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SOCIAL BEHAVIOUR AND DISPERSION OF THE BLACKSHOULDERED KITE

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SUMMARY

MENDELSON, J. M. 1983. Social behaviour and dispersion of the Blackshouldered Kite. *Ostrich* 54:1-18. Colour-marked Blackshouldered Kites *Elanus caeruleus* were studied at Settlers in the Springbok Flats, South Africa. Males usually established territories where females joined them as mates after moving around between territorial males. There were always more resident males than females. Territories were exclusive nesting and hunting areas. The number of territories decreased, but mean territory size increased during the study. Unpaired kites held smaller territories than other residents. Males usually established territories when occupied areas fell vacant, but females usually paired when most other pairs were starting to breed. Both sexes abandoned territories when food supply was poor. Unpaired males deserted more frequently and had longer temporary absences than paired or breeding males. Most kites (86%) were resident for periods of less than 100 days. Females spent either most or very little of their time breeding. The longer males were resident, the greater the proportion of their time spent paired and breeding. Population size varied between 19 and 35 kites ($\bar{x}=26$); about 13% of the population was replaced each half-month. More nomads visited the study area when feeding and breeding conditions were good. After deserting territories, males usually became nomads while females probably moved to new territories. The social organization of Blackshouldered Kites is discussed with reference to food supply (Mendelsohn 1982), population dynamics, and breeding biology (Mendelsohn 1981).

INTRODUCTION

Although many raptor populations have been studied (reviewed by Newton 1979), most research has been done in the temperate Holarctic and several subjects await investigation. Among these are the proximate effects of food on individual performance and how these relate to the behaviour of whole populations. The social behaviour of raptors is also little known, mainly because few colour-marked birds have been studied.

Populations of Blackshouldered Kites *Elanus caeruleus* are described as unpredictable and irruptive with great numbers congregating in rich feeding areas (Brown & Amadon 1968; Morel & Poulet 1976; Skead 1974). Although it is suggested (e. g. Cramp & Simmons 1980) that these movements are responses to local changes in rodent prey numbers, little is known of how, when and by whom the movements are made. This paper presents data on the performance of resident kites, their movements, and the associations and differences in be-

haviour between the sexes. These aspects are then related to the supply of rodent prey (Mendelsohn 1982a), breeding and successive polyandry (Mendelsohn 1981, in press), and the dynamics of kite populations.

STUDY AREA AND METHODS

Blackshouldered Kites were studied in a 6 900-ha area at Settlers (24 57S; 28 33E; 1 048 m a.s.l.) in the Springbok Flats, South Africa, from 1 March 1977 to 30 September 1978. The topography was flat with a 60-m drop over 12 km from north to south. Soils consisted of black turf (64%) or red clay (36%). About 72% of the area was cultivated; the remaining vegetation consisted of *Acacia* woodland (17%) and grassland (5%) in small patches, and road and field verges (5%) and farmyards (1%). The study area is described in greater detail by Mendelsohn (1982a), while the geography of the whole Springbok Flats was studied by Van der Riet (1974).

The presence or absence of birds in the study area was determined by recording the identity and position of all kites sighted. Sixty-seven birds were colour-tagged (Mendelsohn 1981) and each kite was seen an average of nine times per month. Dates of arrival (when kites became resident) or desertion (when they left the area) were taken as the dates individuals were first or last seen. The composition of the population was assessed each half-month (see below) and a bird not seen during a particular half-month was assumed to have deserted. An individual was considered resident only if it was seen repeatedly in an area over several days.

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

Identification of sexes was based on observed sexual behaviour or a discriminant analysis of certain body measurements (Mendelsohn 1981). A bird that paired with one of known sex was assumed to be of the opposite sex. Residents were also classified into one of three mutually exclusive mating classes: *unpaired*, *paired* (but not breeding) or *breeding*. Not all breeding birds were paired because most females left males before their young became independent (Mendelsohn 1981); such deserted, unpaired breeding males were classed as breeders. A bird that first occupied a territory was termed a *territory-holder*, while one that joined a territory-holder to form a pair was a *mate*. Periods spent as territory-holders and mates, and in each class, were measured separately for each bird.

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

A kite seen only once in an area was classed as a *nomad*, but a resident intruding on a neighbouring territory was not included in this category.

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

All sightings and movements were plotted on 1:50 000 maps. After August 1977, composite maps were drawn at the end of each month of all territories in the study area. Boundary positions were based on plotted sightings, territorial conflicts and a knowledge of boundary positions in previous months. Changes in the use of small areas of territories meant that kites were not always seen regularly throughout their territories. Unless observation showed that such apparently vacant areas had been expropriated by other birds, I assumed they still belonged to ones that occupied them in previous months. Territory sizes were measured on the maps to the nearest 0,25 km².

RESULTS

A high degree of individual variation in behaviour was one of the most striking findings in this study. Through necessity most results have been presented as group or population parameters, but individual performances should be emphasized throughout. A brief summary of the social and spatial behaviour of each kite is available in Mendelsohn (1981).

Differences in behaviour between males and females should also be stressed at the start, for these were important to all aspects of social organization. Males were resident for average periods of 205,5 days ($n=38$) and females for 97,3 days ($n=51$) on each territory ($\chi^2=41,8$; $p<0,001$). Females frequently moved territories but each male occupied one territory only during the study. Males were unpaired residents for 3 222 bird-days and females for 751 bird-days only. There were therefore more resident males than females. Throughout the study the mean proportion of males was 60% (range 52-71%). This could be because females spent more time as nomads, but of 20 sexed nomads only seven (35%) were females.

Most males and females were territory-holders and mates respectively (Table 1), because males usually established territories where females joined them. Males were territory-holders for at least 6 298 bird-days, and probably for 7 592 bird-days (Table 1). Only five females were territory-holders for substantial periods (91-249 days).

Unsexed kites (Table 1) were not marked, but most behaved as males by occupying territories alone. All were resident for short periods ($\bar{x}=27,5$ days; $n=18$).

TABLE 1

TOTAL TIME (BIRD-DAYS) SPENT BY MALE, FEMALE AND UNSEXED BLACKSHOULDERED KITES AS TERRITORY-HOLDERS AND MATES, AND AS UNPAIRED, PAIRED OR BREEDING RESIDENTS. MALES AND FEMALES PRESENT AT THE START OF THE STUDY, AND THOSE THAT ESTABLISHED TERRITORIES TOGETHER (TABLE 2.1 f & g) WERE ASSUMED TO BE TERRITORY-HOLDERS AND MATES RESPECTIVELY.

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

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

Males spent more time breeding (2 207 bird-days) than females (1 821 bird-days) (Table 1) because most females deserted before their young became independent (Mendelsohn 1981). Males were then left to care for their flying young.

Pairing

Twelve pairs were present at the start of the study. A further 63 pairs were formed during the following 19 months. Most pairs established for the first time were formed by new birds joining resident territory-holders (Table 2.1 a-e). Where the sexes were known, 32 were females and three were males new to the area. Although six territories may have been established by pairs (Table 2.1 f), nomads were never seen in pairs, suggesting that the kites did not arrive paired. Slight differences in the arrival times of pair members might not have been recorded.

TABLE 2

MOVEMENTS OF BLACKSHOULDERED KITES ASSOCIATED WITH PAIR FORMATION AT SETTLERS IN 1977 AND 1978.

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

The four kites that joined territories (Table 2.1 g) had been unpaired residents for long periods (75-249 days) before pairing.

Eighteen pairs were re-established after one of the birds had been absent from the territory (Table 2.2). More females (ten) than males (five) were absent temporarily. One pair (Table 2.2 d) were seen together immediately before and after their absence but may have separated as nomads during their absence.

Several observations suggest how males and females behave during the first stages of pair formation. On 15 March 1978 I saw ♂71 associating with an untagged intruder for 15 min. On six occasions ♂71 flew towards the intruder which then flew off with ♂71 in pursuit. The six pursuits ended with both

TABLE 3

CAUSES AND FREQUENCIES OF PAIR SEPARATION IN BLACKSHOULDERED KITES AT SETTLERS IN 1977 AND 1978.

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

birds landing on bushes 20-50 m apart. With the intruder perched, ♂71 several times flew to another bush, hovered and descended into the foliage (pairs starting to breed often did this, the behaviour probably representing nest-site inspection and/or advertisement (Mendelsohn 1981)). The pursuits finally ended about 750 m into a neighbouring territory with the intruder flying away and ♂71 stopping his pursuit. Normally, territorial conflicts ended near territorial boundaries and displays to potential nest sites were never seen during conflicts (Mendelsohn 1981). Similar combinations of aggressive and sexual behaviour were seen in recently established pairs. For example, on the day that ♂34 and ♀62 were first seen paired I saw the male fly at the female six times in 155 min. Each time she crouched horizontally in a posture normally adopted by copulating kites. Five of the male's flights ended with him dive-bombing her and on the sixth

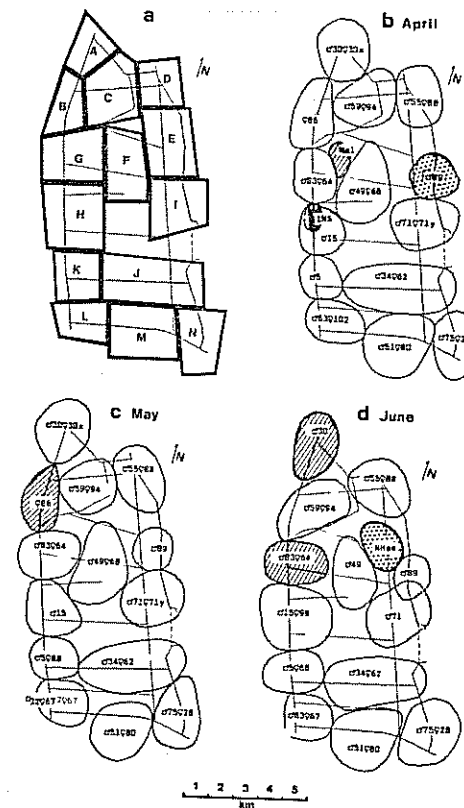


FIGURE 1

(a) 14 areas in which most Blackshouldered Kite territories were situated. (b-d) territories and their occupants during April-June 1978. Stippled and hatched territories were established or/and deserted during the month.

he attempted to copulate. In other new pairs dive-bombing was always the aggressive component, but sexual behaviour included copulations, displays to nest sites and prey being offered to the female (Mendelsohn 1981).

Pairs separated 67 times during the study (Table 3). Mates deserted more often than territory-holders and females deserted more often than males. The members of eight pairs are listed as having deserted simultaneously (Table 3.2 & 3.5), but slight differences in their departure dates might have been missed.

Territoriality

All residents occupied territories which they defended vigorously, except at dusk when intruders flying to or attending communal roosts were not repelled (Mendelsohn 1981). Fig. 1a shows 14 areas

in which most territories were situated, and Fig. 1b-d show examples of month-to-month changes in boundary positions. Territorial boundaries varied according to the presence of neighbours and the use of favoured hunting areas (see example in Fig. 2). The vertical extent of territories is unknown but kites rarely flew above 150 m. Intruders flying overhead were often chased (see Mendelsohn (1981) for a description of territorial defence). Each territory had a focal area consisting of one or more trees used for nesting and roosting during the day or night.

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

Twenty-five new territories were established in vacant areas and 10 in poorly frequented parts of existing territories (Fig. 2). The mean interval between a territory being vacated and being occupied by a new bird was 25.7 days (S.D.=18.0 days; $n=12$). The 10 existing territories which became divided were particularly large and the established occupants concentrated their activities in the remaining areas. Territories formed in vacant areas were occupied longer ($\bar{x}=146.5$ days; S.D.=153.1 days) than those established within existing territories ($\bar{x}=38.0$ days; S.D.=68.3 days) (Mann Whitney $U=213.5$; $p<0.001$).

Two independent juveniles established territories within their parents' territories. Territorial conflicts between these parents and juveniles were often observed.

Several observations suggested that kites might select territories instead of merely arriving in an area and settling there immediately. Five males remained for 1-3 days where they were first found and caught, and only 3-9 weeks later did they become permanent residents in the same areas. Another male was initially present for four days, absent for six weeks, and finally resident for the next nine months. ♂34 showed similar behaviour; he was present for one day, absent for ten weeks (when seen once as a nomad elsewhere), present for one day, absent for four weeks, and then resident in the same area for the next ten months. These seven kites represent 10% of all marked residents, suggesting that their behaviour was not irregular. Some of the 46 unmarked kites that were seen once and

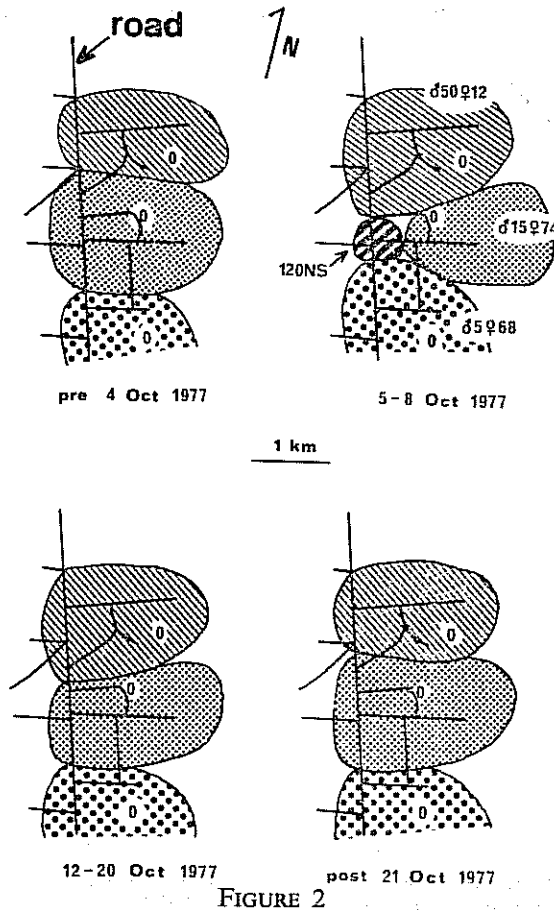


FIGURE 2

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

treated as nomads may have later returned as territorial birds.

The mean sizes of "stable" territories, *i.e.* those occupied continuously during each month, are shown in Fig. 3. The size of a territory usually changed when new birds or neighbours annexed parts of it, or when some parts were vacated and other areas became occupied. Persistent fighting between neighbours also resulted in boundary changes; some borders moved 100-500 m in 1-4

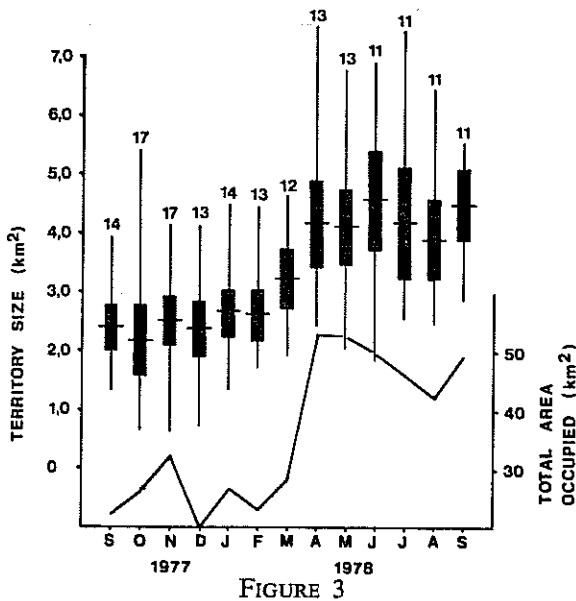


FIGURE 3

Changes in size of "stable" territories (see text) and total area occupied by Blackshouldered Kites between September 1977 and September 1978. Means, 95% C.I., ranges and sample sizes are shown.

weeks of repeated disputes. Two territories formed after unpaired neighbours paired with each other were unusually large (6-7 km²).

From September 1977 to February 1978 territories were both smaller and more numerous than between March and September 1978 (Fig. 3). The inverse relationship between size and number of territories was highly significant (Spearman's $r_{13} = -0.92$; $p < 0.001$). The total occupied area (sum of all territory sizes) also increased between September 1977 and 1978 (Fig. 3), indicating that areas vacant in 1977 became occupied in 1978.

Territories held by unpaired birds were smaller than those occupied by pairs. Sixteen territories were significantly smaller in the month before arrival of a mate ($\bar{x} = 2.49$ km²) than in the next month ($\bar{x} = 3.36$ km²; Matched Pairs $t_{15} = 3.39$; $p < 0.005$). By contrast, paired territories were similar to breeding territories in size; sizes in the month before breeding (when the pair was hunting) were close to size in the following month when the female was restricted to the nest area ($t_8 = 0.42$; NS).

Territories probably became larger the longer they were occupied. Within the periods September 1977-February 1978 and April-September 1978 territory sizes did not vary significantly (Fig. 3), but territory size and duration of tenure were positively correlated (Spearman's $r_{22} = +0.35$; $p < 0.1$ and

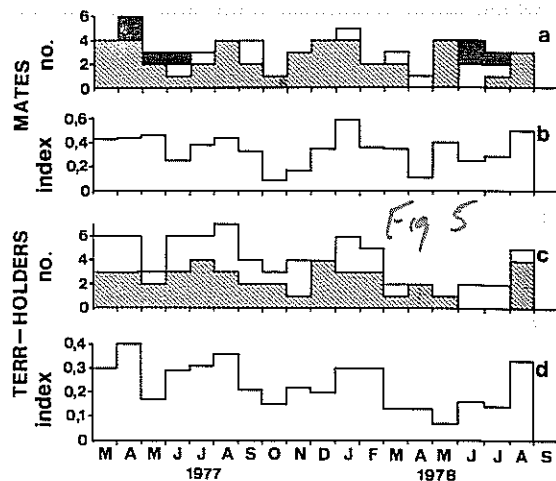


FIGURE 4

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

$r_{13} = < 0.39$; $p < 0.1$ respectively). The mean size of each territory was calculated from measurements made within each test period and the tenure of a territory was the time it was under observation.

Territory desertion was preceded by apparent restlessness. I often saw kites hunting in areas they usually avoided, and also failed to find them regularly in their preferred hunting areas. Two males abandoned territories while tending flying young. The chicks followed their fathers when they left. One of the males nested outside the study area but moved with his single chick into the area for 18 days.

Factors associated with arrivals and desertions

In this section I consider temporal factors associated with kites becoming residents (arrivals) and deserting their territories (desertions). The timing of these events is related first to variations in food supply and breeding activity, and second to the length of stay of residents. Arrivals and desertions by mates and territory-holders (treated separately) could usually be equated with the formation and separation of pairs (see METHODS and Table 3) and the establishment and desertion of territories

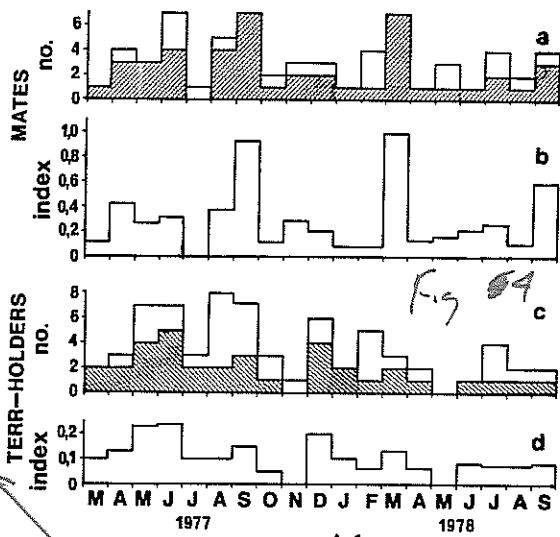


FIGURE 3

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

respectively. Territories became vacant after 68 of the 74 desertions by territory-holders; mates remained resident in the six other cases. Territories were established after 64 of the 68 arrivals by territory-holders; mates were already present in the remaining four cases. Analyses here exclude desertions by mates with flying chicks because these were considered different from other desertions (see DISCUSSION).

Monthly variations in arrivals and desertions (Figs 4 & 5) were significantly correlated with several factors (Table 4). These results indicate that most mates arrived when most pairs were starting to breed, and that most new territory-holders arrived when previously occupied areas fell vacant. Most desertions by mates and territory-holders occurred when few pairs were breeding and feeding conditions were poor. The inverse correlations between the index of new territory-holders and measures of food supply and breeding activity simply indicate that few vacant areas were available when most kites were breeding and food supply was good.

TABLE 4

TESTED RELATIONSHIPS BETWEEN MONTHLY INDICES OF ARRIVALS, DESERTIONS, PAIRS STARTING TO BREED, PAIRS BREEDING AND FOOD SUPPLY IN THE BLACKSHOULDERED KITE. TESTS ARE SPEARMAN'S RANK CORRELATIONS AND SHOW SIGNIFICANCE LEVELS (+p<0.1; ++p<0.05; +++p<0.025; ++++ p<0.005; N.S.—NOT SIGNIFICANT) AND DEGREES OF FREEDOM. NEGATIVE CORRELATION IN PARENTHESES.

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

^ano. new mates/mean no. unpaired territory-holders (Fig. 4b)

^bno. new territory-holders/mean no. territory-holders—two-month samples (Fig. 4d)

^cno. desertions by mates/mean no. mates (Fig. 5b)

^dno. desertions by territory-holders/mean no. territory-holders (Fig. 5d)

^e% of pairs starting to breed (Mendelsohn 1981)

^f% of pairs breeding (adapted from Fig. 7)

^gindex of food supply (Mendelsohn 1982a)

In relation to the length of time they were resident, paired and breeding mates deserted at the same rate (Table 5; $\chi^2_1=1.09$; NS). By contrast, among territory-holders resident for longer than 100 days (Table 6), unpaired kites deserted more often than paired and breeding birds ($\chi^2_1=12.18$; $p<0.005$). Paired and breeding territory-holders resident longer than 100 days deserted equally often ($\chi^2_2=1.97$; NS). Desertion by territory-holders resident for less than 100 days was not related to mating class ($\chi^2_2=0.77$; NS).

Territory-holders returned to their territories more often than mates (Table 5 & 6; $\chi^2_1=4.83$; $p<0.05$). However, among residents of less than 100 days, territory-holders returned less frequently than mates ($\chi^2_1=4.23$; $p<0.05$; corrected for continuity).

The longer a territory-holder was resident, the

TABLE 5

FREQUENCIES OF PERMANENT (PERM.) AND TEMPORARY (TEMP.) DESERTION OF TERRITORY BY MATES ACCORDING TO MATING CLASS AND DURATION OF OCCUPATION IN THE BLACKSHOULDERED KITE.

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

TABLE 6

FREQUENCY OF PERMANENT (PERM.) AND TEMPORARY (TEMP.) DESERTION BY TERRITORY-HOLDERS ACCORDING TO MATING CLASS AND DURATION OF OCCUPATION IN THE BLACKSHOULDERED KITE.

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

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

Although some short temporary desertions were probably not detected, many others evidently lasted for substantial periods. Those by mates lasted an average of 35,7 days (S.D. = 16,1 days) and those by territory-holders 35,2 days (S.D. = 22,9 days). Un-

paired territory-holders deserted for longer periods ($\bar{x} = 39,6$ days; $n = 23$) than paired and breeding territory-holders ($\bar{x} = 25,2$ days; $n = 10$; Mann Whitney $U = 149$; $p < 0,05$).

Occupancy

There was great variation in the length of time kites were resident. This section describes the variation and attempts to relate it to social activities and food supply. Mates were usually resident for short periods (Table 5); 33 (59%) stayed less than

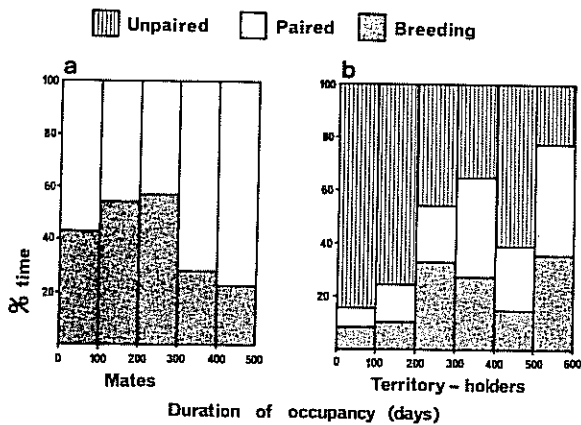


FIGURE 6

The percentage time spent by Blackshouldered Kite mates (a) and territory-holders (b) as unpaired, paired or breeding residents; calculated from data in Tables 5 & 6.

50 days and only five (9%) more than 200 days. Unlike territory-holders (see below), occupancy by mates was not directly related to the proportion of time spent breeding (Fig. 6a). Instead, mates seemed to show two trends, one of intense breeding activity among short-term birds, and the other of little breeding by long residents. The second trend was shown by nine mates resident for longer than 150 days; there was a significant inverse correlation between "occupancy" and "percentage time breeding" (Spearman's $r_s = -0.75$; $p < 0.025$). However, the first trend was not confirmed by comparing the same variables for 47 mates resident less than 150 days (Spearman's $r_{47} = +0.20$; NS). In spite of these inconclusive tests, further data in Table 7 suggest at least two categories of mates could be identified: 1) short to medium-term birds resident only while breeding or while prospects for breeding were probably favourable, and 2) long-term mates that spent little time breeding. The contrast between these groups was emphasized by the performance of several mates. From November 1977 to February

1978 little breeding occurred (Mendelsohn in press), yet five mates remained throughout this period and then started breeding in March 1978. ♀68, in particular, showed how a mate changed groups. In 7½ months before March 1978 she copulated only occasionally with ♂5. Then on 21 March 1978 she deserted and paired with ♂49. They started breeding activity that same day and four days later started a nest; this was abandoned after 10 days of building. They then copulated and displayed to nest sites sporadically, and after 16 days started a new nest. This nest, too was abandoned. On 5 May 1978 she was back with ♂5 and remained with him until at least 30 September 1978. She spent 85% of her 54 days with ♂49 breeding, but only 9% of 367 days breeding with ♂5.

Like mates, most territory-holders were resident for short periods (Table 6). Forty-four (73%) were resident for less than 200 days, but their residence comprised only 28% (2 557 bird-days) of the total time spent by territory-holders. The remaining 16 birds (27%) spent 6 476 bird-days (72%). Two territory-holders even occupied and vigorously defended territories for less than five days (e.g. Fig. 2). Three territory-holders were resident for longer than the 579-day census period. There were many intermediates between these extremes and breeding was observed in all groups (Table 6; Fig. 6b).

The longer a territory-holder was resident the greater the proportion of time it spent paired and breeding (Fig. 6b). For data in Table 6, there were positive correlations between "occupancy" and "paired bird-days/unpaired bird-days" (Spearman's $r_s = +0.83$; $p < 0.025$), and between "occupancy" and "breeding bird-days/total non-breeding bird-days" (Spearman's $r_s = +0.77$; $p < 0.05$).

Long-term territory-holders also had a greater number of mates than short-term territory-holders (Table 8a). Ten of the 12 kites with more than one mate were resident for longer than 300 days. Table 8b compares the occupancy of mates paired with territory-holders resident for different periods. These data show that mate occupancy varied greatly in relation to that of the territory-holders they partnered. Specifically, percentages in Table 8b indicate that the occupancy of a mate was not proportionately related to the occupancy of its

TABLE 7

NUMBER OF MATES AND PERCENTAGE TIME OF TOTAL OCCUPANCY SPENT BREEDING IN THE BLACKSHOULDERED KITE. ONLY MATES RESIDENT FOR 30 DAYS OR LONGER ARE INCLUDED.

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

TABLE 8

- (a) BLACKSHOULDERED KITE TERRITORY-HOLDERS GROUPED ACCORDING TO HOW LONG THEY WERE RESIDENT AND THE NUMBER OF MATES THEY PAIRED WITH.
 (b) COMPARISON OF HOW LONG MATES WERE RESIDENT WHILE PAIRED WITH TERRITORY-HOLDERS RESIDENT FOR DIFFERENT PERIODS.

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

TABLE 9

THE HUNTING SUCCESS OF BLACKSHOULDERED KITE TERRITORY-HOLDERS AND MATES RESIDENT FOR DIFFERENT PERIODS. SEE MENDELSON (1982a) FOR EXPLANATION OF HUNTING TERMS. +p<0,1; ++p<0,05; +++p<0,005; ALL OTHER COMPARISONS NOT SIGNIFICANT.

Territory-holders							
Occupancy group (days)	Perched-hunting			Hovering			
	Minutes Observed	Min./ all strikes	Min./kill	Minutes Observed	Min./ all strikes	Min./kill	Hovers/ descent (no. descents)
1—150	606	12,6+++	60,6+	332	9,2	30,2	6,94 (77)
151—300	1262	21,8+++	157,7	297	10,6	59,4	7,88 (26)
301—500	1309	30,4	145,4+	565	9,6	29,7	7,95 (155)
501—600	2325	28,3	178,8	625	7,8	36,8	6,40 (165)
Mates							
1—100	395	32,9	131,7	182	13,0	22,7++	5,8 (71)
101—500	1978	21,5	94,2	541	21,6	60,1++	6,8 (130)

territory-holder partner. The greater proportion of time spent paired by long-term territory-holders was therefore largely due to their greater number of mates, and not because their mates remained for long periods.

Since kites abandoned territories when food supply was poor (Table 4), I expected hunting

success to be directly correlated with occupancy. Tests of several measures of hunting success (Table 9), however, do not support this prediction, but rather suggest that short-term residents had better success than other kites. The hunting success of territory-holders deserting their territories at different frequencies was similarly compared (Mendelsohn 1981), but the results were inconclusive.

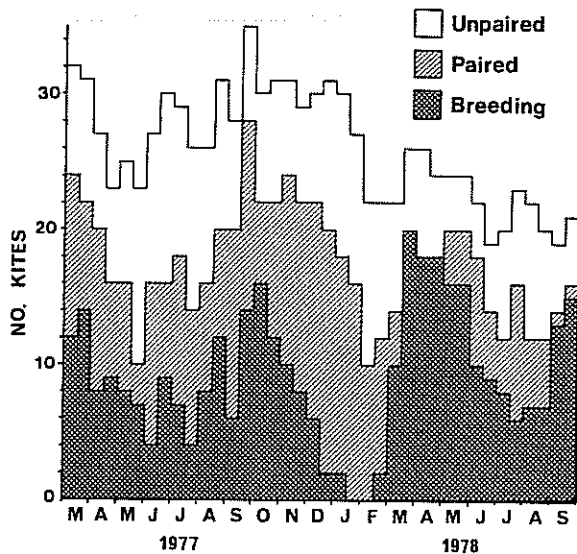


FIGURE 7

Half-monthly counts showing the total number of Blackshouldered Kites resident and in each mating class.

Population dynamics

In 38 half-month counts population size varied between 19 and 35 kites with a mean of 26,0 (S.D. = 4,2 kites) (Fig. 7). The numbers of paired (\bar{x} = 17,6; S.D. = 4,2; range 10-28) and breeding (\bar{x} = 9,4; S.D. = 5,2; range 0-20) kites present each half-month also varied substantially. There was an average of 17,1 territory-holders in the study area (S.D. = 2,8; range 12-22). There were 124 arrivals and 135 desertions during the study, or an average 3,3 new birds and 3,6 desertions each half-month. In a mean population of 26 kites, therefore, about 13% of residents were new and 14% deserted each half-month. These rates varied with more arrivals and desertions in 1977 than in 1978 (Figs 4 & 5).

In 1978 the population was generally smaller and the population of paired and breeding kites greater than in 1977 (Fig. 7). Factors affecting increases and decreases have been considered previously (Table 4). However, neither the percentage of the population paired (Spearman's $r_{19} = +0,15$; NS) nor the percentage breeding (Spearman's $r_{19} = -0,29$; NS) was significantly correlated with population size. Significant correlations between these variables were found for certain periods only. For example, "population size" and "percentage of kites paired" were positively correlated between March 1977 and February 1978 (Spearman's $r_{12} = +0,80$; $p < 0,005$).

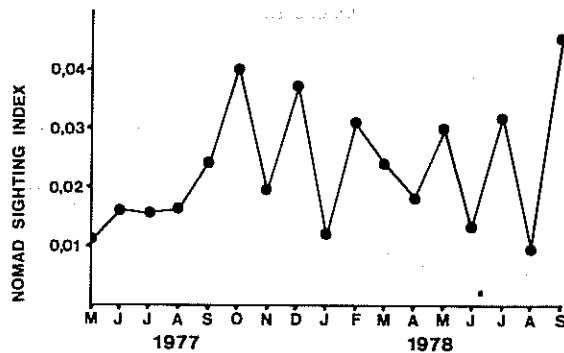


FIGURE 8

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

Population size and food supply Mendelsohn (1982a) were not positively correlated; instead they may have varied inversely (Spearman's $r_{17} = 0,38$; $p < 0,1$), with the population low when food was abundant.

Three adult residents were found dead and a fourth probably died. The last bird was often seen perched with drooped wings and closed eyes during the last week before disappearing. It was also abnormally tame compared with its previous reactions. These four birds represent about 4% of the 102 residents recorded over 19 months. Since some dead birds were certainly not found, a 5-10% mortality rate among adults while resident may be a reasonable estimate. However, adults probably suffered a higher mortality rate as nomads because of their poor condition (see *Movements*). Seven (26%) of 27 young birds died between leaving the nest and becoming independent (Mendelsohn 1981).

Movements

Ninety nomads were seen in the study area between May 1977 and March 1978. Those that intruded on occupied territories were rapidly repulsed (Mendelsohn 1981). I observed one nomad cross three territories while flying a distance of 6 km.

Sixteen of the nomads were marked and three of these were seen in the same place more than once. One nomad was caught in area J (Fig. 1a) on 22 February, resighted after 19 days and again 30 days later in area H, recaptured eight days later in area J, and finally resighted four days later in area H. These records suggest that movements by nomads were not random.

An index of the number of sightings of nomads

TABLE 10

THE NUMBER OF MOVEMENTS BY BLACKSHOULDERED KITES ACCORDING TO THE DISTANCE BETWEEN CAPTURE AND RECAPTURE OR RESIGHTING. COLOUR-MARKED KITES RESIGHTED IN THE SETTLERS STUDY AREA ARE NOT INCLUDED IN THESE DATA.

Distance (km)	<2	2-10	11-30	31-100	>100	Total
No. of records	25	23	14	9	11	82

each month (Fig. 8) was inversely correlated with frequencies of desertions by mates and territory-holders (Fig. 5b & d) (Spearman's $r_{17} = -0.57$; $p > 0.01$; and -0.55 ; $p > 0.025$ respectively). Most nomads were therefore seen in months when few residents were deserting. The nomad index was, however, not significantly related to indices (as in Table 4) of new mates, new territory-holders, pairs copulating, pairs breeding, food supply, or population size (Fig. 7). In most cases, though, levels of significance were to $p < 0.1$, suggesting that the presence of most nomads was positively related to good feeding and breeding conditions.

The weights of nomads were significantly lower than those of residents (Mendelsohn 1981). One bird weighed 255 and 271 g as a resident and 212 g as a nomad. Another weighed 246 g as a resident and 185 g as a nomad, while a third bird weighed 273 and 231 g while resident and 12 days later 209 g as a nomad.

Deserting territory-holders usually became nomads. Ten territory-holders were seen as nomads before or after being residents, and none of the territory-holders occupied more than one territory during the study. By contrast, many deserting mates may not have become nomads. Only two mates were ever seen as nomads and, after deserting, seven mates moved immediately to other territories. These seven desertions form 11.5% of all desertions by mates, and other mates probably paired immediately on territories outside the study area.

Table 10 shows distances between ringing and recapture or recovery for 82 kites. Distances of less than 2 km probably indicate that the birds were recorded again on the same territories. Long-distance movements are shown in Fig. 9; the four longest were 656, 810, 859 and 1 311 km. Most movements were by kites ringed as adults or sub-adults; only three birds in Table 10 were ringed as nestlings and two as possibly dependent young.

DISCUSSION

Male strategies

Males normally established and maintained

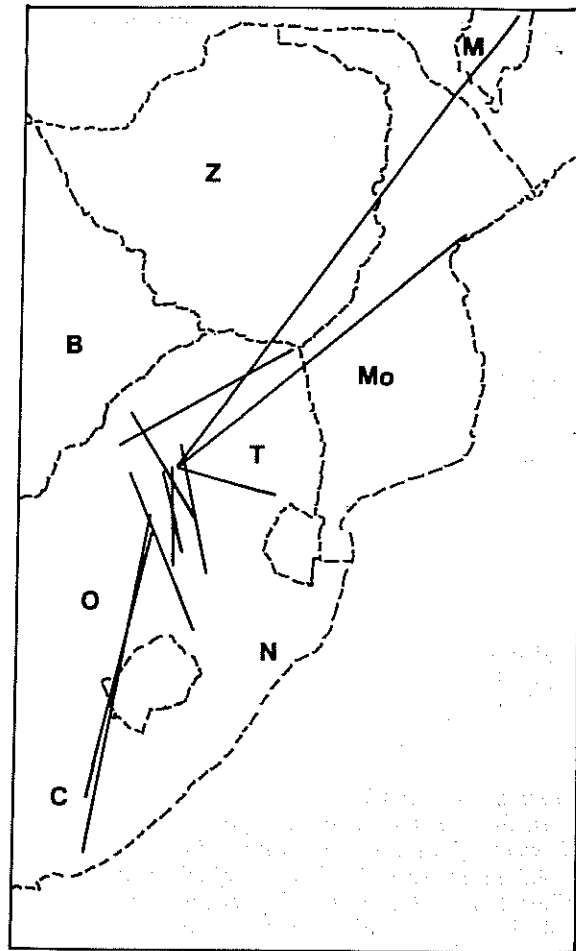


FIGURE 9

Movements of >100 km of Blackshouldered Kites in southern Africa, as shown by ringing recoveries. B—Botswana, C—Cape, M—Malawi, Mo—Mozambique, N—Natal, O—Orange Free State, T—Transvaal, Z—Zimbabwe.

occupancy of territories (Table 1 & 2). Similar behaviour has been recorded for other raptors with males establishing territories before females arrived, being more attached to territories while not breeding and returning more frequently to the same areas each breeding season. These features have been recorded in at least 14 species of the genera *Milvus*, *Circus*, *Hieraaetus*, *Buteo*, *Pandion* and *Falco* (Brown & Davey 1978; Enderson 1960; Green 1976; Newton 1979; A. C. Kemp pers. comm.). Males of these species and of Blackshouldered Kites feed their females while breeding (Mendelsohn 1981).

By establishing territories early, males probably gain more experience of the best hunting areas and this may improve their ability to provide sufficient food for females and young. A good food supply may also allow the pair to start breeding immediately after pair formation; pairs starting to breed earliest usually have the highest success (Drent & Daan 1980; Mendelsohn 1981). It may therefore be significant that in the two pairs formed by males joining resident females (Table 2) breeding started only after delays of 12 and 15 weeks.

Some male kites apparently arrived with females and established territories (Table 2). Similar behaviour has been noted in Pallid Harriers *Circus macrourus*, Black Kites *Milvus migrans*, Peregrines *Falco peregrinus* and American Kestrels *F. sparverius* (Balgooyen 1976; Cade 1960; Desai & Malhotra 1979; Lundevall & Rosenberg 1955). Some of these records, and those for kites, may be inaccurate in failing to recognize small differences in the arrival times of males and females. Nevertheless, the observations do show that males could occasionally pair without long periods of previous experience. It would seem more efficient for males and females to search for territories independently, and for either to pair with any appropriate unpaired residents they might find. It might also be important for lone males or females to pair with residents that have already tested the feeding quality of their territories.

Several observations indicated that males occupied territories for as long as feeding conditions permitted. Firstly, they usually deserted when their food supply was poorest (Table 4). Secondly, deserting males became nomads and, since nomads were in poorer condition than residents, it is probable that food shortages forced them into this condition. Thirdly, sustained occupancy was associated with increasing social success in pairing and breeding (Fig. 6b), these in turn being related to good food supply because unpaired kites had the poorest and breeders the best feeding success (Mendelsohn 1982a). Finally, deserted territories were normally re-occupied quickly (see *Territoriality*) in contrast to several smaller areas that were never occupied by kites (Fig. 1a). These vacant areas consisted largely of cultivated fields which supported few small mammals (Mendelsohn 1982b).

However, in contrast to these observations, data on hunting success (Table 9) suggested that short-term males had at least equal, if not better feeding conditions than longer-term residents. One explanation may involve the positive correlation between occupancy and territory size (see *Territoriality*). Long-term males might have been able to counter local food shortages by hunting elsewhere on their larger territories. Their territories would thus have provided more stable feeding conditions than those

of short-term residents. Short-lived territories may have been occupied only during periods of high prey availability. A further explanation is that short-term males formed part of a nomadic group of kites that sought mainly rich, eruptive food sources (see *Overall strategies*).

The rapid re-occupation of deserted territories and the frequent sightings of nomadic males suggested that territories with good feeding conditions were at a premium. However, males evidently also selected territories because some areas remained vacant, the movements of nomads were not random, and males visited areas they later occupied. These observations suggest that nomadic males assessed the feeding conditions of several areas before settling. The indiscriminate occupation of vacant areas would have been inefficient because there were probably more unsuitable than suitable vacant areas.

Temporary absences may have been "exploratory" trips for males searching for better territories. Similar trips with perhaps the same function have been noted for Prairie Warblers *Dendroica discolor* (Nolan 1978). Alternatively, males, especially unpaired ones with a poorer food supply than others (Mendelsohn 1982a), may simply have deserted as a result of food shortage and then returned after failing to find suitable territories.

Female strategies

The behaviour of males and females probably differed mainly because females were less spatially restricted than males. An excess of males in the population meant that females had greater opportunities for settling than males. Thus, they spent shorter periods on each territory, deserted more often, returned to territories less frequently (Tables 5 & 6), and spent less time as nomads than males. These observations could also be explained by females having poorer hunting success than males, and therefore experiencing more frequent food shortages which could have caused them to desert. However, this hypothesis is not supported by a comparison of hunting success by paired males and females (Mendelsohn 1982a).

Females seldom established territories and probably did so only when food supply was poor and breeding impossible. If prey later became abundant, lone females could attract males and attempt to breed. The five females that maintained territories alone for long periods all paired when other pairs were starting to breed and feeding conditions were improving.

The presence of paired females appeared to be related to breeding and they probably moved between males in search of the best breeding prospects. These conclusions are based on several observations. Firstly, most females arrived and

paired when the greatest proportion of pairs was starting to breed (Table 4). The link between pair formation and breeding was, however, not invariable; some long-established pairs started breeding and some recently-established pairs did not attempt to breed. Secondly, rapid movements by females between males in the study area seemed to be associated with breeding. In each case the female had had poor success with one male and immediately attempted breeding with a new mate. Thirdly, females were paired only when diurnal prey was abundant (Mendelsohn 1982a), this being a probable prerequisite for breeding. Similarly, females were paired only when prey availability was greater than that needed for their own energy requirements. By feeding substantially on nocturnal rodents (active at dawn and dusk), deserted, lone males showed that there was still sufficient food to support non-breeders. Finally, females usually deserted once their chicks had left the nest, and then probably paired and attempted to breed with new males (Mendelsohn 1981).

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

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

I have suggested that there were two categories of breeding behaviour by mates, one in which they spent most of their time breeding, while in the other they spent long periods as non-breeding residents. There were many intermediates (Tables 5 & 7) and these categories may better be considered extremes. However, the behaviour of long-term mates appeared distinctive in that, against expectations, they did not go off in search of males on other territories. To this category may be added the performance of

females that spent long periods as unpaired residents, since they too could have searched elsewhere for better breeding prospects. Possibly long-term female residents were caught in a "bind", with feeding conditions good but not enough to attempt breeding. Evidence for this comes from the better hunting success and greater proportion of diurnal prey of paired versus unpaired kites (Mendelsohn 1982a).

Short-term mates apparently had better hunting success than longer residents (Table 9). This result is hard to explain, but, as with males, may suggest that short-term residents remained paired only under conditions of above-average food supply (see *Overall Strategies*).

Sex ratio and mating system

The ratio of males to females during the study was about 3:2. This ratio may not have been representative of kite populations in general, since weight data for 816 birds (Mendelsohn 1981) indicate roughly equal numbers or only slightly more males. Sex ratios probably also varied according to food supply. During lean periods the majority of residents would probably have been males as unpaired residents. With abundant prey, and most of the residents paired, the ratio would have approached parity.

Elsewhere (Mendelsohn 1981) I discuss relationships between successive polyandry and multiple

brooding by kites. Elsewhere (Mendelsohn 1981) I discuss relationships between successive polyandry and multiple brooding by kites. Females deserting dependent young and pairing with new males could have bred three times each year. The parental investment (Trivers 1972) of males was greater than that of females because they spent longer feeding chicks. Evidently, one parent could care for the flying young as effectively as two. Furthermore, any reduction in success caused by one parent deserting was presumably balanced by advantages (for the female) of another breeding attempt. With this background, it is of interest in this paper to examine the relationships between female desertion, the site tenacity of males, and the greater number of males than females. Three hypotheses are suggested.

Traditionally sex ratios were thought to determine mating systems (Lack 1968) and this could explain why females deserted. With a surplus of males, females could pair with those males that had remained unpaired. If females deserted, males were obliged to remain and complete the breeding effort, so as to avoid complete failure. In this view, then, the sex ratio determined that females could desert and that males remained resident.

Alternatively, selection could primarily have favoured the continued occupation by males

(Lundberg 1979). Since territories with good feeding conditions were in short supply, breeding males on good territories may seldom have found better alternatives. Males may also have remained resident because they hunted most efficiently in the areas where they had most experience. Sex ratios and repeat breeding by females may therefore have been incidental; females deserted because only one bird could leave. Interestingly, high levels of paternal care in most animals are associated with male territoriality (Ridley 1978).

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

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

The suggestion that either the skewed sex ratio or site-tenacity by males could provide females with the opportunity to desert may be equally probable. However, deserting females could only attempt breeding again if there were surplus males, and if feeding conditions were suitable for breeding again. This latter aspect may be the one most relevant to kites because unpredictable changes in rodent densities (Mendelsohn 1982a, b) may often have provided suitable conditions for repeat broods (Mendelsohn 1981). Temporal changes in food supply that allow females to breed again may predispose birds to polyandry (Graul *et al.* 1977), but relatively few raptors exploit prey populations that show the necessary unpredictable increases or sustained high densities.

Territoriality

Territory size and food supply vary inversely in most animals (Ebersole 1980; Hixon 1980). However, kite territories became larger (Fig. 3) as prey density increased during the study (Mendelsohn 1982a). Similar trends are reported for other birds of prey and carnivores defending large territories (Brown & Watson 1964; Lockie 1966; Southern & Lowe 1968). This suggests that large predators maximize the area they defend and ensure greater reserves for periods of food scarcity (Hixon 1980). The upper limits to territory size are probably determined by energy constraints involved in defence against competitors.

However, very high densities of kites have been reported at rich food sources (see *Overall strategies*), suggesting that at some threshold of food supply, territoriality, as observed at Settlers, breaks down. During a period of escalating prey density residents would presumably attempt to prevent new birds from establishing territories. Newton *et al.* (1977) suggest that aggression may be reduced when food is abundant. Alternatively, a great number of invading birds attracted to a rich food source may make it energetically impossible for residents to defend large areas.

Overall strategies

Most studies of birds have considered the social and spatial organization of species, or at least populations, as characteristic and fixed. Even genera and families are often said to have set mating systems and patterns of dispersion (Lack 1968). While such generalizations may sometimes be valid, many studies of marked birds now show a high degree of individual variability in these behaviour patterns (Birkhead 1981; Emlen 1978; Hamerstrom 1969; Newton & Marquiss 1982; Nolan 1978). This is true even of Holarctic birds that migrate, establish territories and breed at set times of the year. This study has shown a similar high degree of individual variation in the behaviour of kites. For example, kites varied in their occupancy as residents and in the number of times they left an established territories (Tables 5 & 6), males and females sometimes exchanged roles (Table 1), not all females deserted fledged young to pair with other males, and kites roosted either communally or alone (Mendelsohn 1981).

My impression of social and spatial behaviour at Settlers was one of relative, or at least attempted, stability. Kites, especially those males that spent a high proportion of their time paired or breeding, were dispersed on large territories and showed considerable site-tenacity. Many females, too, probably remained as long as feeding and breeding conditions were favourable. However, the majority

TABLE 11

TWO SETS OF BEHAVIOUR STRATEGIES ADOPTED BY KITES AND THE ENVIRONMENTAL CONDITIONS TO WHICH THEY ARE PROBABLY RELATED. SEE TEXT FOR FURTHER EXPLANATION.

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

of residents were short-term territory-holders or mates and their performance did not seem to depend on prey abundance alone. Indeed, it seems that kites show two main sets of life-history tactics, one described as "stable" and the other as "unstable" (Table 11). The "stable" strategies were typical of the behaviour of many kites at Settlers, while "unstable" behaviour is shown vividly by the records of several observers.

In August 1975 Collett (1982, *in litt.*) counted 200-300 kites hunting over 30 ha of cultivated land in the eastern Cape (an equivalent density in the Settlers study area would have involved 16 000-25 000 birds). The kites arrived together, stayed for a week, and suddenly departed. This area normally held two pairs of kites. A high density of *Rhabdomys pumilio* and another rodent (probably *Praomys natalensis*) was noted at the time. Similar irruptions of kites during rodent plagues have been observed in the Transvaal (Malherbe 1963; Skead 1974; A. C. Kemp pers. comm.), Zimbabwe (J. Cooper *in litt.*), and Senegal (Morel & Poulet 1976). Irruptiveness is also said to occur in India (Brown & Amadon 1968).

While many other raptors also mass at sporadic rich food sources (Brooke *et al.* 1972; Galushin 1974; Newton 1979), most occupy large territories when breeding. Kites differ from these species by also

breeding at high densities. Malherbe (1963, pers. comm.) found at least eight pairs of kites breeding in an area of about 6 km² that usually held one pair. Vernon (SAOS nest record cards) and Madden (1977) found occupied nests 140 and 200 m apart. A. C. Kemp (pers. comm.) found three active nests in an area with a 200-m radius. These nest densities were far greater than any seen at Settlers, where the nearest active nests were about 900 m apart.

Communal roosting may be another aspect of nomadic and irruptive behaviour since these roosts could serve as "information centres" (Ward & Zahavi 1973). Kites usually formed communal roosts when food supply was poor at Settlers and information from these roosts may have helped birds in moving to more profitable feeding areas (Mendelsohn 1981).

The behaviour described as "stable" and "unstable" probably depends on different feeding conditions (Table 11) similar to those described for other nomadic and site-tenacious birds (Andersson 1980; Galushin 1974; Maclean 1973; Newton 1972, 1979). Populations of several rodents (mainly *Praomys natalensis*, *Tatera leucogaster* and *Lemniscomys griselda*) fluctuate markedly and unpredictably in southern Africa (Choate 1972; Coetzee 1975; Mendelsohn 1982b; Van der Merwe & Keogh 1970; Wilson 1970). Nomadic kites probably gather at plagues of these species, while stable residents depend on rodent populations that remain relatively even. The number of available prey species may also influence the feeding conditions of kites. Those feeding on one or two species may experience greater changes in food supply than those that depend on several different sources of prey. Unpaired kites at Settlers demonstrated this by preying largely on *Praomys natalensis* (Mendelsohn 1982a) and being more erratic residents than other kites (Table 6). Paired and breeding kites caught roughly equal numbers of three species and were stable residents for long periods.

The three other *Elanus* kites also feed mainly on rodents (Mendelsohn 1982a) and show close parallels to the behaviour of Blackshouldered Kites. Whitetailed Kites *E. leucurus* and Blackwinged Kites *E. notatus* may roost communally and mass and breed at rich food sources, while at other times they defend large areas (Brown & Amadon 1968; Dixon *et al.* 1957; Hayward & Macfarlane 1971; Hobbs 1971; D. G. W. Hollands *in litt.*; Waian 1973). The Letterwinged Kite *E. scriptus* is an arid-zone species that has specialized in the kind of nomadism, irruptiveness and sociability sometimes shown by the other species. It appears always to move in flocks, roosts communally, and breeds in loose colonies (Beruldsen 1971; Holland 1977;

Parker 1971). The species breeds only during rodent plagues and great numbers apparently starve to death in the absence of high prey densities (Hollands 1979; Klapste 1979).

The two sets of strategies in Table 11 show several features suggestive of *r*- and *K*-selection (Pianka 1970). While they may only be opposite ends of a spectrum of variation with many intermediate conditions, they are useful reference points and show that kites use different patterns of behaviour to survive and breed under a variety of feeding conditions. Real (1980) has shown that animals facing uncertain conditions evolve diverse strategies. This would appear to be true of kites where the nature of rodent population dynamics is often unpredictable; densities may vary erratically or remain reasonably stable. Nomadic and sociable behaviour, as responses to erratic prey densities, probably evolved in fairly dry conditions where rainfall is unpredictable. Similar behaviour is shown by many arid-zone birds (Maclean 1973; Serventy 1971). Rodent breeding is strongly affected by rainfall and plant growth (Perrin 1980; Taylor & Green 1976) and rodent densities are therefore likely to be erratic in dry areas. "Stable" strategies by contrast, probably evolved in wetter areas where rainfall is more predictable and prey densities show more regular and less drastic changes. The wet and dry conditions suggested here are probably both experienced by kites. The species occupies a wide range of habitats with varying rainfall regimes and, in southern Africa, wet and dry periods alternate about every ten years (Tyson & Dyer 1978). Thus the variety of rainfall regimes, both geographically and temporally, could be the ultimate factor favouring the evolution of diverse strategies in kites. If kites lived under dry conditions alone, they would probably show only the kind of behaviour seen in the highly nomadic and sociable Letterwinged Kite.

Crop cultivation may also affect the behaviour of kites by adding heterogeneity to an area. The Settlers study area was probably as climatically unstable as most parts of the bird's range. However, with 72% of the area under a variety of crops, prey availability may have been more stable than in other homogeneous areas (W. R. Tarboton pers. comm.).

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