

Population Biology and Breeding Success of Blackshouldered Kites *Elanus caeruleus*

John M. Mendelsohn

ABSTRACT

The study investigated factors affecting the population density and breeding success of Blackshouldered Kites. Males established territories on which they either lived alone or paired with a succession of mates: as a consequence there were always more resident males than females in the study area. Males resident for long periods spent proportionately more time paired and breeding than those occupying territories for shorter periods. The area was saturated with territories, so most new males only occupied territories when resident males left. The success of males thus depended on their ability to find and occupy territories for long periods on which they could pair and breed. Some parts of vacated territories were incorporated into those of neighbouring males, resulting in a decline in the number (and density) of territorial males and an increase in average territory size.

Female success depended on moving around to find resident males occupying territories with the best breeding prospects and food supply; proportionately more females paired and bred with territorial males when prey was most available. As a result the behaviour of males and females had different effects on population density. The behaviour of resident males limited the density of territories, while the density of pairs depended on females as they either paired or left resident males in response to fluctuations in food supply.

Males participated in each successful breeding cycle for an average of 25 weeks, while most females spent only 16 weeks breeding, leaving their mates once their young started flying. Some males bred twice a year and females may have bred three or more times a year. Clutches averaged 3.4 eggs, while average broods of 3.05 nestlings and 2.9 post-nestlings indicated low rates of loss in successful nests. However, productivity was low because of high rates of complete nest failure throughout the cycle; only 6 of 58 attempts produced independent young. Some males made up to seven breeding attempts in 19 months but there was much individual variation in the number of independent young they produced.

INTRODUCTION

The success of a population depends on the pooled achievements of its constituent individuals. Each individual contributes to the parameters of the population according to its ability to occupy an area and use its resources, obtain a mate, breed, and survive. The behaviour required to meet

these individual goals was, for present purposes, described by five factors that largely accounted for the performance of a population of Black-shouldered Kites *Elanus caeruleus*. Population size and composition was determined largely by (1) territoriality and (2) pairing, while breeding performances depended on (3) clutch and brood sizes, (4) success rates, and (5) numbers of broods. This paper describes these components and attempts to account for some of the variation in their contributions to population success. I follow many other studies (reviewed by Newton 1979) in exploring how the variable qualities of individuals, different areas, times of year, etc., account for variation in success. However, individuals may pursue the same goals in different ways using a variety of options or strategies that will, cumulatively, have different consequences for the success of the population.

Black-shouldered Kites are small, diurnal raptors, widely distributed in North and South America, Africa, southern Europe, southern Asia and Australia. They typically occur in open grasslands, cultivated areas and clearings in woodlands. Males are smaller than their mates and while breeding do the great majority of hunting to provision for themselves, their mates and young. Breeding females very seldom hunt. The results reported here were obtained at Settlers (24° 57S, 28° 33E) in South Africa in a 19-month study of several aspects of their general biology. The study area was occupied by between 19 and 35 residents at different times. All residents lived on territories that were actively defended against any intruders. Males usually established territories where females joined them as mates. Unpaired residents had the poorest and breeding birds the best food supply; paired residents were intermediate. The territories were exclusive areas containing the nesting and foraging areas of residents who sometimes joined communal roosts elsewhere at night. Residents frequently deserted their territories or mates, but also often later returned. Many adults and sub-adults were nomads and ringing recoveries showed that they often moved long distances. They fed largely on rodents, especially three species that made up 92% of prey biomass, that fluctuated widely and unpredictably in availability. Intervals between successive prey captures were often long, so hunting success varied substantially from day to day. Breeding occurred throughout the year, some individuals breeding more than once. Each cycle lasted an average of 25 weeks from the start of nest building to independence of the young. Many nests failed to produce young, and failures occurred at any stage of the breeding cycle. In successful nests, clutches of 2-5 eggs yielded 1-4 young, but because not all eggs gave rise to young, mean brood size was lower than mean clutch size. More information can be found in Mendelsohn (1981, 1982a, 1982b, 1983, 1984).

STUDY AREA & METHODS

The study was conducted in a 6900 ha area at Settlers (24° 57S, 28° 33E; 1,048m a.s.l.) in the Springbok Flats, South Africa, from 1 March 1977 to 30 September 1978. Most of the area was cultivated with grain crops, while the remainder consisted of small patches of *Acacia* woodland and grassland, road and field verges and farmyards (Mendelsohn 1982a).

The presence or absence of birds was determined by recording the identity and position of all kites sighted. Sixty-seven birds were colour-marked (Mendelsohn 1981) and each individual was seen an average of nine times per month. Dates on which kites became resident or left the area were taken as the dates on which they were first or last seen, respectively. Sexes were identified by behaviour or from a discriminant analysis of body measurements (Mendelsohn 1981). Residents were placed in one of three mating classes according to their status or behaviour: *unpaired*, *paired* (but not breeding) or *breeding*. Not all breeding birds were paired because some females left their mates before the young became independent. A bird that first occupied a territory was functionally termed a *territory-holder*, while one that joined it to form a pair was called a *mate*. A kite seen only once in an area was classed as a *nomad*, but residents that intruded on neighbouring territories were not placed in this category. All sightings were plotted on 1:50,000 maps. After August 1977, composite maps were drawn at the end of each month to determine territory boundaries and sizes.

All breeding activity in the study area was recorded and some data from elsewhere were used, especially information from the Southern African Ornithological Society's (SAOS) nest record cards. Nests were usually checked every second day and dates on which breeding started were normally taken as the dates on which breeding activity was first seen. In some cases average incubation

tion and nestling periods were used to estimate dates. Nestlings were ringed at about three weeks of age; most were later trapped and marked with patagial tags.

Changes in food supply were monitored by trapping rodents, weighing pellets, and counting the number of birds seen with prey; there were good correlations between these three measures. Methods of obtaining these other data on food supply and hunting behaviour were obtained using methods described by Mendelsohn (1982a,b).

RESULTS

Territorial occupancy

Changes in the occupants, sizes and numbers of territories were largely due to the presence or absence of males, which established and occupied most territories. Each marked male occupied only one territory during the study on which it usually had a number of mates in succession. Females, by contrast, paired successively with different males on different territories; no female associated with more than one male while she was on one territory. Thirty-two single males were resident for 3,222 bird-days, whereas only nine females held territories alone for 751 bird-days. Five of these females were resident alone for substantial periods (53, 91, 102, 179 and 249 days respectively). These differences meant that there were always more resident males than females in the area. The proportion of males varied between 53% and 71% (\bar{x} =60%) in different half-months during the study. There was probably a similar sex ratio among nomads since 13 (65%) of 20 sexed birds were males.

New territories were established 25 times in areas that had recently been vacated by territory-holders that left the study area, while 10 other new territories were formed in poorly-frequented parts of very large occupied territories. The interval between a territory being vacated and occupied by a new bird averaged 25.7 days (range 1-58 days). There was a positive correlation between the monthly incidence of territories being deserted and new territories being formed (Table 1), so most new territories were only formed when vacant areas became available. There was thus a shortage of suitable territories and existing territories were indeed vigorously defended against neighbours and intruding nomads. Nevertheless, kites probably did not settle immediately and, perhaps, indiscriminately in areas becoming vacant. Of 24 birds marked when first seen in vacant areas, six (25%) were present for 1-7 days only. They then disappeared for 3-9 weeks before returning to become permanent residents in these areas. Some nomadic kites were seen visiting the same areas repeatedly, suggesting that they did not move around at random. Furthermore, more nomads were seen on the study area when prey were abundant than at other times (Mendelsohn 1983).

Table 1. Correlations between monthly rates of movements by territory-holders and mates into or out of the study area, numbers of pairs starting to breed, numbers active breeding at all stages, and food supply (after Mendelsohn 1983).

CATEGORY	Mates arrive	Territory-holders arrive	Mates leave	Territory-holders arrive
Territory-holders arrive	NS			
Mates leave	NS	+++		
Territory-holders leave	NS	+++	+++	
♂pairs start breeding	++	-	---	---
♂pairs breeding	NS	--	-	----
Food supply	NS	----	---	----

Positive correlations ++ $p < 0.05$; +++ $p < 0.005$
Inverse correlations - $p < 0.1$; -- $p < 0.05$; --- $p < 0.025$; ---- $p < 0.005$
NS - not significant

Territories were probably deserted as a result of food shortage, since most desertions occurred when feeding conditions were poorest (Table 1). Furthermore, none of the territory-holders that left their territories was ever seen on another territory, but 10 were seen as nomads that were in poorer condition than residents (Mendelsohn 1981,1983).

Territory-holders deserted territories 72 times during the study, and 41 of these kites were never seen again, their territories being taken over by other birds. In the remaining 33 cases, the birds returned to their areas an average of 35.2 days (SD=22.9 days) later. For nine kites, resident for more than 200 days and, between them, making 23 temporary desertions, there was an inverse correlation between the length of time that each occupied its territory and the frequency with which it temporarily left the territory (Mendelsohn 1983). Thus the longer a kite held a territory the less likely it was to leave temporarily.

Some areas were occupied continuously by the same males throughout the study, while others had a succession of occupants. Of a total of 60 territory-holders, 44 (73%) were resident for less than 200 days; two birds even held territories for less than 5 days (e.g. Fig 1). Three of the remaining 16 (27%) kites were resident for longer than the 579-day census period. The longer a kite held a territory, the greater the proportion of time it spent both paired and breeding (Fig 2). This was largely attributable to the fact that long-term territory-holders had a greater number of mates than shorter term kites, and not because their mates stayed with them for long periods (Mendelsohn 1983).

Most territories covered 1 to 7 km², average sizes varying between 2 and 4 km² at different times of the study. The boundaries and sizes of those occupied by the same birds changed little from month to month, although some repeated disputes led to boundaries moving 100-500m over a few weeks. Territorial birds often adopted parts of neighbouring territories when they became vacant, so some small territories in 1977 were included in larger ones present in 1978 (Fig 3). This led to a decline in the number of territories and increase in territory size during the study, the inverse relationship between these variables being significant (Mendelsohn 1983). Furthermore, certain areas that were vacant in 1977 were occupied in 1978, as shown by changes in the total occupied area. Territories held by unpaired residents were smaller than those held by pairs, and the longer a territory was occupied by the same bird(s), the larger it apparently became.

Pairing

The presence or absence of pairs was usually dependent on the behaviour of females since it was they who joined males on territories and remained there for variable periods before moving elsewhere. New females joined established territorial males 29 times but only three males settled with territorial females. In 18 instances in which a pair was temporarily separated, females arrived back to rejoin their mates 10 times while males moved away temporarily 5 times. Pairs broke up 48 times after females left, but only twice as a result of males leaving.

Most mates were present for short periods; 33 (59%) stayed less than 50 days and only five (9%) more than 200 days. Unlike territory-holders, females that spent long periods paired did not spend greater proportions of the time breeding than those resident for shorter periods. Instead, two trends were apparent, one in which there was intense breeding activity for the duration of the female's stay, and the other in which females paired for long periods without spending much time breeding (Fig 2). The behaviour of ♀68 illustrates the contrast between the two kinds of behaviour. She spent 3 1/2 months with ♂5 and they only occasionally copulated. Then on 21 March she left and paired with ♂49. They started breeding activity that same day and four days later had started a nest which they abandoned after 10 days of building. They continued showing signs of breeding by copulating and displaying at nest sites and after 16 days started a new nest. This was also abandoned and on 5 May she returned and remained with ♂5 for at least five more months. She showed breeding activity on at least 46 (85%) of the 54 days she spent with ♂49, but signs of breeding were seen on only 33 (9%) of the 367 days spent with ♂5. She and other females probably remained with males for long periods without breeding because feeding conditions were too poor to attempt it. Most of them started breeding when other pairs started breeding as feeding conditions were about to improve (Mendelsohn 1984). Their behaviour was probably functionally equivalent to the few females that held territories alone, since they also paired when others started breeding.

Several observations suggested that the presence of females and their movements were related to breeding prospects. Firstly, most females arrived to pair with territory-holders during months in which most pairs also started breeding (Table 1). Secondly, most pairs broke-up as females left

when there was a shortage of food (Table 1), especially of diurnal rodents. Kites were only paired when diurnal prey was abundant (Mendelsohn 1982a) and a regular supply of prey throughout the day was probably necessary for breeding. Females thus appeared to leave when this was no longer available. The fact that their mates remained as unpaired residents, and fed more on nocturnal rodents active at dawn and dusk, showed that there was sufficient food to support the daily food requirements of adults. Thirdly, rapid movements by females between males appeared to be associated with breeding. In each case, the female had poor success with one male and then immediately attempted breeding with the new male, as illustrated by the movement of ♀68 between ♂5 and ♂49. While all territory-holders that left their territories were never seen on other territories, most mates probably soon moved to other territories.

Only two mates were seen as nomads and seven that left their territories were subsequently observed paired with other males. These seven represented 11.5% of all the desertions by mates and many others may have paired on territories outside the study area. Finally, females that moved away once their young fledged (see below) probably attempted to breed with other males (see DISCUSSION).

Population dynamics

Changes in territorial behaviour and pairing had substantial effects on the dynamics of the population. There were 19 to 35 residents ($\bar{x}=26$) in the study area in the 38 half-month counts (Fig 4). Numbers of territory-holders, and thus territories, varied between 12 and 22 ($\bar{x}=17.1$), while numbers of paired kites, i.e. 2x number of pairs, ranged from 10 to 25 ($\bar{x}=17.6$). Any relationship between changes in population size and food supply was confounded by the effects of the numbers of territory-holders and mates on population size. The proportion of paired birds in the resident population varied in direct relation to food supply, reflecting the attraction of mates when feeding conditions were good. However, this response and its effect on population size was offset by the decline in number of territories (which varied inversely with food supply) and thus numbers of both territory-holders and mates, during the study (Fig 4).

Although 49% of arrivals and 36% of the desertions involved the same birds leaving and returning, kites arrived to settle in the area a total of 124 times and 135 desertions were recorded. Over the 19-month study and against a population of 26 residents, an average of 6.5 arrivals and 7.1 desertions, or a turnover of about 25%, was recorded each month. As discussed earlier, these turnovers or rates of movement changed from month to month in relation to changes in prevailing feeding conditions, availability of vacant territories and breeding activity (Table 1).

Number of breeding birds

The number of kites breeding in the area depended on the number of occupied territories and pairs. However, it also depended largely on fluctuations in food supply since most pairs were breeding when prey was most abundant (Fig 4). Seasonal changes in other environmental factors, such as temperature and day-length, were probably irrelevant because breeding started in all months of the year. Comparing changes in food supply with changes in the proportion of birds starting to breed suggested that kites anticipated increases in prey populations, perhaps in response to the breeding activities of rodents (Mendelsohn 1984).

Number of broods

Kites could breed more than once a year. The frequency with which this happened depended on the duration of suitable feeding conditions and length of time needed to complete each breeding cycle.

Each cycle lasted an average of 172 days (about 25 weeks or just under six months) from the start of the pre-laying period to independence of the young. There was limited variation in the duration of incubation and nestling periods, but great differences between the shortest and longest pre-laying and post-nestling periods (Table 2). Adding the observed minimum and maximum periods for each stage of breeding, shows that the whole cycle could have taken as little as 125 or as long as 224 days. Food supply was the only factor I could relate to some of the variation. Pairs that laid quickly produced larger pellets than those that laid after long pre-laying periods (Table 3). Food supply was also apparently related to lower growth rates, so long nestling periods might have been due to poor feeding rates (Mendelsohn 1981).

Table 2. The duration of stages of the breeding cycle and the number of cycles possible each year if breeding was continuous.

STAGE	Males		Females	
	Mean	Range	Mean	Range
Pre-laying	24	10-46	24	10-46
Incubation	31	29-33	31	29-33
Nestling	35	32-38	35	32-38
Post-nestling	82	54-107	20	0-83
TOTAL	172	125-224	110	71-299
Breeding cycles/year	2.1	2.9-1.6	3.3	5.1-1.8

While males contributed to the breeding cycle for its entire duration, most females departed soon after their chicks left the nest. Females at eight nests left an average of 20 (range 0-49) days after the young started flying, while the female at a ninth nest remained and helped the male feed and defend her chick throughout its 83-day post-nestling period; she left her mate eight days after the young bird became independent. One female moved immediately to an unpaired male on an adjoining territory and remained with him for 46 days. The other females simply disappeared from the study area, but three later returned after their young became independent, having been away for 50, 56 and 61 days respectively. Two of them rejoined their unpaired mates, while the third stayed for 15 days on the territory alone, her mate and chicks having died during her absence.

Table 3. Weights of pellets produced by different groups during the pre-laying and incubation periods.

	Eggs:		Period before laying:		Clutch	
	laid	not laid	<24 days	>24 days	hatched	deserted
Mean	1.53	1.34	1.64	1.27	1.33	1.16
S D	0.79	0.48	0.76	0.59	0.67	0.48
No.	78	55	27	26	127	69
Difference	p < 0.05		p < 0.05		p < 0.025	

The departure of females meant that they participated in each breeding cycle for an average of 110 days only, compared to the 172 days spent by males for the full cycle. Males could therefore breed twice each year (Table 2), as did ♂15 and ♂51 who started breeding again 40 and 14 days respectively after successfully rearing young to independence. Intervals between independence of their fledglings and the acquisition of new mates were even shorter, 8 and 13 days respectively. Both second attempts were successful (at least until young of ♂51 left the nest) indicating that continuous breeding was possible. ♂15 spent 346 out 386 days breeding while, except for an interval of 14 days, ♂51 was engaged in breeding activity for at least 251 days.

Table 4. The sizes of clutches, nestling broods and post-nestling broods observed at Settlers and elsewhere in southern Africa.

Number eggs/young	Clutches		Nestlings		Post-nestlings
	Settlers	s. Africa	Settlers	s. Africa	Settlers
1	0	0	1	4	1
2	3	4	4	7	2
3	6	18	7	21	2
4	9	25	5	8	3
5	1	4	0	3	1
6	0	1	0	0	0
Number	19	52	17	43	9
Mean	3.4	3.6	3.05	3.0	2.9

Clutch and brood sizes

Clutch sizes at Settlers varied between 2 and 5 eggs, with a mean of 3.4 eggs (Table 4). This was similar to a larger sample from elsewhere in southern Africa (mean=3.6 eggs). Brood sizes at Settlers area (mean=3.05 young) were also similar to those elsewhere (mean=3.0 young). Post-nestling broods at Settlers consisted of an average of 2.9 young. These figures indicate that few eggs and young were lost from successful nests during the cycle. However, overall success rates were low (Table 5) because complete clutches and broods were lost in a high proportion of nests.

Table 5. Percentage success rates for nests, clutches and broods in this study at Settlers and others elsewhere in the Transvaal, South Africa by W. R. Tarboton (MS) and A. C. Kemp (pers. comm.). The second column shows the number of attempts that remained at each stage after starting with 100 breeding attempts.

Stage	Settlers		Tarboton	Kemp
	% success	No. surviving	% success	% success
Pre-lay	60	100	-	-
Nest building	50	60	62.5	84
Incubation	59	30	40	37.5
Nestling	67	18	83	-
Post-nestling	73	12	-	-
Independence		9	-	-

Success rates

The following success and failure rates (summarised in Table 5) were recorded at Settlers:

- Of 40 pairs that started copulating and displaying at nest sites etc., 24 (60%) built nests and 16 (40%) failed to build.
- Of 40 nests seen being built, eggs were laid in 20 (50%) and 20 (50%) were abandoned.
- Of 22 clutches, 13 (59%) produced nestlings and nine (41%) failed. In those clutches in which at least one egg hatched, 43 eggs produced 37 (86%) chicks.
- Of 18 broods, 12 (67%) produced flying young and six (33%) died. In those broods that produced flying young, 30 (88%) out of 34 nestlings left the nest.
- Of 11 flying broods, 8 (73%) produced independent young and 3 (27%) whole broods died. Excluding complete broods that died, 22 (96%) out of 23 fledglings became independent.

Similar high overall failure rates have been found by A.C. Kemp (pers. comm.) and W. Tarboton (MS) (Table 5). Kemp found 19 nests, 16 clutches were laid, but only six nests survived to produce 14 flying young. In Tarboton's study, 24 nests were built, 15 clutches (45 eggs) were laid, six clutches (19 nestlings) hatched and five broods (14 young) fledged.

Two peaks of breeding activity were observed during this study, one starting in July 1977 and the other in March 1978 (Mendelsohn 1984). Within each peak, the small samples (Table 6) suggested that those pairs which started breeding earliest had the best success.

Table 6. Nest success in relation to when breeding started in each of two peaks of breeding activity

Year and month	No. pairs start breeding	No. (%) laying	No. (%) producing young
1977			
July	2	1 (50)	1 (50)
August	6	1 (17)	1 (17)
September	5	1 (20)	0 (0)
1978			
March	10	6 (60)	3 (30)
April	4	1 (25)	0 (0)
May	3	0 (0)	0 (0)
June	2	0 (0)	0 (0)

Many failures were probably due to food shortages. Smaller pellets, indicating lower food intakes, were produced by pairs that failed to lay or deserted clutches during incubation than those that were successful (Table 3). Several observations indicated that females became inattentive towards their nests (see similar results for Tawny Owls *Strix aluco* by Hirons 1985a), followed their mates foraging away from the nest, or hunted themselves when feeding conditions were poor. This allowed various predators access to their nests, resulting in the loss of nest contents. Seasonal differences in success rates also suggest that kites were most productive when food was most abundant.

Between March and June 1977, eight breeding attempts produced only two fledglings; between July and September 1977, 10 attempts produced only three fledglings; and 13 attempts started between March and May 1978 resulted in 13 fledglings. The greater success rates coincided with better feeding conditions in 1978 than in 1977 (Mendelsohn 1982a).

Some failures were also associated with strong winds. Three eggs, in two clutches, were broken after a strong wind in October 1978. In the SW Cape, South Africa, at least 10% of 61 nests were destroyed by wind (SAOS nest records).

Productivity

The productivity of the population was low, mainly because the poor success rates (Table 5) meant that only about 9% of all nests started produced independent young. If each successful attempt produced 2.9 independent young, 100 breeding attempts would have produced about 26 young. Only 15 independent young were produced in the study area during the 19 month census period; equivalent to 9.5 young/year. Against an average population of 26 residents, productivity was $9.5/26=0.365$ independent young/resident/year.

These calculated rates represent the whole population, but most kites produced no young. Twenty-nine territory-holders did not breed, 10 territory-holders made one attempt to breed, 4 made two, 1 made three, 2 made four, 2 made five, 2 made six, and 1 territory-holder made seven breeding attempts. Of these 58 different breeding attempts during the 19 months, only six produced young. The majority were thus repeat attempts following previous failures. The extent of individual variation in productivity is shown in Table 7 for seven males who were monitored for most of the study and whose total productivity during the 19 month period was therefore known. Five of the males produced no young, although each had a number of mates and tried to breed several times. Both males that produced young had two successful breeding attempts each. The fathers of the remaining four independent young produced during the study left the area after much shorter periods and could have bred elsewhere.

Table 7. The productivity of seven males whose breeding performance throughout the 19-month study was known.

Male	Days observed	Number of mates	Number breeding attempts	Number Independent young
5	579	2	5	0
15	579	3	4	6
49	484	5	5	0
51	516	4	3	7
59	559	2	5	0
63	579	3	5	0
71	495	3	4	0

DISCUSSION

Population size

The densities of many raptors vary from place to place and year to year according to prey availability (Newton 1979). It was therefore surprising that population size did not vary in a direct and simple way with changes in food supply in this study. This was true whether population size was expressed as the total number of residents or as the number of territories (Fig 4). The saturation of the study area with large territories defended by males meant that other males had little opportunity to establish new territories which would have increased the density. Similar results were obtained for Tawny Owls (Hirons 1985b) and Common Kestrels *Falco tinnunculus* (Village 1983) where territorial behaviour limited non-residents from establishing their own territories and breeding. Furthermore, territories expanded as some males left, leading to a decline in the density of territories and number of residents in the area. The overall trend in the population was therefore downward, numbers dropping when food shortages caused desertions but not increasing when prey became more abundant. If one male could conceivably have defended the whole 69km² study area, the process might have ended in a population consisting of that male and perhaps its mate.

Although male territoriality limited density, movements by females led to changes in the size and composition of the population which were directly related to food supply. As prey availability increased, more females became resident in the area, the total number of residents increased and the sex ratio became more balanced. By contrast, when feeding conditions were poor, females left, population size declined and males further outnumbered females. The behaviour of males and females thus had different effects on the dynamics of the population.

The success of males and females

Males of many other raptors usually establish and occupy territories, on which females then settle (Newton 1979; Mendelsohn 1983). These roles in kites, functionally described as territory-holders and mates respectively, were not invariable, however. Some females held territories alone where a few males joined them as mates to form pairs. Male and female roles were thus not fixed, but were probably flexible responses to prevailing opportunities for acquiring territories, pairing and breeding. The saturation of the area with resident males was probably a major factor in this respect. While some males and their territories may have been less attractive than others, females nevertheless had the opportunity of choosing between different territories. Had the area been saturated with females, they would have had fewer opportunities for making alternative choices, as was the case for males, although other factors may have also mitigated against them making frequent moves (see below).

The availability of 'choices' to females was also related to their behaviour in seeking the best breeding prospects by pairing with established males. Although females sometimes probably sought and occupied better feeding areas, they would have competed directly with territorial males if that was their sole requirement. The area would then have been saturated with unpaired residents of both sexes, each holding its own territory. Females could not have settled on occupied territories if males did not anticipate breeding with them.

Differences in hunting success between males and females might also have contributed to their different behaviour. If females hunted less efficiently than males they might have been forced to leave their territories more frequently and move around in search of better feeding areas. Although comparisons of the hunting success of paired males and females (Mendelsohn 1982a) suggest that there was little difference in hunting success, more data are required to test this possibility.

Having established a territory, a male's performance evidently improved the longer it stayed; the size of the territory probably increased, it obtained mates rapidly and spent much of its time breeding. This doubtless reflected a continuous good food supply, both of the territory and probably the male's improved experience in finding the best hunting areas. Rijnhsdorp *et al.* (1982) found that Common Kestrels hunted according to the times that their prey was active and that they returned to areas on which they had hunted profitably during the past one or two days. This suggests a substantial capacity to learn both when and where to hunt. The ability to find prey will be most important during breeding, when males hunt to provide all the food for their mates and young. A strong need for familiarity with feeding areas might explain why males that provide paternal care usually establish and hold territories (Ridley 1978). Moreover, males that rapidly provide their mates with food to lay down body reserves and produce eggs early in the season should have the best breeding success (Table 6; Drent & Daan 1980). These factors suggest that even if they found alternative areas, males that move might take some time before achieving adequate levels of competence on their new territories.

Males obtained two probable advantages by expanding their territories. First, by preventing other males from acquiring territories and breeding, territorial males would have contributed proportionately more offspring to future generations (Verner 1977). Their offspring would, in turn, have greater access to resources since there would be fewer unrelated competitors. Second, the expansion of territories maximised the area they defended and ensured greater reserves for periods of food scarcity (Hixon 1980). This is particularly relevant to kites that often encounter unpredictable changes and shortages of prey. These changes occur seasonally, as a result of irregular fluctuations in rodent density, and from day to day because hunting success is so variable (Mendelsohn 1982a, b).

The behaviour of females appeared to be opportunistic, as suggested by the frequent moves and attempts to breed with different males. Since successful breeding occurred on relatively few territories, there was perhaps strong competition among females for these areas. Their success probably depended on their ability to compare breeding prospects on their own territories with those available elsewhere, and to select and move to those offering the best opportunities. This might explain why most females moved onto established territories when prospects for breeding improved, few females moved as nomads, and some birds were seen changing territories within a day or so. Although I noted that females were often temporarily absent for a few days or weeks, they might have made frequent short trips (undetected by me for a few hours only) in search of alternative prospects. Telemetry studies of females should provide useful information on how, when and where they move.

Productivity

The very low productivity recorded during this study was similar to that recorded elsewhere (Table 5), suggesting that such rates might be usual in Black-shouldered Kites. In terms of overall strategy, their poor success was probably balanced by the ability to attempt breeding repeatedly and at any time of the year. Much of their breeding thus appeared to be opportunistic, most likely in response to unpredictable fluctuations in rodent densities.

The low productivity, as the pooled result of a number of factors, was largely due to high failure rates. Very few kites bred as often as they could and there was relatively little variation in the sizes of successful clutches and broods, so these components had little effect on productivity. Even though the number and proportion of breeding pairs varied substantially (Fig. 4), this, too, had little effect, since the great majority of the many breeding attempts made during the study failed. Clearly, then, very little of the potential productivity of the population was realised.

Most failures during the pre-laying and incubation periods were probably attributable to food shortages which might also have impaired the growth rates of nestlings. Successful nests were therefore those at which there was a satisfactory supply of food throughout the breeding cycle. This depended ultimately on the hunting success of males and prey density, since this was closely

related to food intake (Mendelsohn 1982a). While it seems plausible that food shortages would interrupt breeding behaviour, it is not clear what proximate processes were involved. On the one hand, shortages might limit energy expenditure on demanding activities such as nest building, egg formation and additional hunting to feed nestlings. However, kites might also "voluntarily" cease breeding if a shortage of prey indicates that the breeding cycle has a poor chance of success anyway. Similarly, fewer eggs might be laid if feeding conditions indicate that only small broods will be fed adequately. These facultative and predictive processes have been suggested to play a role in determining clutch sizes of Dunnock *Prunella modularis* (Davies 1985) and Eastern Kingbirds *Tyrannus tyrannus* (Murphy 1986).

The number of breeding pairs was limited by the number of territories and declined as male territories expanded. However, the proportion of breeders was largely determined by the presence or absence of females and related changes in food availability (Fig 4). This relationship was due to two responses. Firstly, kites started breeding in anticipation of increasing food supply, so the numbers of kites breeding increased sharply before food supply peaked, as in March 1978. Secondly, the numbers of breeders dropped as feeding conditions diminished, both as a result of failures and because successful pairs reached the end of their cycles when food supply dropped.

Few raptors breed more than once a year, so this component of productivity is not relevant to most species. The average duration of male and female participation in each breeding cycle, 172 and 110 days respectively, suggests that if they bred continuously, males could produce two and females three broods each year. Perhaps fortuitously, this ratio (2:3) was the reciprocal of the average sex ratio (3:2) among residents in the study area; three males, each breeding twice would have produced a total of six broods with two females that each bred three times. I found that males could indeed breed twice a year successfully and argue that females may also breed continuously. If continuous breeding was possible, the number of broods produced each year might depend on the duration of each cycle. Minimum periods over which a cycle could be completed (Table 2) suggest that males might breed about three times and females five times each year. Good evidence of such breeding rates has yet to be found, but there are indications in the literature of repeated, continuous breeding when food is superabundant (Malherbe 1963; see also Hollands (1977) for the similar Letter-winged Kite *Elanus scriptus*).

The observations of eight out of nine females leaving their mates and fledglings suggests that this occurs regularly. Similar behaviour has been observed in Black-shouldered Kites in California (Waian 1973, pers. comm.; Henry pers. comm.), Snail Kites *Rostrhamus sociabilis* (Beissinger & Snyder 1987) and Tengmalm's Owls *Aegolius funereus* (Solheim 1983). Desertions in all these species probably occurred because females could breed again with other males and there are indeed four records of this for Tengmalm's Owls, one for Snail Kites, and one probable record for Black-shouldered Kites in California. These observations support the idea that females at Settlers also left to find new males with whom they could breed. Further evidence for this is as follows. First, the female that paired with a neighbouring single male would doubtfully have done so if breeding was not intended, given the functional relationship between pairing and breeding. Second, if females had no chance of improving their reproductive fitness elsewhere, they would probably have not left their young, considering the additional costs of paternal care to their single mates (as shown by Beissinger (in press)) and reduction in level of protection for the offspring. Third, if either one of the pair was unable to leave and find a new mate once the chicks fledged, females had the best chance of finding new mates because there was an excess of males. Selection for continued occupation of their territories also meant that males were unlikely to leave. Females thus behaved as expected in terms of the prevailing sex ratio and male territoriality. The paucity of observations of repeat breeding in the study area and elsewhere is doubtless due to the difficulty in tracking the movements of individual females, often over considerable distances of up to 10km (Tengmalm's Owls) and 160km (Snail Kites).

Overall Patterns

Although there were many residents and frequent movements in and out of the study area, the general impression of the dynamics of the population at Settlers was one of relative stability. The population density was comparatively low. Males that attracted a succession of mates and bred successfully were dispersed on large territories which they occupied for long periods. Many females, too, stayed several months and many breeding attempts lasted substantial periods, some of them producing a few young. The frequency of breeding was low, new attempts being made only

after previous broods became independent. This stability was probably related to comparatively small changes in food supply. Populations of the three species of rodents that dominated their prey did not fluctuate synchronously (Mendelsohn 1982b), so a decline in the density of one species may have been compensated by increases in others.

The relative stability was especially evident when compared to events recorded elsewhere. There are many records of quite different conditions when rodent densities fluctuate widely and prey is sporadically superabundant (reviewed in Mendelsohn 1983). Kite densities may be several times greater than those observed at Settlers, and populations are often irruptive. Great numbers suddenly arrive in an area and leave just as quickly. The birds also often join large communal roosts. Such high densities suggest that territories must be very small if any areas are defended at all. Adjacent nests may be as close as 100-200m and second clutches are probably started when previous broods are still being fed (Malherbe 1963).

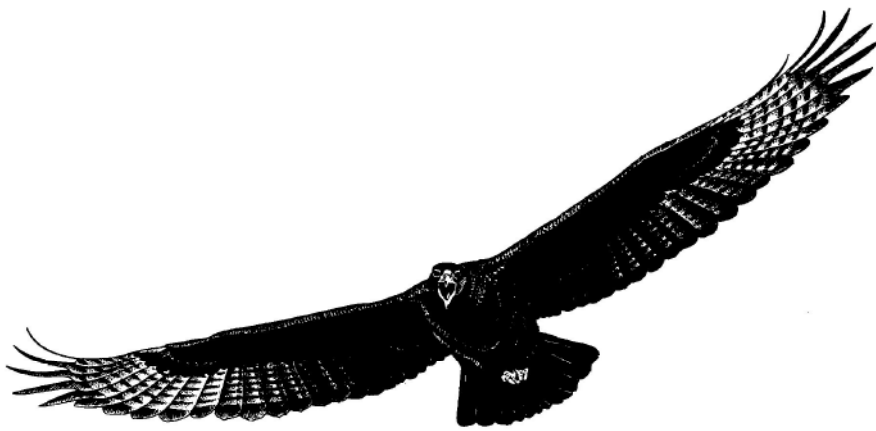
These conditions, and those observed in this study, differed substantially and show features suggestive of r and k -selected strategies. However, they are probably opposite ends of a spectrum of responses that varies according to feeding conditions. Some elements of irruptive kinds of behaviour were observed at Settlers. For example, the high turnover rate was largely due to rapid movements on and off territories that could not provide a stable food supply (Fig 1; Mendelsohn 1983). The presence of nomadic kites suggested that the study area offered opportunities for these birds to exploit sudden changes in food supply. Communal roosting was probably related to feeding conditions, since those that slept in these roosts had a poorer food supply than kites that spent the night alone on their territories (Mendelsohn 1981).

The behavioural responses of kites to different feeding conditions will have quite different consequences for population parameters, resulting in different population densities, dispersions, sex ratios, chances of acquiring mates or territories, and reproductive rates. My observations at Settlers probably show just one of the many ways in which variable opportunities and responses can affect population size and productivity in Black-shouldered Kites.

REFERENCES

- BEISSINGER, S.R. & N. F. R. SNYDER 1987. Mate desertion in the Snail Kite. *Anim. Behav.* 35: 477-487.
- BEISSINGER, S.R. *In press*. Mate desertion and reproductive effort in the Snail Kite. *Anim. Behav.*
- DAVIES, N.B. 1985. Co-operation and conflict among Dunnocks *Prunella modularis*, in a variable mating system. *Anim. Behav.* 33: 628-648.
- DRENT, R.H. & S. DAAN 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- HIRONS, G.J.M. 1985a. The importance of body reserves for successful reproduction in the Tawny Owl (*Strix aluco*). *J. Zool., Lond (B)* 1: 1-20.
- HIRONS, G.J.M. 1985b. The effects of territorial behaviour on the stability and dispersion of Tawny Owl (*Strix aluco*) populations. *J. Zool., Lond (B)* 1: 21-48.
- HIXON, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* 115: 510-530.
- MALHERBE, A.P. 1963. Notes on birds of prey and some others at Boshoeke north of Rustenburg during a rodent plague. *Ostrich* 34: 95-96.
- MENDELSON, J.M. 1981. A study of the Blackshouldered Kite *Elanus caeruleus*. Ph. D. thesis, University of Natal, Pietermaritzburg.
- MENDELSON, J.M. 1982a. The feeding ecology of the Blackshouldered Kite *Elanus caeruleus* (Aves: Accipitridae). *Durban Mus. Novit.* 13: 75-116.
- MENDELSON, J.M. 1982b. Notes on small mammals on the Springbok Flats, Transvaal. *S. Afr. J. Zool.* 17: 197-201.
- MENDELSON, J.M. 1983. Social behaviour and dispersion of the Blackshouldered Kite. *Ostrich* 54: 1-18.
- MENDELSON, J.M. 1984. The timing of breeding in Blackshouldered Kites in southern Africa. *Proc. 5th Pan-Afr. Orn. Congr.* 799-808.
- MURPHY, M.T. 1986. Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds. *Auk* 103: 465-476.
- NEWTON, I. 1979. *Population Ecology of Raptors*. Berkhamsted: T. & A. D. Poyser.
- RIDLEY, M. 1978. Paternal care. *Anim. Behav.* 26: 204-302.
- RIJNSDORP, A., S. DAAN & C. DIJKSTRA 1981. Hunting in the Kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. *Oecologia* 50: 391-406.
- SOLHEIM, R. 1983. Bigyny and biandry in the Tengmalm's Owl *Aegolius funereus*. *Ornis Scand.* 14: 51-57.
- VERNER, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111: 769-775.
- VILLAGE, A. 1983. The role of nest-site availability and territorial behaviour in limiting the breeding density of kestrels. *J. Anim. Ecol.* 52: 635-645.
- WAJAN, L.B. 1973. The behavioural ecology of the North American Whitetailed Kite (*Elanus leucurus majusculus*) of the Santa Barbara coastal plain. Ph. D. thesis, University of California, Santa Barbara.

John M. Mendelsohn
Durban Natural History Museum
P. O. Box 4085
Durban 4000
South Africa



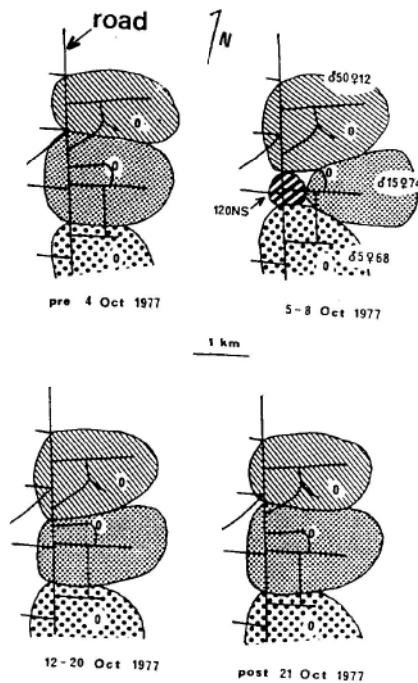


FIGURE 1. Rapid territory changes during October 1977. Focal areas of each territory are indicated by "0". The unmarked bird, 120NS, occupied a territory for two days when ♂15, ♀74 withdrew from part of their normal range. ♂50, ♀12 and ♂5, ♀68 also extended their territories to fill part of the vacant area. ♂15, ♀74 then returned, the other kites withdrawing and 120NS leaving the area (after Mendelsohn 1983).

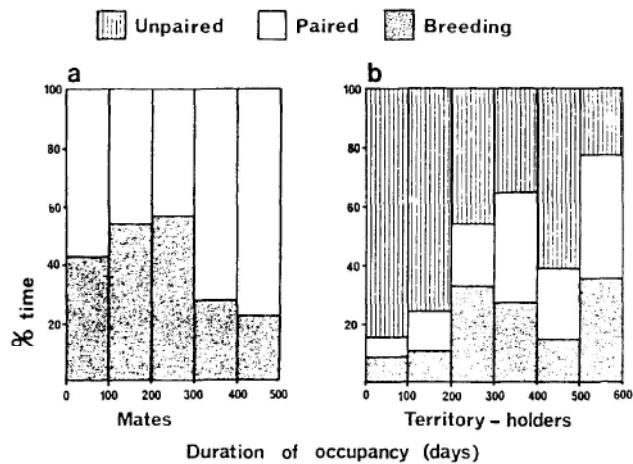


FIGURE 2. The relationship between the time (a) territory-holders and (b) mates were resident and the proportion of that time spent unpaired, paired, or breeding (after Mendelsohn 1983).

FIGURE 3. The sizes of "stable" territories, i.e. those occupied continuously during the month and the total area occupied by all residents. Means, 95% CIs, ranges and sample sizes are shown (after Mendelsohn 1983).

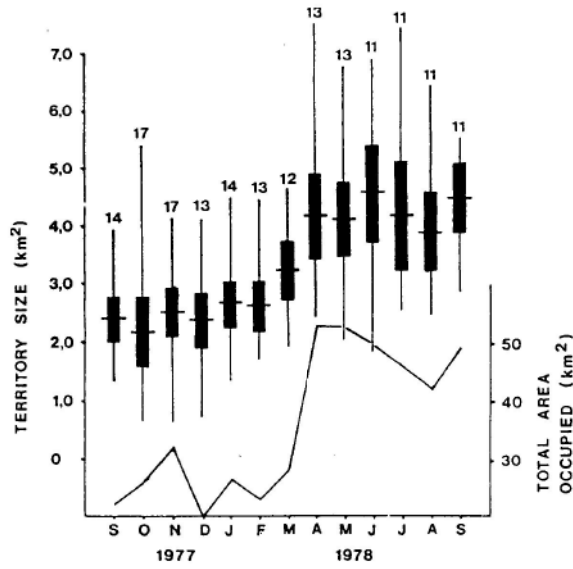


FIGURE 4. Monthly changes in food supply, population size, number of territories, and the percentage of residents breeding or paired. Spearman's Rank Correlations between these variables were: food supply vs population size +0.36; NS; food supply vs % paired +0.67; $p < 0.01$; food supply vs % breeding +0.71; $p < 0.01$; no. territories vs population size +0.81; $p < 0.01$.

