

PARENT-OFFSPRING RELATIONS DURING THE POST-FLEDGING DEPENDENCY PERIOD IN THE BLACK KITE (*Milvus migrans*) IN JAPAN

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ABSTRACT.—The transition to independence of the juvenile black kite (*Milvus migrans*) was investigated in four families near the tip of Nagasaki Peninsula in Japan, where the kite is resident. The juveniles fledged at 58–63 d of age, and they became independent at 46.8 d on average after fledging. The frequency of begging and approaches by the juvenile toward the parents did not change through the post-fledging dependency period. With respect to parental effort, the frequency of parental approaches toward the juvenile and the parental feeding frequency decreased with juvenile age. Furthermore, the parents in the two families studied in detail avoided juvenile approaches, and the female parent of one family dived her offspring two d before juvenile independence. Thus, the parents decreased the parental care over time. This suggests that decreases in parental effort are related to the juvenile independence of the resident black kite.

KEY WORDS: *black kites; juvenile independence; Milvus migrans; parental care; post-fledging dependency period.*

Relación padre-cría durante el período de dependencia post-volantón en *Milvus migrans* en Japón

RESUMEN.—Se estudió la transición a la independencia en los juveniles de *Milvus migrans* de cuatro familias, cerca del extremo de la península de Nakasaki en Japón, donde esta ave es residente. Los volantones juveniles de 58 a 63 días de edad, llegaron a ser independientes en un promedio de 46.8 días, después de volar. La frecuencia con la que los juveniles se acercaron a sus padres para pedir alimento no cambia a través del período de dependencia post-volantón. Respecto al esfuerzo parental, estos disminuyeron la frecuencia de alimentación a los juveniles a medida que aumentaba su edad. Así, el cuidado parental decrece en el tiempo, patrón que puede estar relacionado con la subsecuente independencia de los juveniles.

[Traducción de Ivan Lazo]

In many bird species, juvenile birds depend on their parents for some period even after leaving the nest (Ashmole and Tovar 1968, Alonso et al. 1987, Kopachena and Falls 1993 and references therein). Relations between parents and offspring during this transition to independence have been studied in some raptors. According to these studies, the independence of juveniles is brought about largely by parental aggression toward juveniles (Alonso et al. 1987; *Aquila heliaca*), by decreasing parental efforts toward juveniles (Wyllie 1985; *Accipiter nisus*, Ceballos and Donazar 1990; *Neophron percnopterus*), or abrupt dispersal of juveniles still under parental care (Walker 1987; *Aquila chrysaetos*). A breakup of a family tie is influenced by migration in European breeding populations of black kites (*Milvus migrans*), which

winter in Africa (Bustamante and Hiraldo 1990). In Japan, however, the black kite is resident. Therefore, one can expect either of the following transitions to juvenile independence: (1) parents initiate the process (e.g., by parental aggression or a reduction in parental effort), or (2) juveniles become independent without a decrease in parental care. The purpose of this study is to examine parent-offspring relations during the post-fledging dependency period in the resident black kite, and to describe the factors leading to juvenile independence.

MATERIALS AND METHODS

During June–August of 1986, 1991 and 1992, four families (families A and B in 1986, family C in 1991, and family D in 1992) were studied near the tip of Nagasaki Peninsula (32°30'N, 129°45'E). In this study area, pairs of kites maintain their territories through the year (Koga and Shiraishi 1994). Since the above four families occupied their territories at separate sites, we regarded these pairs as different. The topographic relief is relatively steep with

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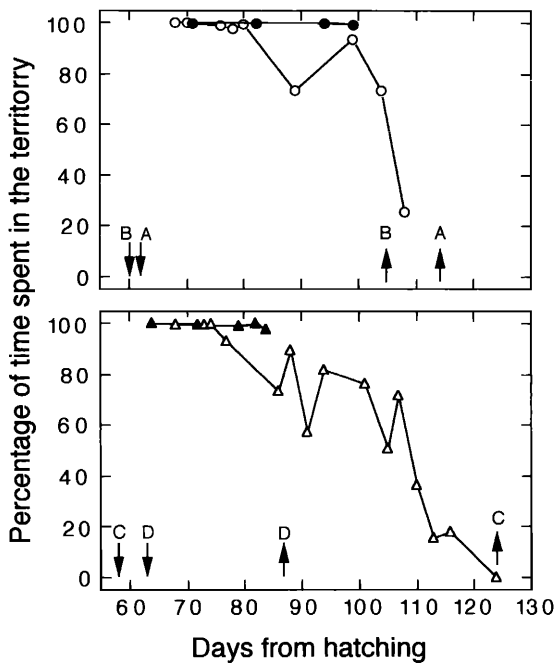


Figure 1. Percentage of time the juveniles spent in the natal territories, according to age of the first hatched young. ○—○, the juvenile of family A; ●—●, the juvenile of family B; △—△, the juvenile of family C; ▲—▲, the juvenile of family D. Fledging age is represented by (↓) and independent age by (↑). A–D represents the juveniles of families A–D, respectively.

an elevation of ca. 200–260 m. The main tree species in the study area are *Castanopsis cuspidata* and *Quercus glauca*, with small stands of *Q. acutissima*. In this area, black kites usually foraged in two fishing ports (about 3 km away) and on coasts or shores, and breeding individuals defended a radius of ca. 50–100 m centered on their nesting trees.

The date when the first egg was laid was 4 March in family A, 10 March in family B, 21 March in family C and 1 April in family D. The clutch size was two in families A and C, and one in family D. One nestling hatched in families A, B, and D, two nestlings hatched in family C, and all nestlings fledged. All the nestlings studied were radiotagged and marked with a colored band about 10 d prior to fledging. The nestling of family D was also fitted with a colored tail streamer (Konrad and Gilmer 1986). Nestlings of families A and B were fitted with radiotransmitters (50–53 MHz range) attached by a backpack harness (Kenward 1985). The transmitter and harness weighed approximately 30 g (ca. 3% of the body weight). Because the transmitters failed ca. 3 wk after the attachment, data on activities of the juveniles out of their natal territories were not obtained. Nonetheless, transmitters were useful markers for individual identification

during watching in the territories. Juveniles of families C and D had transmitters operating in the 144–146 MHz range (ca. 14 g, Architect Co., Tokyo) attached to their backs with a fast-drying glue. Sex distinction and individual identification of the parent birds were based on the color of body feathers (usually light in males, and dark in females) and the plumage characters (e.g., slightly different patterns of the breast feathers, white feathers around the base of the bill, or broken flight feathers), respectively.

Field work started after fledging (ranging from mid-June to early July), and it was ended when the juveniles became independent: the day of independence was defined as the first time that the juveniles were not seen in the natal territories during observation. In families A and B, a half-day observation was made 5 and 10 d after independence, and the juveniles were not found in their natal territories. In family C, the elder juvenile provided all its own food and roosted out of the territory before the independence day (see the Results section for the death of its younger sibling). The juvenile of family D was pursued on the first and fifth days after it left the home territory, and then radio signals were monitored around the territory every morning and evening for about a month. As a result, it seemed that the juvenile did not return to the parental territory, although it suddenly appeared near the natal territory 25 d after independence. Thus, our definition of independence may be acceptable.

On rainy days observations were not carried out because of difficulty in the identification of wet individuals. In our study area the rainy season extended from mid-June to mid-July. Consequently, intervals between observations were irregular (2–14 d, see Fig. 1). Observations were made through binoculars (8 × 30) and a telescope (25–40×). The duration of each observation was 5–7 hr between 0600 and 1900 H in families A and B, and 13–14.5 hr (from dawn until dusk) in families C and D. The number of observation bouts was nine in family A (49 hr), four in family B (24 hr), 16 in family C (221.6 hr), and seven in family D (98.1 hr).

Observed behaviors were recorded in a notebook in as much detail as possible or recorded on a tape recorder. The locations of the juveniles in families C and D were determined visually, then plotted on a map of a scale of 1:2500 or 1:25 000. If visual contact was lost, the juveniles were located by radio-triangulation. The daily total of durations of visual contact with the juveniles in families C and D was at least 522 min and usually more than 700 min. In the present analysis of parent-offspring relations, the following measures were used as variables indicating juvenile interest in maintaining contact with the parents, parental interest in maintaining contact with the juveniles, and parental effort to care for the juveniles.

Juvenile Interest. (1) Frequency of approaches by the juvenile (FAJ) toward the parents when at least one parent and the juvenile were present together (times/hr). A juvenile approach occurred when the juvenile flew to the parent(s) and landed usually ≤ 1 m of them. (2) Frequency of begging by the juvenile (FAB) when at least one parent and the juvenile were present together (times/hr). We regarded each behavioral sequence comprising various consecutive begging and silent periods as one begging activity. If different behaviors (e.g., preening) were observed

Table 1. The number of samples used for analyses of each variable.^a

FAMILY	FAJ	FBJ	FAP	NPE/FAJ	NPF	TSJ	TSP	TSF	HRS
A	9	9	9	— ^b	9	9	9	— ^c	— ^c
B	4	4	4	— ^b	4	4	4	— ^c	— ^c
C	14 ^d	14 ^d	14 ^d	12 ^e	16	16	9 ^f	12 ^f	12 ^f
D	5	5	5	5	5	5	5	7 ^g	7 ^g

^a See Materials and Methods for abbreviations.

^b The analysis was not conducted, owing to a small number of juvenile approaches (in many cases, less than three times per observation bout).

^c The sufficient data were not obtained, because of failure in transmitters.

^d The data from two observation bouts were omitted from the analysis, because the parents and juvenile were not present together.

^e The data from four observation bouts near the independent day were not used, owing to a small number of juvenile approaches (less than three times per observation bout).

^f Since it was impossible that the juvenile flight activities (TSF and HRS) and TSP near juvenile independence were measured at the same day, the sample sizes of these variables were smaller than the number of observations.

^g The data from two observation bouts after independence were added, to estimate the development of the flight ability more correctly

between two such begging sequences, we considered each begging activity to be a separate one.

Parental Interest. (3) Frequency of approaches (FAP) by the parent toward its juvenile when at least one parent and the juvenile were present together (times/hr). When the parent flew to a juvenile and landed within 1 m of it, we considered this to be a parental approach. (4) The ratio of the number of parental escapes from the juvenile (NPE) to that of juvenile approaches (FAJ). A parental escape occurred if the parent left a tree just before or ≤ 30 sec after the juvenile landed near the parent.

Parental Effort. (5) The number of parental feedings (NPF) per young per hr. We regarded as parental feedings when the parents tore prey and offered pieces of meat to the juveniles, when the parents transferred prey to their offsprings, or when the juveniles snatched prey held by the parents on a branch. Feeding of an unmarked, begging juvenile was observed twice 11 d after fledging of the first hatched young in family C. Although such feedings might make the adults waste their time and energy, we omitted these feedings from our data.

In addition to these variables, the total time spent by both the juvenile (TSJ) and at least one parent (TSP) in the parental territory was also recorded. Furthermore, the daily amount of time spent in flying by the juveniles (TSF) of families C and D was examined, and their home range sizes (HRS) were estimated using the minimum polygon method.

Since the first author conducted observations by himself, it was impossible to monitor simultaneously the behavior of the parents in the vicinity of the nest and that of the juvenile outside the territory. Moreover, in several observation bouts of family C, the parents and juvenile were not present together, or the number of juvenile approaches during watching was too small to create detectable changes in the ratio of NPE/FAJ. Consequently, the number of samples used for analyses of some variables in family C was smaller than that of observations conducted (Table 1). In family D, TSFs and HRSs were examined for additional days after independence to estimate the development of the flight ability more accurately.

For each family, we calculated simple linear regression correlation coefficients between age of the first hatched young and each of the variables. Further, to examine the relationship between age and each of the variables used to describe parent-offspring relations (FAJ, FBJ, FAP, NPE/FAJ and NPF) for all the families pooled together, we calculated partial correlation coefficients using multiple regression models of the form $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$, where Y was each of the five variables all of which were standardized, β_0 was a constant, β_1 was the coefficient for standardized age of the first juvenile (X_1), β_2 was the coefficient for the family groups (X_2) that were assigned scores. The scores were calculated using the following equation: $Sc = Ni - S/F$, where Sc was the score, Ni was the number of observation bouts in family i, S was the sum of all Ni, and F was the number of families examined. Correlation coefficients were computed also between age and logarithmic-transformed data on TSFs and HRSs for the juveniles of families C and D. Statistical significance was set at 0.05. Means were expressed with SD.

RESULTS

Activities of the Juveniles. Young black kites fledged at 58–63 d. The younger juvenile of family C died of unknown reason 25 d after fledging (83 d of age). Therefore, the analysis of juvenile activities in this family was based on the data obtained from the elder juvenile. The juveniles of families A, B and D became independent at 114, 105 and 87 d of age, respectively. The elder juvenile of family C attended the communal roost out of its home territory at 111 d of age, and then spent most time in resting and soaring out of the natal territory. This juvenile did not appear in the parents' territory on 124 d of age. The average length of the post-fledging dependency period was 46.8 ± 17.5 d ($N = 4$).

Table 2. Simple or partial correlation coefficients (r) between the age in days of young and the variables concerning the parent-offspring relation.

VARIABLE ^a	FAMILY	r	RANGE	PROBABILITY
FAJ	A	0.118	0-1.62	0.762
	B	0.936	0.31-0.53	0.064
	C	0.413	0.28-1.63	0.142
	D	0.328	0.44-0.91	0.590
	pooled	0.232	-1.33-1.99	0.209
FBJ	A	0.447	0-4.00	0.228
	B	-0.311	0.33-0.92	0.689
	C	0.180	0.59-2.90	0.539
	D	0.473	1.38-2.66	0.421
	pooled	0.04	-1.45-2.60	0.831
FAP	A	-0.693	0-1.25	0.039
	B	-0.972	0.52-0.92	0.028
	C	-0.927	0-0.84	<0.001
	D	-0.921	0.07-0.42	0.027
	pooled	-0.649	-1.05-2.44	<0.001
NPF/FAJ	C	0.968	0-1.00	<0.001
	D	0.908	0.27-0.67	0.033
	pooled	0.962	-1.74-1.51	<0.001
NPF	A	-0.652	0-0.80	0.057
	B	-0.030	0.35-0.67	0.970
	C	-0.833	0-0.63	<0.001
	D	-0.857	0.14-0.63	0.070
	pooled	-0.659	-1.31-1.95	<0.001

^a See Materials and Methods for abbreviations.

In families A and B, the juveniles did not forage during observation, but the 82-d-old juvenile of family B plucked leaves from a tree twice while in flight. In the family C juvenile, such a plucking behavior was occasionally observed from 86-105 d old ($N = 15$). This juvenile began foraging at 101 d of age, and captured 13 prey by itself during observations. The juvenile of family D was once observed plucking leaves 83 d after hatching. On the same day the juvenile picked up and ate one earthworm, yet it apparently depended on its parents for almost all food until it became independent.

Sufficient data on the development of flying ability were obtained only from the two juveniles of families C (the elder juvenile) and D, owing to failure in transmitters of the juveniles in families A and B and to the death of the younger juvenile in family C. TSFs of the elder juvenile in family C varied from 0.5-12 min before 74 d of age, and then increased

(303 min at the maximum, $r = 0.83$, $df = 10$, $P < 0.01$). The juvenile of family D devoted 4-14 min to flying until 82 d of age, and then increased TSFs (294 min at the maximum, $r = 0.89$, $df = 5$, $P < 0.005$). HRSs of these two juveniles also increased exponentially with their age (the juvenile of family C ranged from 0.05-423.5 ha, $r = 0.94$, $df = 10$, $P < 0.001$, and the juvenile of family D ranged from 0.7-119.5 ha, $r = 0.792$, $df = 5$, $P = 0.034$).

TSJs in families A and C decreased with age (family A, $r = -0.77$, $df = 7$, $P = 0.014$; family C, $r = -0.940$, $df = 14$, $P < 0.001$; Fig. 1). In contrast, the juveniles of families B and D devoted all or almost all of their time in their parents' territories until they gained full independence (family B, $r = -0.66$, $df = 2$, $P = 0.336$; family D, $r = -0.591$, $df = 3$, $P = 0.249$). FAJs and FBJs were not correlated with age even when each juvenile was considered separately (Table 2), indicating that the juvenile solicitation for food and juvenile interests in the parents did not decrease through the post-fledging dependency period.

Activities of the Parents. The parents of all the four families roosted in their territories during the study period. In families A and C, TSPs tended to decrease through the post-fledging dependency period (family A, $r = -0.85$, $df = 7$, $P = 0.004$; family C, $r = -0.85$, $df = 7$, $P = 0.004$), although a slight increase occurred around juvenile independence (Fig. 2). In contrast, there was no relationship between TSPs and juvenile age in families B and D (family B, $r = -0.60$, $df = 2$, $P = 0.403$; family D, $r = -0.43$, $df = 3$, $P = 0.472$). Nevertheless, the parents of the family B evidently decreased the time spent in its territory just before the juvenile independence.

Although both parents carried food for their juveniles, the male parent delivered most of the prey to the juveniles (males, 0.32 ± 0.11 prey/hr, $N = 4$; female, 0.04 ± 0.02 prey/hr, $N = 4$). The parents usually carried prey to the place where the juvenile perched (family A, $N = 15$; family B, $N = 11$; family C, $N = 51$; family D, $N = 11$), while the juvenile occasionally flew to the place where the parent landed with food (family A, $N = 2$; family B, $N = 1$; family C, $N = 15$; family D, $N = 15$). In family C, NPFs decreased with juvenile age (Table 2). NPFs in families A and D also tended to decrease during the post-fledging dependency period, although this tendency was not significant. When data from all of the pairs were pooled, a decrease in NPFs was apparent. The parents of families A and C stopped feeding 1 and 2 wk before the juvenile independence,

respectively. FAPs significantly decreased through time, even when each pair was considered separately. The avoidance of juveniles by parents was examined in families C and D in which the juveniles approached their parents more frequently than in the other two families. The ratio of NPE/FAJ was positively correlated with juvenile age. These results suggest that the effort of parental care decreased gradually during the post-fledging dependency period.

In families A, B and C, there was no evidence that the parents attacked their juveniles. In contrast, the female parent of Family D made steep dives (four occasions) at her juvenile 2 d before juvenile independence (85 d of age), when the juvenile began to increase its flying activities. Three of these dives occurred in succession when both the female parent and her juvenile soared together within the home territory. The fourth dive was directed at her juvenile perching on a branch. During these dives, the male remained perched on a branch and silently watched.

DISCUSSION

As observed in other birds (Morehouse and Brewer 1968, Moreno 1984, Alonso et al. 1987, Lett and Bird 1987, Ceballos and Donazar 1990), black kites, migrating from Europe to Africa, decrease the frequency of parental feeding around juvenile independence (Bustamante and Hiraldo 1990). However, because the decline in the feeding frequency is slight (a decrease of only 0.3 feedings/day, using the equation fitted by Bustamante and Hiraldo (1990)), reduction of parental effort is not a determining factor that leads to independence. It has been suggested that the initiation of migration influences a rupture of family ties (Bustamante and Hiraldo 1990). On the other hand, although the juveniles of Japanese black kites continued to solicit parental care through the post-fledging dependency period, the parents evidently reduced NPFs. In the absence of measurements of weight loss by the juveniles, this finding is not direct evidence that the juveniles did not receive sufficient food. However, in two families the parents cut off feeding. Furthermore, a decrease in FAPs in all the four families and an increase in the ratio of NPE/FAP in the two investigated families indicate that the parents became reluctant to look after their juveniles with time. Additionally, in one family juvenile independence occurred 2 d after parental aggression. Thus, our observations suggest that the juvenile independence in the resident black kite may be encouraged by decreased parental effort.

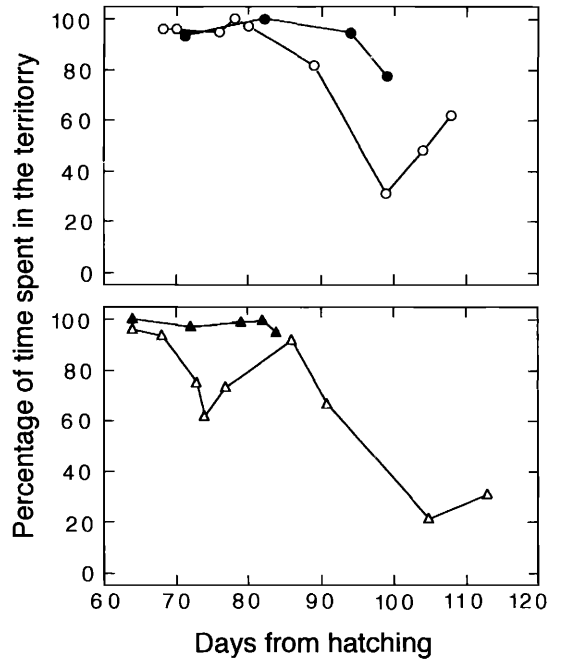


Figure 2. Percentage of time at least one parent spent in the territories, according to age of the first hatched young. O—O, the parents of family A; ●—●, the parents of family B; △—△, the parents of family C; ▲—▲, the parents of family D.

In black-capped chickadees (*Parus atricapillus*), parental aggression has been interpreted as a behavior to encourage juveniles to feed independently (Leonard et al. 1991). Davies (1976, 1978) has shown that in two passerine species juveniles become independent when they can obtain food more efficiently by self-feeding than by begging from their parents which decrease feeds. In contrast to this, it has been suggested that independence in marsh tits (*Parus palustris*) is initiated by juveniles themselves because it is more likely that juveniles dispersing earlier obtain territories as adults (Nilsson and Smith 1985, Nilsson 1990). Kenward et al. (1993) have indicated that juvenile goshawks (*Accipiter gentilis*) may disperse abruptly after maturation of hunting behavior, for there may be little advantage for juveniles to remain where there is an adult pair because of low adult mortality and decreasing food availability. In resident black kites the juveniles might not have pressure to leave the parents' territories early, unlike marsh tits and goshawks, because kites probably start to breed at 2–3 yr of age (Newton 1979), and

in our study area the birds fed mainly on discarded fish which obviously does not require complex capture techniques. On the other hand, such food habits may allow the parents to end their parental care without giving a serious disadvantage to the juveniles in flying ability.

Parents and offspring are expected to disagree about the amount of parental investment, and overt conflicts between them are predicted (Trivers 1974). As considered in other birds (Davies 1978, Alonso et al. 1987, Hiraldo et al. 1989, Ceballos and Donazar 1990), it is possible that parental aggression and decreased parental effort in black kites may be related to this parent-offspring conflict (but see Mock and Forbes 1992). However, the level of begging by juvenile black kites tended to be unchanged during the post-fledging dependency period, which is not consistent with the expectation from Trivers' theory, i.e., juveniles should solicit food more intensively when parents withhold prey. Since parental and juvenile behaviors are influenced also by various factors unrelated to parent-offspring conflict (see Clutton-Brock 1991, Mock and Forbes 1992), further studies are required in order to show whether parent-offspring conflict exists in this species.

In conclusion, although our results based on only four families should be regarded as preliminary, they suggest that decreases in parental effort may be the main factor which leads the juvenile to independence in the resident black kite.

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