min/kill) in Africa. These averages suggest that African birds took more than double the time to catch prey than those in the Americas. If prey in the two areas had been caught at the same rate, the expected values would be 223,6 and 168,0 kills during the periods of hunting observed in the New World and Africa, respectively. The expected values, however, differ significantly from the observed number of kills (χ^2 = 53,6; p <0,001), supporting the conclusion that hovering success in Chile and California was better than that in Africa.

In South Africa, the rate of prey capture by perch-hunting was substantially lower than by hovering. For all birds throughout the year, each prey item was caught after 280 min (11 kills) (Tarboton 1978), and 127 min (67 kills) (Mendelsohn 1982). On average, therefore, hovering yielded prey items 3–4 times more quickly than perch-hunting. However, because kites spent more time perch-hunting, there was less of a difference in the numbers of prey yielded by two hunting methods (Table 1). Prey caught by hovering was significantly smaller (22,2 g) than that caught by perch-hunting (29,6 g), because hovering and perch-hunting tended to occur in different habitats where prey of different sizes predominated (Mendelsohn 1982).

Several studies reported seasonal and other variation in hunting success. In Chile, hovering yielded prey every 18,9 min in spring and 26,8 min in summer on average, while in autumn and winter no prey was caught during a sample of 289 min of hunting (Jaksić *et al.* 1987). In California, Warner & Rudd (1975) reported that 47 % of hovering bouts yielded prey during nesting, while only 31 % were successful at other times of the year. Mendelsohn (1982) found no significant difference in the rate at which breeding (34,6 min/kill) and non-breeding (39,1 min/kill birds obtained prey by hovering. However, breeding birds made significantly more descents while hovering towards prey than non-breeders. Furthermore, perch-hunting by breeding kites (75,1 min/kill) was much more successful than that by non-breeding residents (164,3 min/kill). Using these and other measures of hunting success, Mendelsohn (1982) also found that success varied significantly between different times of the day, seasons and habitats.

Few data are available on the number of prey caught each day. During 54 full days of obser-

vation in California, kites caught an average of 3,1 prey items (average weight — 24,7 g) per day; the monthly averages varied between 2,8 and 3,5 items/day over the five winter months (November–March) (Bamman 1975). These were non-breeding kites hunting to feed themselves. No other studies regularly measured the number of prey caught per day, but Tarboton (1977) estimated that two items, of about 30 g each, were eaten daily. Mendelsohn (1982) estimated that 1–3 items were usually eaten each day. The number of prey caught varied according to prey size and breeding males killed many more prey each day to feed their mates and young. For example, Stendell (1972) observed a breeding male throughout the day in California, during which it killed 21 mice in 168 min of hunting.

Tarboton (1978), Koplin et al. (1980) and Mendelsohn (1982) estimated energy intake and expenditure using various models for time-activity budgets and estimates of food consumption. Based on the turnover of tritiated water, Sapsford & Mendelsohn (1984) estimated a daily energy expenditure 287 kJ for non-breeding, South African kites weighing an average of 244 g. Scaled to a body mass of 244 g, the other models provided comparative estimates for non-breeders of 411 kJ (Tarboton 1978), 348 kJ (Koplin et al. 1980) and 280 kJ/day (Mendelsohn 1982). Sapsford & Mendelsohn (1984) also provide various estimates of daily energy turnover for breeding males and females that are, respectively, 25 % higher and 14 % lower than those for non-breeders. Tarboton (1977) discovered that kites usually produce one pellet each day and that pellet weight closely reflects the weight of prey ingested the previous day. Pellet weights thus provide good estimates of food consumption, but regressions reflecting this relationship will vary according to the weights of indigestible material that remain from different prey species.

Hunting habitat

Many studies provide general descriptions of the habitats favoured for hunting (Stendell 1972; Bamman 1975; Thiollay 1977; Amat 1979; Schlatter et al. 1980; Bergier 1982; Mendelsohn 1982; Baker-Gabb 1984a; Jaksić et al. 1987). The preferred habitats were those in which rodents were both abundant and accessible to kites. Dense cover usually supported good rodent populations, but kites avoided very long grass where prey was inconspicuous. Barnard (1987) found that more hovering occurred over undisturbed grasslands than over those with sparse plant cover as a result of recent burning. The terms used to describe habitats varied between studies, but most habitats were described as: grassy foothills, flat grasslands, pastures, crop lands (alfalfa, wheat, sugar beet, various cereal crops), creek bottoms or ditch edges, salt and fresh-water marshes, woodland clearings, open savanna, orchards, low, dense scrub and grass, and road and field verges. These habitats fit the broad categories of grasslands, low scrub, open woodlands or cultivated fields. In woodlands and orchards, kites frequented clear-ings and hunted between trees wherever there was sufficient cover to support rodent populations. Areas in which kites were most abundant were usually heterogeneous mosaics of cultivated fields, pastures, verges, ditches, small marshes and patches of rank grass. Certain microhabitats were usually selected for hunting. For example, Bamman (1975) reported that 93 % of hunting was over tall rank grass, short rank grass and salt marshes, even though these three habitats together comprised only 5 % of his Californian study area. In one area in South Africa, 51 % of hunting was over road and field verges which made up 5 % of the ground area (Mendelsohn 1982).

Composition and size of prey

Table 4 summarises the results of 19 studies of prey composition in which over 19 000 prey items were identified. The analyses indicate that, with the exception of Morocco, rodents made up more than 85 % of the diet, either by frequency or biomass. A similar pattern was found in a small sample from the Ivory Coast where 21 prey items consisted of 12 rodents, 5 lizards, 3 grasshoppers and 1 bird (Thiollay 1978). In most areas rodents formed more than 95 % of the diet and this component was largely due to the presence of one, two or three species (Table 5). The major exceptions were in Spain and Morocco where birds and insects made up substantial portions of the diet, although even these were usually small in terms of prey biomass. Elsewhere, birds, lizards and insects were not important components of the diet and in many areas these items were not preyed upon at all. The frequency of insect prey might be exaggerated if pellets containing their remains also held lizard remnants, since the insects may have been lizard prey.

The predominance of a few rodent prey species (Table 5) was notable in that these items comprised over 70 % of the numbers of prey in all studies except one each in Spain and Morocco. Their contribution to prey biomass was probably substantially greater, but this could not be calculated for most studies. *Mus musculus*, the feral house mouse, was an important prey item in such widely separated areas as Chile, California, Spain and Australia. The average body weights of the predominant prey species varied between 16 and 83 g, although most species averaged 30–40 g in weight. The heaviest *Otomys angoniensis* reached weights of 150 g (Mendelsohn 1982) while Forbes-Watson (1977) recorded a 210 g kite carrying an *Otomys* sp. weighing 160 g in Kenya. The smallest insects, small lizards, rodents, and shrews weighed less than 1–2 g, by contrast.

Comparative morphology

Table 6 compares some morphological aspects that may affect flight dynamics and forging behaviour in different populations. Standard errors of means for parameters of South African kites provide indications of how the populations differ. Wing areas were estimated from a regression (developed from 156 measured wing areas of South

TABLE 4

PREY COMPOSITION AS A PERCENTAGE OF THE TOTAL NUMBER (N) OF PREY ITEMS IDENTIFIED. FOR SOME STUDIES THE PERCENT-
AGE FREQUENCY OF PREY BIOMASS IS GIVEN IN PARENTHESES

Locality	Total N	Mammals	Birds	Lizards	Insects
Chile[1]	766	98,7	0,6	0	0,7
Chile[2]	718	97,2	2,8	0	0
Chile[3]	151	98,0	2,0	0	0
California[4]	5 977	99,8	0,2	0	0
California[5]	74	100	0	0	0
California[6]	214	100	0	0	0
California[7]	202	99	2	0	0
California[8]	876	>99	?	?	?
California[9]	219	98,2	0,5	0	1,4
California[10]	131	>97,9	?	?	?
California[11]	3 266	>99,8	0,2	0	0
Spain[12]	149	43,6 (91,9)	1,3 (4,1)	1,3 (1,0)	53,7 (3,0)
Spain[13]	130	77,0 (85,7)	5,4 (10,6)	6,9 (3,2)	10,7 (0,4)
Morocco[14]	196	48 (42)	40 (57)	1 (0,5)	11 (0,6)
South Africa[15]	3 408	96,7 (98,2)	2,0 (1,4)	1,3 (0,4)	0 (0)
South Africa[16]	341	99,4	?	?	?
South Africa[17]	1 777	98	0,8	1,0	0,2
South Africa[18]	97	84	0	12	4
Australia[19]	332	94,4	3,0	2,7	0

[1]Meserve (1977) — Polpaico, Santiago Prov.; [2]Schlatter *et al.* (1980) — Pudahuel, Santiago Prov.; [3]Schlatter *et al.* (1980) — La De-
hesa, Santiago Prov.; [4]Stendell (1972) — San Francisco Bay; [5]Bond (1942) — Los Angeles Co.; [6]Hawbecker (1940) — Santa Cruz
Co.; [7]Dixon *et al.* (1957) — San Diego Co.; [8]Waian (1973) — Santa Barbara Co.; [9]Stendell & Myers (1973) — Monterey Co.; [10]T. St.
John, cited by Meserve (1977) — Orange Co.; [11]Wright (1978) — San Diego Co.; [12]Heredia (1983) — Salamanca, central Spain;
[13]Amat (1979) — NW Cáceres, western Spain; [14]Bergier (1982) ; [15]Mendelsohn (1982) — Settlers, Transvaal; [16]Tarboton (1978) —
Nylsvlei, Transvaal; [17]Slotow (1987) — Settlers, Transvaal; [18]Siegfried (1965) — Stellenbosch, Cape; [19]Baker-Gabb (1984a) —
coastal Victoria.

TABLE 5

THE FREQUENCY OF DOMINANT RODENT PREY SPECIES (THOSE COMPRISING MORE THAN 10 % OF THE DIET) AS A PERCENTAGE OF
THE TOTAL NUMBER OF PREY ITEMS

Country and Source	Rodent species (Body weight—g)	Frequency	Total
CHILE Schlatter *et al.* (1980)	*Akodon olivaceus* (40)	35,2	
	Mus musculus (17)	24,1	
	Oryzomys longicaudatus (45)	27,7	87,0
CHILE Schlatter *et al.* (1980)	*Akodon olivaceus* (40)	34,5	
	Oryzomys longicaudatus (45)	37,1	71,6
CHILE Meserve (1977)	*Akodon olivaceus* (40)	75,2	
	Mus musculus (17)	20,2	95,4
CALIFORNIA Wright (1978)	*Reithrodontomys* sp. (10)	10,2	
	Microtus californicus (39)	84,5	94,7
CALIFORNIA Stendell (1972)	*Mus musculus* (14)	21,1	
	Microtus californicus (39)	74,5	95,6
CALIFORNIA Other studies (see Table 4)	*Mus musculus* (18)	20, 2–85, 2	
	Microtus californicus (39)	10, 8–88, 1	72, 1–97, 9
SPAIN Heredia (1983)	*Microtus arvalis* (33)	31,5	31,5
SPAIN Amat (1979)	*Apodemus sylvaticus* (25)	15,4	
	Pitymys duodecimcostatus (17)	25,4	
	Mus musculus (32)	35,4	76,2
MOROCCO Bergier (1982)	*Mus musculus/spretus* (36)	18	
	Lemnyscomys barbarus (32)	16	34
SOUTH AFRICA Tarboton (1978)	*Rhabdomys pumilio* (34)	43	
	Otomys angoniensis (83)	30	
	Praomys natalensis (31)	14	87
SOUTH AFRICA Mendelsohn (1982)	*Rhabdomys pumilio* (34)	29,5	
	Otomys angoniensis (83)	27,6	
	Praomys natalensis (31)	29,8	87
SOUTH AFRICA Slotow (1987)	*Rhabdomys pumilio* (34)	16	
	Otomys angoniensis (83)	51	
	Praomys natalensis (31)	31	98
SOUTH AFRICA Siegfried (1965)	*Rhabdomys pumilio* (34)	84	84
AUSTRALIA Baker-Gabb (1984a)	*Mus musculus* (16)	93,4	93,4

TABLE 6

MORPHOMETRICS OF FLIGHT-RELATED STRUCTURES OF BLACKSHOULDERED KITES IN CHILE, CALIFORNIA, SOUTH AFRICA AND AUSTRALIA. WING AREA = 1,13 [(WING + ULNAR LENGTHS) (SECONDARY LENGTH)/100] + 304,5; WING SPAN = 2,40 (WING + ULNAR LENGTH) − 15,0 (SEE TEXT). LINEARIZED TAIL LOADING = (BODY WEIGHT $^{1/3}$/(TAIL LENGTH[1]); SEE JAKSIĆ & CAROTHERS (1985). MEANS OF WEIGHTS (G), LENGTHS AND SPANS (MM), AREAS OF BOTH WINGS (CM^2); MEAN ± SE ($\bar{x}$) FOR *caeruleus*.

	Chile *leucurus*	California *majusculus*	South Africa *caeruleus*	Australia *notatus*
Body weight	294	309	244 ± 1,71	280
Wing length	300	320	267 ± 0,62	295
Secondary length	?	158	146 ± 0,42	148
Wing span	?	1 001	843 ± 7,51	927
Wing area	?	1 061	891 ± 4,40	961
Ulnar length	?	103	89 ± 0,25	97
Tail length	169	171	117 ± 0,39	140
Wing/Secondary	—	2,03	1,82	1,99
Wing/Ulna	—	3,11	2,99	3,04
Secondary/Ulna	—	1,53	1,64	1,53
Linear tail load	0,393	0,395	0,534	0,467

DATA SOURCES: *leucurus* — body weight from Schlatter *et al.* (1980), wing and tail lengths from Johnson (1965). Wing, tail, secondary and ulnar lengths for *majusculus* and *notatus* from skins (A.C. Kemp unpubl.). Weights of *notatus* (n = 20) from Baker-Gabb (1984b), of *majusculus* (n = 17) from Stendell (1972) and Jaksić (unpubl.). All data for *caeruleus* from Mendelsohn (unpubl.).

African kites) that uses wing, ulnar and lengths (see Biggs *et al.* 1978 for methods of measurement) to indicate the area of a rectangular wing shape. The correlation obtained for the 156 birds was highly significant (r = 0,54; p < 0,001), and the predicted wing area for South African birds differed by <0,1 % from the measured average. Wing spans for non-South African birds were estimated using a different regression that relates [wing length + ulnar length] to wing span (r = 0,997; p < 0,001). This equation was obtained from measured wing spans.

Body weights, wing and tail lengths follow an increasing trend from *E. c. caeruleus* in South Africa, to *notatus* in Australia, *leucurus* in Chile and *majusculus* in California (Table 6). The wing proportions of *notatus* lie between those of *majusculus* and *caeruleus* which have the broadest wings and lowest aspect ratios. The longer, narrower wings of kites hovering in California and Australia provide greater support at lower energy costs (Greenewalt 1975) than those of South African birds. Masman & Klaassen (1987) provide a regression to estimate flight costs that uses body weight, wing span and wing area as variables. From the figures in Table 6, *caeruleus* expends 15,2 W, *notatus* 14,6 W and *majusculus* 13,6 W in flapping flight.

E. c. leucurus in Chile resemble *majusculus* in having much longer tails and ligher tail loadings than *caeruleus*. The longer tails are probably related to (a) the need for greater lift while hovering in light winds when their tails are spread, and (b) use as rudders to provide stability during stronger, buffeting wind. The tail loading of *notatus* lies between those of *caeruleus* and the New World kites.

CONCLUSIONS

The studies reviewed here suggest that many aspects of hunting behaviour are similar in different parts of the world. We found no differences in the general sequence of events and patterns of hunting behaviour. Although the duration of hovering bouts, hovers, and flights between hovers were highly variable, the average periods in different areas were similar, as was the number of sites over which kites hovered. Hunting occurred predominantly early and late during the day except where low temperatures prevailed throughout the day. The habitats preferred for hunting were structurally similar, but varied according to local conditions of rodent abundance and accessibility. Although strike success rates varied seasonally, many of the overall averages were similar. Good samples of prey (Table 4) showed that kites throughout the world (except in Spain and Morocco) feed predominantly on diurnal rodents. Most of these similarities are probably attributable to the fairly uniform morphology of kites, availability and behaviour of prey, and habitats selected in different parts of the world.

Despite this relative uniformity, there were conspicuous differences in the proportions of hovering and perch-hunting in different areas. All hunting was adjudged to be by hovering in California, although some observations showed that these birds could occasionally catch prey from perches. (Incidentally, there are probably more suitable hunting perches, such as utility poles, in California than in most other parts of the world). By contrast, South African kites spent up to 75 % of their hunting time perched and this yielded a substantial proportion of their prey, with the balance being caught by hovering. These differences also meant that South African kites hunted for about twice as long each day as Californian ones (Table 2). In Chile and Australia limited use was made of perch-hunting, while in Spain, Morocco and the Ivory Coast perch-hunting was more regular; no information was available on the amount of time kites hunt each day in these areas.

The duration of hunting before prey was caught varied substantially (Figs. 1c, d) and hunting success was therefore unpredictable. In terms of time intervals, hovering was a more predictable

method of hunting, but it might have been less predictable energetically because of higher energy costs. Differences in energy yield and costs between hovering and perch-hunting raise questions of why kites hunt by both hovering and perch-hunting and in the proportions observed. There is also the question of why these and other large birds hunt for such a small proportion of the day and spend the remaining time apparently loafing. The best answers to these problems may be found by establishing whether strategies are minimizing time or energy costs, maximizing energy gain, or some variable combination of these goals (Herbers 1981; Mendelsohn 1982; Jaksić & Carothers 1985; Masman 1986). Variation in the relative use of hunting methods is unlikely to affect total energy expenditure, since metabolic rates are largely determined by body mass (Walsberg 1983) and maximum rates of energy assimilation (Kirkwood 1983). Rather, by using hovering and perch-hunting in different proportions, kites possibly allocate their energy resources in various ways, perhaps in accordance with expected benefits and cost constraints. Two observations in this paper suggest that hunting strategies are used to minimize energy costs and maximize gains.

First, some kites may be better suited to hovering than others. Compared with birds elsewhere, the longer wings and tails of kites in the New World (Table 6) probably reduce their hovering costs, so a link between structural proportions and frequency of hovering suggests that costs are minimized. (This implies some disadvantage to long tails and wings in African kites, otherwise selection for these features would lead to a reduction in the costs of their hovering too). Second, the predominance of hovering may be attributable to its greater efficiency and energy gain in North and South America, where prey was caught about twice as quickly as in South Africa. If kites can obtain all their food requirements by hovering for short periods, there might be no need for more time-consuming perch-hunting. In fact, kites in Africa may be forced to do more perch-hunting because they have poor success in hovering, yields simply being inadequate to cover the costs of this energetically expensive method of hunting. This would seem to be true in South Africa where seasonal, daily and individual variation in the proportion of hunting by hovering was positively related to variation in hovering yields (Mendelsohn 1982). Data are not available to test this prediction in the New World, where we would expect occasional perch-hunting to occur when hovering yields are poor.

Several studies reported relationships between the timing of hunting and temperature. While kites may indeed have preferences for certain ambient temperatures, it is perhaps more likely that hunting is related to the timing of activity and, thus, availability, of their prey. Evidence of this is lacking for kites, but Common Kestrels *Falco tinnunculus* time their hunting in response to changes in the activity patterns of voles (Raptor Group R.U.G./R.I.J.P. 1982). The effects of temporal changes in wind velocity on the timing of hunting, in particular that of hovering (Videler *et al.* 1983), also need to be investigated.

All the work reviewed here has been on residents, most of which were adult or, at least, subadult kites. No data are thus available on the development of hunting skills or changes in hunting methods or success as birds age. Some changes are to be expected, since juveniles are probably less adept at selecting the best hunting areas and killing prey than adults. In addition, juvenile South African kites have shorter wings and longer tails than adults (Mendelsohn 1981), so their proportional use of hovering and perch-hunting may differ from adults.

Results summarized in Table 4 demonstrate that Blackshouldered Kites are clearly rodent specialists and that, compared with most other diurnal raptors, they have a comparatively narrow range of diet (Jaksić & Carothers 1985). The high frequency of birds, lizards and insects in the prey of Mediterranean kites is an interesting exception. A study experimentally comparing processes of prey selection in generalist kites from the Mediterranean and specialists elsewhere would be useful.

There have probably been more studies, worldwide, of the foraging behaviour of kites than of any other raptor. In reviewing these studies we have pooled available data and hope to provide a source of data on behavioural variation for a species with an extensive distribution. Although more information is needed from most areas, some aspects of foraging behaviour are evidently quite uniform, while others vary seasonally, individually, temporally, and regionally. This raises questions about the origins and causes of stability and variability in complex foraging behaviour. Being common in many areas and living in open country where they can be observed for long periods, kites can provide large samples of data required to understand variation in foraging behaviour, activity budgets and energetics. In his study of Common Kestrels, Masman (1986) and co-workers provide excellent examples of the methods and analyses to be used in understanding the development and evolution of foraging behaviour in different areas. Finally, most theoretical and experimental work on optimal foraging has been devoted to animals that consume small prey frequently over long periods. Blackshouldered Kites provide good opportunities to investigate these questions in a predator that encounters large prey unpredictably, and uses different methods to search for food, and forages over comparatively short periods.

REFERENCES

AMAT, J. A. 1979. Notas sobre la ecología alimenticia del Elanio Azul (*Elanus caeruleus*). *Doñana Acta Vertebrata* 6: 124–128.

BAKER-GABB, D. J. 1984a. The feeding ecology and behaviour of seven species of raptor overwintering on coastal Victoria. *Aust. Wildl. Res.* 11: 517–532.

BAKER-GABB, D. J. 1984b. Morphometric data and dimorphism indices of some Australian raptors. *Corella* 8: 61–63.

BAMMAN, A. R. 1975. Ecology of predation and social interactions of wintering White-tailed Kites. M.Sc. thesis, Humboldt State University, Arcata, California.

BARNARD, P. 1986. Windhovering patterns of three African raptors in montane conditions. *Ardea* 74: 151–158.

BARNARD, P. 1987. Foraging site selection by three raptors in relation to grassland burning in a montane habitat. *Afr. J. Ecol.* 25: 35–45.

BERGIER, P. 1982. L'Elanion Blac au Maroc premeirs resultats. *Bulletin de l'Institut Scientifique* No. 6: 187–206.

BIGGS, H. C., BIGGS, R. & KEMP, A. C. 1978. Measurement of raptors. *Proc. Symp. African Predatory Birds* 77–82. Pretoria: Northern Transvaal orn. Soc.

BOND, R. M. 1942. White-tailed Kites feeding on house mice. *Condor* 44: 231–232.

DIXON, J. B., DIXON, R. E. & DIXON, J. E. 1957. Natural history of the White-tailed Kite in San Diego County, California. *Condor* 59: 156–165.

FORBES-WATSON, A. D. 1977. Maximum carrying potential of a Blackshouldered Kite *Elanus caeruleus*. *Scopus* 1: 44.

GREENEWALT, C. H. 1975. The flight of birds. *Trans. Am. Phil. Soc., New Series* 65: 1–67.

HARRIS, T. 1984. Prey immobilisation by the Blackshouldered Kite *Elanus caeruleus*. *In* MENDELSOHN, J. M. & SAPSFORD, C. W. (Eds), *Proc. 2nd Symp. African Predatory Birds*: 195–208. Durban: Natal Bird Club.

HAWBECKER, A. C. 1940. The nesting of the White-tailed Kite in southern Santa Cruz County, California. *Condor* 42: 106–111.

HAWBECKER, A. C. 1942. A life history study of the White-tailed Kite. *Condor* 44: 267–276.

HERBERS, J. 1981. Time resources and laziness in animals. *Oecologia* 49: 252–262.

HEREDIA, B. 1983. Alimentacion invernal del Elanio Azul (*Elanus caeruleus*) en la provincia de Salamanca. *Alytes* 1: 255–266.

HEUNIS, F. 1975. Padtellings van Blouvalke *Elanus caeruleus* in die distrik van Stellenbosch. *Bokmakierie* 27: 53–55.

HUSAIN, K. Z. 1959. Notes on the taxonomy and zoogeography of the genus *Elanus*. *Condor* 61: 153–154.

JAKSIĆ, F. M. & CAROTHERS, J. H. 1985. Ecological, morphological, and bioenergetic correlates of hunting mode in hawks and owls. *Ornis Scand.* 16: 165–172.

JAKSIĆ, F. M., ROZZI, R., LABRA, A. & JIMENEZ, J. E. 1987. The hunting behavior of Black-shouldered Kites (*Elanus caeruleus leucurus*) in central Chile. *Condor* 89: 907–911.

KIRKWOOD, J. K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Physiol.* 75A: 1–3.

JOHNSON, A. W. 1965. The birds of Chile and adjacent regions of Argentina, Bolivia and Peru. Vol. 1. Buenos Aires: Platt Establecimientos Gráficos.

KOPLIN, J. R., COLLOPY, M. W., BAMMAN, A. R. & LEVENSON, H. 1980. Energetics of two wintering raptors. *Auk* 97: 795–806.

MASMAN, D. 1986. The annual cycle of the Kestrel *Falco tinnunculus*, a study in behavioural energetics. Doctoral thesis, Rijksuniversiteit, Groningen.

MASMAN, D. & KLAASSEN, M. 1987. Energy expenditure during free flight in trained and free-living Eurasian Kestrels (*Falco tinnunculus*). *Auk* 104: 603–616.

MENDELSOHN, J. M. 1981. A study of the Blackshouldered Kite *Elanus caeruleus*. Ph.D. thesis, University of Natal, Pietermaritzburg.

MENDELSOHN, J. M. 1982. The feeding ecology of the Blackshouldered Kite *Elanus caeruleus*. *Durban Mus. Novit.* 13: 75–116.

MENDELSOHN, J. M. 1984. The timing of breeding in Black-shouldered Kites in southern Africa. *Proc. V. Pan-Afr. orn. congr.* Johannesburg: Southern African Ornithological Soc.

MENDELSOHN, J. M. 1986. Sexual size dimorphism and roles in raptors — fat females, agile males. *Durban Mus. Novit.* 13: 321–336.

MESERVE, P. L. 1977. Food habits of a White-tailed Kite population in central Chile. *Condor* 79: 263–265.

MOORE, R. T. & BARR, A. 1941. Habits of the White-tailed Kite. *Auk* 58: 453–462.

PARKES, K. C. 1958. Specific relationships in the genus *Elanus*. *Condor* 60: 139–140.

RAPTOR GROUP R.U.G./R.I.J.P. 1982. Timing of vole hunting in aerial predators. *Mammal Rev.* 12: 169–181.

SAPSFORD, C. W. & MENDELSOHN, J. M. 1984. An evaluation of the use of tritium for estimating daily energy expenditure for Blackshouldered Kites *Elanus caeruleus* and Greater Kestrels *Falco rupicoloides*. *In* MENDELSOHN, J. M. & SAPSFORD, C. W. (Eds), *Proc. 2nd Symp. African Predatory Birds*: 183–194. Durban: Natal Bird Club.

SCHLATTER, R. P., TORO, B., YANEZ, J. L. & JAKSIĆ, F. M. 1980. Prey of the White-tailed Kite in central Chile and its relation to the hunting habitat. *Auk* 97: 186–190.

SIEGFRIED, W. R. 1965. On the food of the Blackshouldered Kite. *Ostrich* 36: 224.

SLOTOW, R. H. 1987. The regulation of breeding in Blackshouldered Kites. M.Sc. thesis, University of Natal, Pietermaritzburg.

STENDELL, R. C. 1972. The occurrence, food habits and nesting strategy of White-tailed Kites in relation to a fluctuating vole population. Ph.D. thesis, University of California, Berkeley.

STENDELL, R. C. & MYERS, P. 1973. Whitetailed Kite predation on a fluctuating vole population. *Condor* 75: 359–360.

TARBOTON, W. R. 1977. Food consumption and pellet production in the Blackshouldered Kite. *Zool. Afr.* 12: 252–255.

TARBOTON, W. R. 1978. Hunting and the energy budget of the Black-shouldered Kite. *Condor* 80: 88–91.

THIOLLAY, J-M. 1977. Les rapaces d'une zone de contact savana-forêt en Côte d'Ivoire: modes d'exploitation du milieu. *Alauda* 45: 197–218.

THIOLLAY, J-M. 1978. Les rapaces d'une zone de contact savana-forêt en Côte d'Ivoire: spècialisations alimentaires. *Alauda* 46: 147–170.

VIDELER, J. J., WEIHS, D. & DAAN, S. 1983. Intermittent gliding in the hunting flight of the kestrel, *Falco tinnunculus*. *J. exp. Biol.* 102: 1–12.

WAIAN, L. B. 1973. The behavioral ecology of the North American White-tailed Kite (*Elanus leucurus majusculus*) of the Santa Barbara coastal plain. Ph.D. thesis, University of California, Santa Barbara.

WAIAN, L. B. & STENDELL, R. C. 1970. The White-tailed Kite in California with observations of the Santa Barbara population. *California Fish and Game* 56: 188–198.

WALSBERG, G. 1983. Avian ecological energetics. *In* FARNER, D. S., KING, J. R. & PARKES, K. C. (Eds), *Avian Biology*. Vol. 7. New York: Academic Press.

WARNER, J. S. & RUDD, R. L. 1975. Hunting by the White-tailed Kite (*Elanus leucurus*). *Condor* 77: 226–230.

WATSON, F. G. 1940. A behavior study of the White-tailed Kite. *Condor* 42: 295–304.

WRIGHT, B. A. 1978. Ecology of the White-tailed Kite in San Diego County. M.Sc. thesis, San Diego State University, San Diego, California.