

Factors influencing family rupture and parent-offspring conflict in the Black Kite *Milvus migrans*

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Juvenile and adult behaviour was studied at eight nests of Black Kites *Milvus migrans* within the Doñana Biological Reserve, Spain. Parental investment in vigilance and defence of offspring progressively decreased during the post-fledging dependence period. The number of feeds was also slightly reduced towards the end of the period. However, this does not seem to be the main factor which leads to juvenile independence. The fact that the family rupture is sudden and that the post-fledging dependence period tends to shorten as the season progresses suggests that juvenile and adult migratory urgency may be as important a factor as reduced parental investment in breaking the family ties.

The optimum length of the period of parental care, for the parents, is that which maximizes their net lifetime reproductive success. However, the optimum length of this period for the offspring would be that which makes their own probability of surviving to reproductive age the highest. Parental and offspring interests thus frequently come into conflict (Trivers 1974). A time is reached when parents stop investing in their present offspring (which are capable of looking after themselves) so as to improve their own future reproductive success, either by making another breeding attempt or by starting to recover for the next breeding season. For the offspring an extension of parental care would almost always be profitable even if it meant a lower reproductive success for the parents. Such parent-offspring conflict has been recorded in several passeriform species, in which it has been noted that the parents progressively promote offspring independence by reducing their investment, while offspring still demand the same amount (Davies 1976, 1978, Woodward 1983, Moreno 1984, Edwards 1985).

Studies that have tried to identify which factors affect either the end of parental care or offspring independence during the post-fledging dependence period of raptors are scarce (Brown 1966, Brown & Amadon 1968, Kussman 1976, Konrad & Gilmer 1986, Alonso *et al.* 1987). It has been proposed that in some species the adults initiate offspring independence by a reduction in feeds and an increase in parental aggression towards them (Alonso *et al.* 1987), whereas in others it has been said that juveniles initiate independence by a gradual loss of interest towards adults as soon as they improve in feeding themselves (Brown 1966, 1976).

The aim of the present study is to evaluate parental investment of the Black Kite *Milvus migrans* during the post-fledging dependence period, and the development of juvenile behaviour in relation to the changes in parental investment. In addition, an attempt is made to assess whether a parent-offspring conflict on the length of the post-fledging dependence period exists by trying to identify the factors which bring about juvenile independence.

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Study area and methods

The study was carried out in southwest Spain at the Doñana Biological Reserve (37°N, 6° 30' W) included in the National Park of the same name. A more detailed description of the area can be found in Valverde (1958, 1960), Allier *et al.* (1974) and Rogers & Myers (1980).

Three main biotopes can be distinguished in the area: (a) Mediterranean scrubland formed by *Halimium* spp., *Cistus libanotis*, *Erica* sp. with scattered cork oaks *Quercus suber* and small stone pine *Pinus pinea* woods; (b) the marsh mainly covered by *Scirpus* spp. which remains flooded during winter, though almost dry throughout the season we carried out our research; and (c) the coastal sand dunes with vegetation mainly of *Ammophila arenaria*, *Corema album* and *Juniperus phoenicea*.

The climate is of Mediterranean type with Atlantic influence. There was no rainfall during the study period and the mean temperature was 23°C.

The population of Black Kites at the Biological Reserve of Doñana consisted of 80 breeding pairs. The nests were mainly on cork oaks not far from the marsh border.

The post-fledging dependence period of 15 Black Kite juveniles, belonging to eight breeding pairs was studied during the summers of 1985 and 1986. Of the 15 juveniles, nine were radio-marked with transmitters fixed with backpack harnesses (Beske 1978) and wing-tagged with colour plastic patagial stripes of Saflag (Kochert *et al.* 1983), four were wing-tagged only and two were not tagged at all. One of the wing-tagged juveniles was killed at the nest by a predator before fledging. Three adult males (of the eight breeding pairs) were caught with bow-net traps (Tordoff 1954) and equipped with transmitters and wing-tags. All the other adults could be told apart from other kites by their behaviour, or plumage characteristics under good light conditions.

Observations started in both years by the end of June, before the juveniles fledged, and finished by mid-August when all the tagged individuals had definitely left the study area. Observation periods were complete days, from dawn to dusk (0630–2030 h GMT). A mean number of 8 observation days per breeding pair were carried out. In 1985 observations were carried out regularly every 4 days, while in 1986 there were four observation periods of 2 consecutive days for each breeding pair, previously fixed at those juvenile ages not well covered by 1985 observations, or in which family-conflict was thought to be more probable. Two consecutive day periods were chosen in order to have a better control of the frequency of feeds. A tally of 849 observation hours was made (further details in Bustamante 1986). All the data were registered on tapes as well as on record cards specially designed to record some of the variables quickly and accurately. Observations were made from a vehicle at a mean distance of 235 m from the nest with a 20–40 × 60 telescope and 10 × 50 binoculars.

Special attention was paid to those aspects of adult and juvenile behaviour which were considered to be related to parental investment, or related to the behaviour of juveniles towards adults, to juvenile hunting behaviour, or to those which could be connected with family rupture. The following variables were taken into account: total daily time (in seconds) spent by one or both adults chasing other kites or raptors coming near the nesting area; total daily time (in minutes) spent by one or both adults flying or perching in an area where the nest-tree or offspring were still in sight; the number of intruders, measured as the daily number of raptors which crossed an imaginary line between observer and nest-tree, and whether or not it was being chased by adults; number of times daily a parent flew towards an offspring, whether or not it was carrying food; number of times daily an offspring flew towards a parent, whether or not the parent was carrying food; total daily time (in seconds) spent by a juvenile in begging behaviour; weighted daily mean distance the adults perched from each of their offspring; weighted daily mean distance between perched siblings; number of daily feeds per breeding pair; and total number of daily flights for each juvenile.

Statistical analysis were carried out using the BMDP statistical package (Dixon & Brown 1983). Analyses were first performed for each individual or for each pair. As the lack of significant correlations in many cases seemed to be due to small sample sizes, and individuals or pairs did not seem to differ in their trends, analyses were also performed after pooling the data. For those variables clearly departing from linearity, least-squares fitted orthogonal polynomials were calculated using the BMDP5R program, which performs a goodness-of-fit test on whether polynomials of higher degree would give additional information.

Results

Parental investment

Three variables were considered to reflect parental investment: time spent by adults in the area near the nest, time spent by adults chasing other raptors and daily

frequency of feeds. Time spent in vigilance and defence of the nest has been considered as parental investment—although other authors do not consider it to be so (Davies 1978)—because this is the most time-consuming activity of the Black Kite female during the nestling period (J.P. Veiga & F. Hiraldo unpubl.).

When the relationship between the first two variables and the age of the eldest chick was considered, a similar decrease was observed in the majority of the pairs, although correlation coefficients were not statistically significant in all the cases (Table 1). On pooling the data, a significant decrease was observed both in the time spent near the nest and in the time spent chasing intruders, although the number of these intruders tended to remain constant during the entire period.

Daily feeding frequency was very variable in all the pairs studied (Fig. 1), as may be expected for a raptor feeding on varied and unpredictable prey resources. The variability of feeding frequency and small samples sizes obscured clear trends for each pair. If pairs are pooled and the post-fledging period is divided into four parts for each breeding pair just before the first juvenile fledges; just after all juveniles have fledged; middle period (a week before first departure); and days before departure of juveniles from the nesting area), we find that the feeding frequency for each pair was lower prior to fledging (mean = 0.56 feeds/day, s.d. = 0.73, $n = 9$) than after fledging (2.56 feeds/day s.d. = 2.07, $n = 9$; Mann-Whitney $U = 68.5$, $P < 0.05$) and higher in the middle period (2.57 feeds/day, s.d. = 2.06, $n = 14$) than before departure (0.93 feeds/day, s.d. = 1.00, $n = 14$; Mann-Whitney $U = 51$, $P < 0.05$). On the other hand, there were no significant differences between the feeding frequency after the first flight and middle period (Mann-Whitney $U = 62$, n.s.). The feeding frequency for the pooled data fits better to a parabola than to a straight line ($F_{2,57} = 3.78$, $P < 0.05$). This curve shows the trend of the adults' feeding 'intention', independently of differences in daily hunting success or prey availability; after a period of low feeding frequency before fledging, feeds increased, but slightly decreased again before juvenile departure.

Although we do not have feeding frequency data for the same pairs during the nestling period, observations of other nests within the area over different years

Table 1. Correlation coefficients between age of the eldest Black Kite chick and time spent by adults chasing intruders, time spent by adults near the nesting area and number of intruding raptors. When the sample size for a variable is different to the one tabulated for that pair, it is shown to the left of the correlation coefficient

Breeding pairs	n	Age versus		
		time chasing intruders	time near nest	no. of intruding raptors
A003	8	-0.881† ($n = 9$)	-0.943†	—
A161	7	-0.657	-0.751	—
A157	7	-0.797*	-0.380	—
A101	4	-0.743	-0.711	0.779
PMAR	6	-0.468	-0.605	0.734
A137	5	-0.078	-0.306	-0.766
A165	8	-0.624	-0.960†	0.126
A191	10	-0.405	0.129 ($n = 8$)	0.117
Pooled	55	-0.521‡ ($n = 56$)	-0.288† ($n = 31$)	0.286

* $P < 0.05$, † $P < 0.01$, ‡ $P < 0.001$.

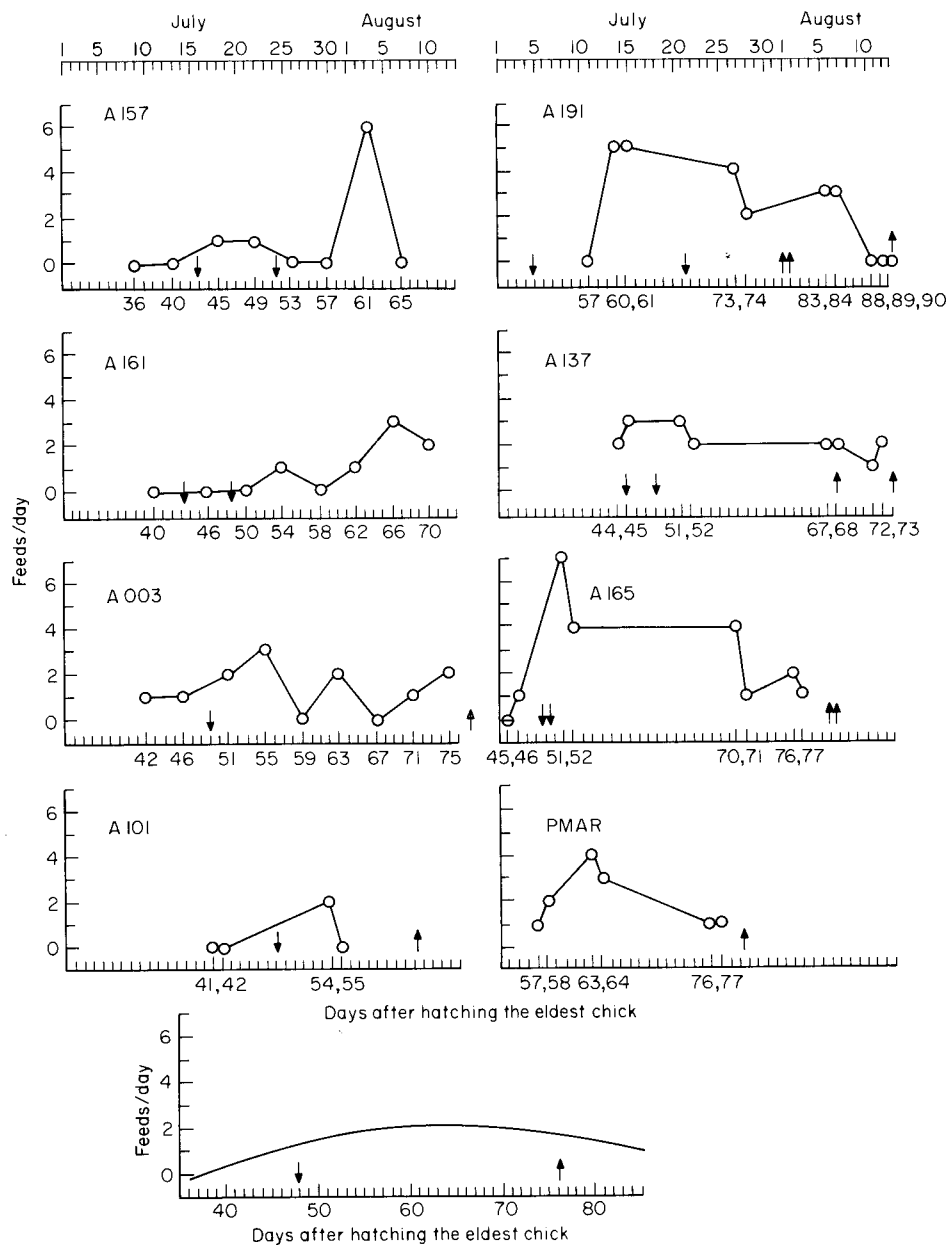


Figure 1. Feeding frequency for each Black Kite pair in relation to age of the oldest juvenile. Open circles are observed values. Pairs A157, A161 and A003 were studied in 1985, the rest in 1986. Pairs A003, A101 and PMAR had only one juvenile; A157, A161 and A165 had two juveniles (the second young was 2 days younger in all cases) and A191 and A137 had three juveniles each (1 and 6 days younger in A191, 2 and 6 days younger in A137). Fledging age and date for each young is represented by (↓) and age and date of departure by (↑). A157 and A161 juvenile departures and A191 eldest juvenile and PMAR juvenile first flights happened out of the range covered by the graph. The third juvenile of A137 died during fledging. The last graph is the least-squares second-degree polynomial fitted to the data pooled according to eldest juvenile age. ↓↑ represent average fledging and departure ages, respectively. Equation of the curve:

$$y = -0.0028x^2 + 0.3701x - 9.8473$$

usually ranged from two to six feeds per day (authors' unpubl. data). Days with no feeds during the nestling period were extremely rare. We believe that the low feeding rate before fledging therefore represents a decrease in feeding frequency. At the same time, the adults spent much of the time flying in the vicinity of the nest with prey in their talons before entering to feed (behaviour which was not observed during the nestling period). The amount of time adults spent flying with prey before entering to feed was significantly higher at the time juveniles fledged (982.7 s, s.d. = 1154.7, $n = 18$), than during the rest of the post-fledging period (159.4 s, s.d. = 365.7, $n = 16$; Mann-Whitney $U = 28$, $P < 0.02$).

Adults frequently flew towards their offspring, sometimes to feed them and sometimes not. The frequency of this behaviour tended to increase slightly with the age of the juveniles. Although this increase was observed in most pairs (Fig. 2) it did not seem to be linear. The small sample sizes prevent further analysis of the data for individual pairs. If data are pooled a significantly better fit is obtained to a second-degree polynomial than to a straight line ($F_{2,57} = 4.04$, $P < 0.05$). The parabola obtained is similar to that of feeding frequency.

Juvenile behaviour

During the post-fledging period juveniles were not observed to beg for food as persistently as noted in other raptors, such as Black Eagles *Aquila verreauxi* (Gargett 1972), Ospreys *Pandion haliaetus* and buzzards *Buteo* spp. (authors unpubl. data). The intensity of begging apparently changed irregularly from day to day and from one individual to another (Fig. 3). With data for all the juveniles pooled, there seemed to be a progressive increase in begging until an age of 69 days, after which it decreased (Fig. 3). The begging behaviour in relation to juvenile age fits a third-degree polynomial significantly better than a second-degree ($F_{1,86} = 4.00$, $P < 0.05$) or a linear equation ($F_{2,86} = 3.36$, $P < 0.05$).

Juveniles frequently flew towards their parents when they were perched in sight of the nest, regardless of whether or not they had food. Some authors have considered these flights as indicating the greater demand of the juveniles for food (Davies 1976, Moreno 1984). The number of these flights pooled increased significantly with age (Table 2) but this behaviour seemed to be highly variable; at the individual level it is correlated with age for only one juvenile. However, if the fraction of the total number of daily flights that is directed towards adults is considered we find that correlation with age is lost ($r_{58} = 0.05$, n.s.). Nevertheless, both these variables are highly correlated with begging for the whole period ($r_{61} = 0.378$, $P < 0.01$ and $r_{88} = 0.521$, $P < 0.01$) probably because both reflect the juvenile level of food demand from the adults.

None of the 15 tagged juveniles was seen to catch prey by itself during the post-fledging dependence period and none showed typical adult hunting behaviour. They did not seem to spend any time searching for food during this period (Bustamante & Hiraldo in press).

Family conflicts

To study possible family conflicts that could cause the breakage of family links, we considered two variables used by other authors: parent-offspring and sibling aggression (Holleback 1974, Woodward 1983, Alonso *et al.* 1987) and the distance between perched individuals of the family unit while within the nesting area (Holleback 1974, Davies 1976, Alonso *et al.* 1987). Among the tagged individuals, no aggression was observed between parents and offspring nor between siblings.

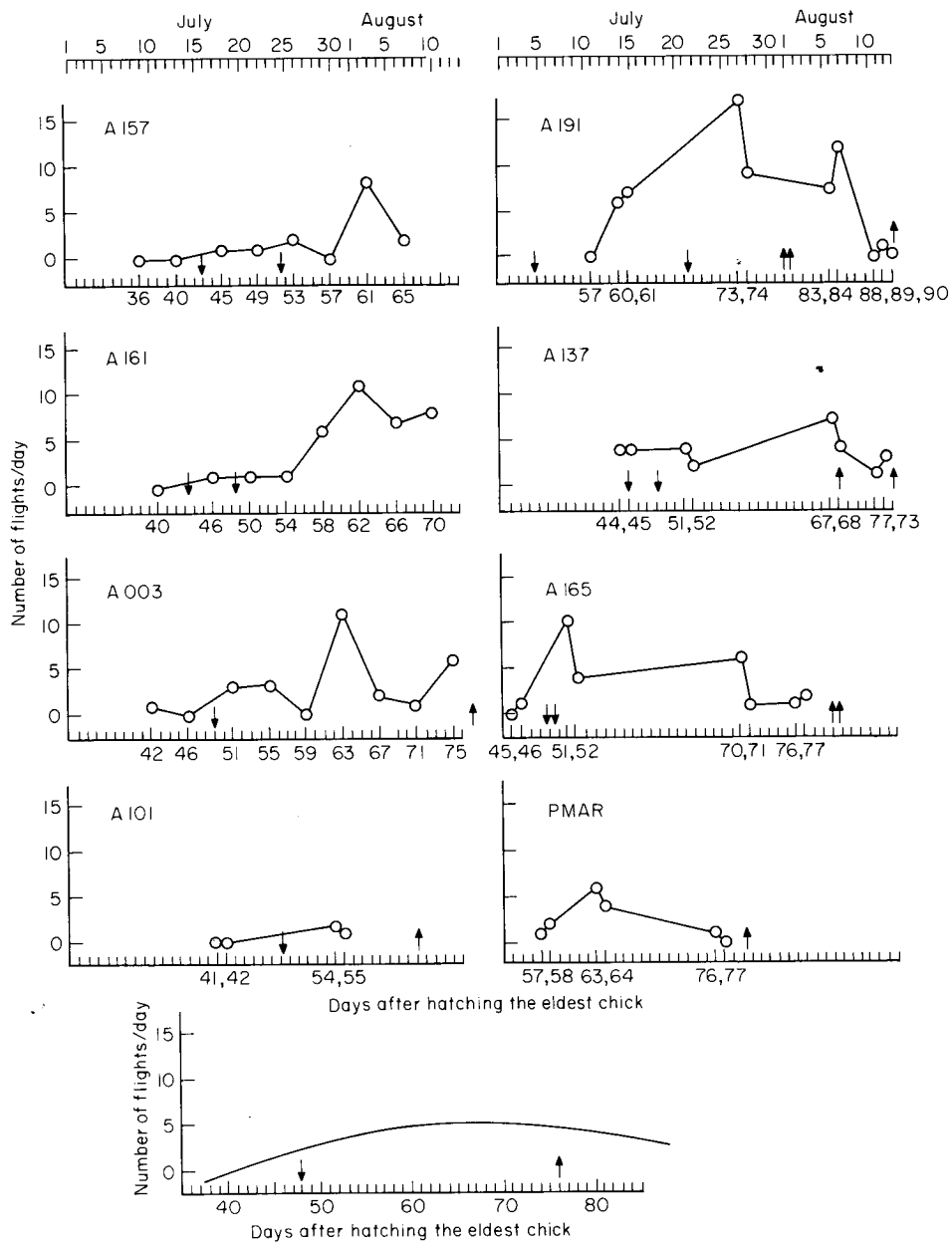


Figure 2. Frequency of flights by parent Black Kites to all offspring in relation to age of the oldest juvenile during the post-fledging dependence period. Other details as in Fig. 1. Equation of the curve:

$$y = -0.0059x^2 + 0.8198x - 23.4416$$

Nevertheless, adults were observed to be aggressive towards juvenile intruders, as were adults of neighbouring pairs towards tagged juveniles if they came near their nests. Although the behaviour was variable in each family, the mean distance between parents and offspring did not change significantly throughout the post-

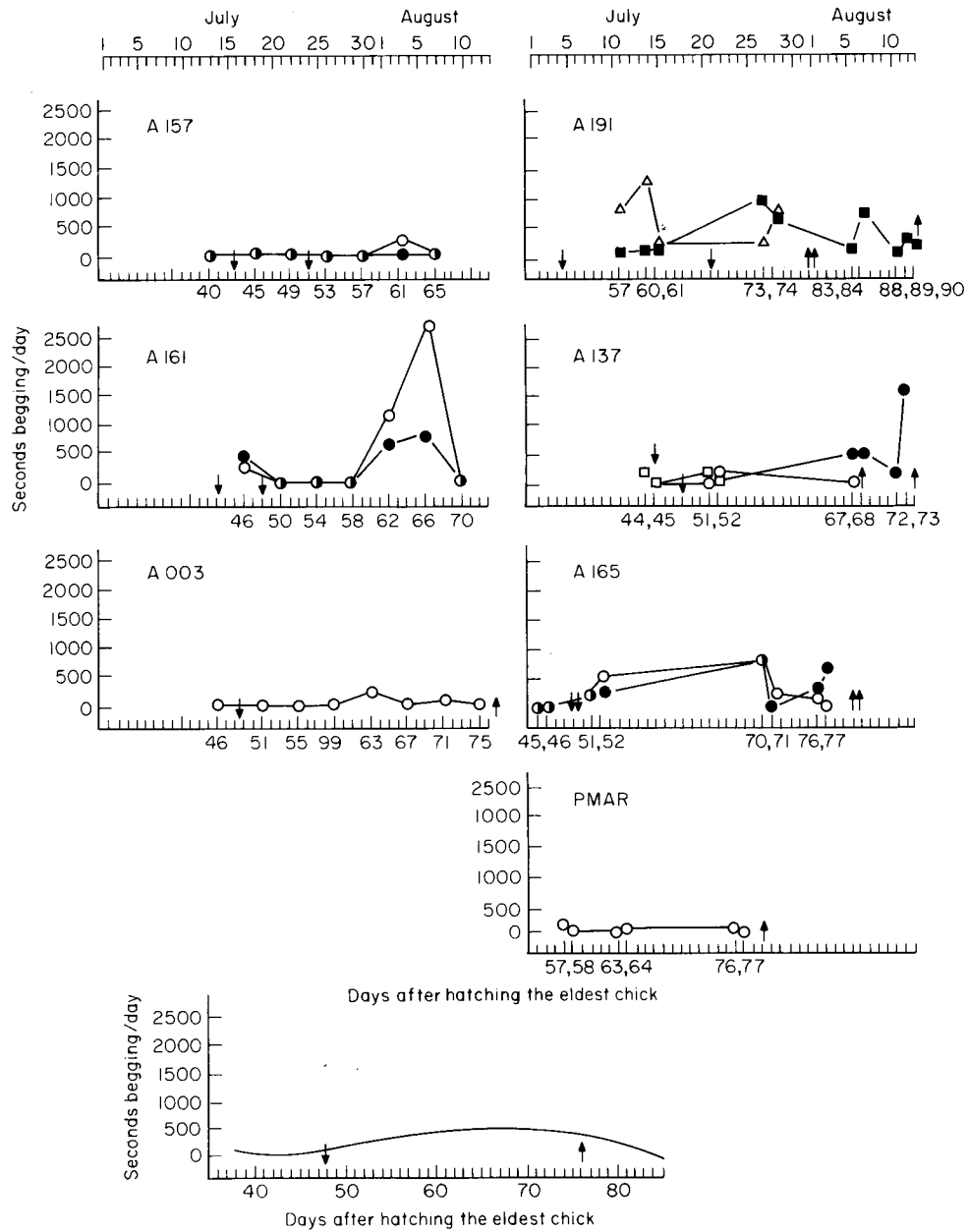


Figure 3. Time spent begging by juvenile Black Kites in relation to their age during the post-fledging dependence period: (O) first juvenile; (●) second juvenile; (■) third juvenile; (Δ) first and second juvenile could not be told apart and an average time begging is given; (□) first, second and third, or second and third could not be told apart and the last graph shows the least-squares curve fitted by a third-degree polynomial to all data pooled according to juvenile age. Other details as in Fig. 1. Equation of the curve:

$$y = -0.0453x^3 + 7.7238x^2 - 415.7339x + 7234.3086$$

Table 2. Correlation coefficients between age of juvenile Black Kites and direct flights of offspring towards parents, mean distance between parents and offspring and mean distance between siblings. J1, J2 and J3 indicate first, second and third juvenile, respectively

Juveniles	Age versus				
	<i>n</i>	flights towards parents	<i>n</i>	parent- offspring distance	distance between siblings
J1 A003	9	0.425	9	0.394	—
J1 A161	8	0.464	8	0.618	8 0.733*
J2 A161	8	0.247	8	0.837†	8 0.857†
J1 A157	8	0.825*	8	-0.076	8 0.857†
J2 A157	8	0.567	8	0.556	8 0.857†
J1 PMAR	6	-0.741	6	-0.469	—
J1 A137	5	0.288	—	—	—
J2 A137	8	0.650	—	—	—
J1 A165	8	-0.399	8	0.044	8 0.923†
J2 A165	8	0.548	8	0.104	8 0.923†
J3 A191	10	0.143	—	—	—
Pooled	86	0.323†	63	0.101	24 0.559†

* $P < 0.05$, † $P < 0.01$.

fledging dependence period. However, the mean distance between siblings tended to increase with age (Table 2), both for pooled data and for each of the families in which it was studied. Mean distance between siblings seems to be strongly related to flying proficiency of the juveniles and shows a significant correlation with the log of the daily total time spent flying by the older sibling ($r_{21} = 0.504$, $P < 0.05$).

Discussion

Before the first flights of the young there was a decrease in the adults' feeding frequency along with an increase in the amount of time adults spent flying with prey in their talons before entering the nest. A similar decrease in food supply when reaching the fledging stage, followed by an increase when the young are able to fly, was observed by Green (1976) in Scottish Ospreys. The behaviour of holding the prey in sight of the juveniles at the time of fledging has also been recorded for the Peregrine *Falco peregrinus* (Ratcliffe 1980). We interpret this behaviour in the Black Kite as an 'intention' of the adults to hasten first flights of the juveniles, perhaps to reduce nest predation risks. Although it seems unlikely, it is possible that the pre-fledging food reduction is an adjustment to lower energy requirements of the young at this stage, or may even be due to observer interference in adult behaviour.

Parental investment, measured as vigilance and defence of offspring, decreased as the post-fledging dependence period progressed. At the same time, juveniles demanded the same attention from their parents, as has been observed in other raptors (Alonso *et al.* 1987). Family tensions, that would be produced by a parent-offspring conflict, appear not to be very intense in this species. There was no aggression and parents did not increase the distance from their offspring while perched; indeed, they flew more frequently towards them as the period progressed, although there was a progressive withdrawal among siblings. Aggression in other species can be interpreted as behaviour directed to chase off offspring from the

adults' hunting grounds, once juveniles can hunt by themselves, so as to avoid an over-exploitation of prey (Holleback 1974, Davies 1976, Alonso *et al.* 1987, although see Brown 1976). Such behaviour would be unnecessary for the Black Kite, since it is a migratory species that leaves the area once it has finished breeding. Similarly in some other migratory raptors no aggression has been recorded during the post-fledging dependence period (Kussman 1976, Beske 1978, Konrad & Gilmer 1986, although see Meinertzhagen 1954 and Johnson 1986). The observed increase in the mean distance between siblings seems to be attributable to the increase in flight ability of the juveniles more than to tension between them (Davies 1976).

The results discussed above could be fitted to a model of juvenile independence due to parental decision, as has been proposed for other species (Davies 1976, 1978, Woodward 1983, Moreno 1984, Edwards 1985). However, there is a set of facts which make us think that reduction in parental investment is not the only or main factor influencing juvenile independence. Reduction of parental investment can also be explained as the reduction of effort as soon as there is no further need of it (Davies 1976). During the nestling period the female devotes all her time to vigilance and nest defence but these are not necessary once the juveniles are able to fly, as predation risk has decreased; it is only then that the female begins to cooperate in feeding. If the reduction in the feeding frequency was the triggering factor of the family split, we might expect this reduction to be more marked. We might also expect that juvenile behaviour would be directed to deceive their parents into donating extra investment (Davies 1978) by, for example, an increase in begging or in the number of times adults are chased by juveniles, as observed in other species (Davies 1976, 1978, Woodward 1983, Moreno 1984). However, as we have already seen (Figs 1 and 3), the period of maximum begging is very close to the period of maximum feeding frequency, and the increase in the number of flights towards their parents is mainly due to greater flying ability. The fact that the decrease in the feeding frequency is not the only factor which triggers family rupture is supported by the observation of three juveniles, belonging to two different multiple broods (A191 and A137), which left the area while the parents were still maintaining a high feeding level and continued to feed the youngest siblings (Fig. 1). On the other hand in at least one case (the youngest of three siblings, J3A191) the parents abruptly cut off feeds 3 days before juvenile departure.

According to Bruun (1986) raptors subsisting on highly seasonal food—as does the Black Kite in Doñana (Delibes 1975)—show greater urgency in migration than species dependent on less variable sources. It could be that migration in some way influences family rupture in this species. This is suggested by the fact that the post-fledging dependence period shortens as the season progresses—there is a significant negative correlation between the length of the post-fledging period and fledging date ($r_{11} = -0.583$, $p < 0.05$)—and that juveniles seem to have higher migratory restlessness by the end of the summer. Those juveniles starting the post-fledging dependence period later in the season show a quicker increase in the number of daily flights (Bustamante & Hiraldo *in press*). The need to migrate at an early date could be the evolutionary force that has priority over the natural tendency of juveniles to try to extend parental care (Trivers 1974, Davies 1978), in such a way that a clear parent-offspring conflict does not necessarily take place. Thus, the rupture of family ties could be produced by adult or juvenile initiative depending on the intensity of their migratory restlessness. Further research is needed to study the factors that favour an early migration and the mortality risk due to late migration, so that their influence on Black Kite juvenile independence can be assessed.

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