

Family break-up in Black and Red Kites *Milvus migrans* and *M. milvus*: is time of independence an offspring decision?

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I observed the natural process of family break-up in 13 families of Black Kites *Milvus migrans* and five families of Red Kites *M. milvus* in which fledglings had been individually marked. In other broods, I performed experiments which modified the parental investment fledglings received by supplementing nests of both species with food or transferring Black Kite chicks to nests with younger or older chicks of the same species.

The time of family break-up in the Black Kite is mainly an offspring decision which is not affected by an artificial increase of parental investment. The duration of the post-fledging period was not increased in Black Kites that were given supplementary food. Chicks transferred to nests with a younger chick did not extend the post-fledging period, nor did chicks transferred to nests with an older chick shorten the post-fledging period. In Red Kites, parental investment seemed to have more influence on the timing of the family break-up. Red Kite adults invested less as parents than did Black Kites during the post-fledging dependence period, and in nests where supplementary food was given, Red Kite fledglings stayed attached for a longer period.

Juvenile raptors continue to depend on their parents for food after fledging during a phase known as the post-fledging dependence period. According to the parent–offspring conflict theory (Trivers 1974, 1985), offspring will be selected to try to prolong the period of parental care, while parents will be selected to stop investing in their present offspring once the cost of parental care surpasses the benefits they obtain in terms of net lifetime reproductive success. In raptors, a parent–offspring conflict can be expected both over the amount of parental investment that offspring should receive during the post-fledging period and over the duration of the post-fledging period.

A parent–offspring conflict over the duration of the post-fledging dependence period has been documented in several species of birds (Davies 1976, 1978, Woodward 1983, Moreno 1984, Edwards 1985, Leonard *et al.* 1988, Turcotte & Bédard 1989). In these studies, the parents progressively reduced investment, promoting offspring independence, while offspring seemed to demand the same amount. Davies (1978) provided the only experimental evidence that the level of parental investment during this period in Great Tits *Parus major* determined when fledglings became independent.

In raptors, family break-up may take place after a period of parent–offspring conflict, the parents being the ones who promote the independence of juveniles by a gradual reduction in the food supplied or even by increased aggression

towards them (Sherrod 1983, Alonso *et al.* 1987, Delannoy & Cruz 1988, Hiraldo *et al.* 1989). Family break-up may also take place without apparent conflict when juveniles lose interest in their parents (Brown 1966, Bustamante & Hiraldo 1990a).

The Black and the Red Kite *Milvus migrans* and *M. milvus* are two medium-sized diurnal raptors with generalist feeding habits. The Black Kite is a summer visitor to the study area, while the Red Kite is resident. The duration and characteristics of the post-fledging dependence period have been documented in both species (Bustamante & Hiraldo 1989, Bustamante 1993). In an observational study of the factors influencing family break-up in the Black Kite, Bustamante & Hiraldo (1990) found no clear signs of parent–offspring conflict and suggested that the need for early migration affected the timing of family break-up.

I chose the Red Kite because its ecology is similar to the Black Kite, but it is a resident in the study area. In the observational study, I monitored variables measuring the level of parental investment and of offspring demand to test for differences between species. I also performed experiments in which I modified the amount of parental investment that fledglings were receiving and studied its influence on the duration of the post-fledging dependence period.

STUDY AREA AND METHODS

The study was carried out in Doñana Biological Reserve (37°N, 6°30'W) inside Doñana National Park, southwest

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Spain. Three main biotopes can be distinguished in the area: (1) Mediterranean scrubland formed mainly by *Halimium* spp., *Cistus libanotis* and *Erica* spp., with scattered Cork Oaks *Quercus suber* and small woods of Stone Pine *Pinus pinea*; (2) marsh mainly covered by *Scirpus* spp., which is almost dry during summer and (3) coastal sand dunes with vegetation mainly of *Ammophila arenaria*, *Corema album* and *Juniperus phoenicea*. A more detailed description can be found in Valverde (1958) and Rogers & Myers (1980).

Observational work

In 1985, 1986 and 1987, I followed the post-fledging dependence period of 25 Black Kite fledglings from 13 broods. In 1987, I followed the post-fledging period of 11 Red Kite fledglings from five broods. Some of the data from the 15 Black Kite fledglings observed in 1985 and 1986 have been published (Bustamante & Hiraldo 1990a). All fledglings were wing-tagged with colour plastic patagial stripes of Saflag (Kochert *et al.* 1983) to allow individual recognition. Only three adult Black Kites and one adult Red Kite were marked, but in most cases adults could be recognized by behaviour and plumage characteristics.

Observations, made by two observers at an average distance of 250 m from the nest with $\times 20$ – 40 telescopes and $\times 10$ binoculars, were started before the juveniles of a brood fledged, continued until all fledglings had left the vicinity of the nest and were considered to be independent. Fledglings equipped with transmitters had shown that parents stopped feeding their young once the fledglings had left the nesting area (Bustamante & Hiraldo 1989, Bustamante *in press*). Broods were observed regularly during the post-fledging period for complete days, from dawn to dusk (0630–2030h GMT). There were 95 observation days for Black Kites (3–10 days/brood) and 38 observation days for Red Kites (5–10 days/brood).

In order to study the existence of a parent–offspring conflict during the post-fledging period, I selected a set of variables as indicators of parental investment, parental interest in the offspring, the level of offspring demand and the amount of parental care obtained by offspring in relation to demand (Appendix).

The feeding frequency by adults and the prey size were very variable, and it was difficult to identify the prey brought to the nest. To obtain a more detailed picture of the changes in food brought to the nest by adults during the post-fledging period, I visited ten Black Kite nests (three in 1987, three in 1988 and four in 1991) and nine Red Kite nests (five in 1988 and four in 1991) every 2 days, recorded the prey remains found and estimated the biomass of prey. All these nests were additional to those under observation. Although this method underestimates the number of prey brought to the offspring, it gives comparable results between the two species as both continued to feed their offspring at the nest during the post-fledging period and rarely fed them at other perches (Bustamante 1990, 1993).

Experiment 1

To test if adults determined the timing of family break-up by reducing the food brought to their offspring during the post-fledging dependence period, I placed food supplements in the nests of both species of kites. Ten Black Kite nests (five in 1987 and five in 1991) received supplements, and 13 nests were used as controls (seven in 1987 and six in 1991). Ten Red Kite nests (five in 1988 and five in 1991) were given supplements, and 12 nests were used as controls (seven in 1988 and five in 1991). For all fledglings, I determined their ages at first flight and at independence.

At experimental nests, 500 g of meat per fledgling was left in the nest every 2 days (daily adult requirements are < 100 g), starting 2 weeks after the first flight of the eldest chick in the brood. The meat used to supplement the nest was eaten by the fledglings and by other kites coming to the nest when the fledglings were absent. I assumed that the effect of supplementing the nest with food was comparable to that of the parents increasing their feeding frequency.

Experiment 2

In order to test if parental investment had any effect on the duration of the Black Kite post-fledging dependence period, I modified the parental investment certain chicks were receiving by introducing them into broods that were more or less advanced than their original brood. I selected 18 Black Kite two-chick broods with a hatching asynchrony no greater than 5 days.

Treatment 1

In six nests, the first-hatched chick was replaced by another Black Kite chick (*foster T1*) 15–20 days older. The remaining original chick is referred to as *original T1*.

Treatment 2

In three nests, the second-hatched chick was replaced by another Black Kite chick (*foster T2*) 15–20 days younger. The remaining original chick is referred to as *original T2*.

Control

In nine nests, one of the chicks was replaced by another chick (*foster C*) of a similar age (0–5 days difference). The remaining original chick is referred to as *original C*.

The number of two-chick broods in the study area and the relative ages of the chicks restricted the allocation of nests to experimental treatments, rendering an unbalanced design. The chicks were exchanged when they were 15–40 days old. No chicks were rejected in their foster nests, and there was no mortality among introduced chicks during the nestling or post-fledging periods, with the exception of a nest

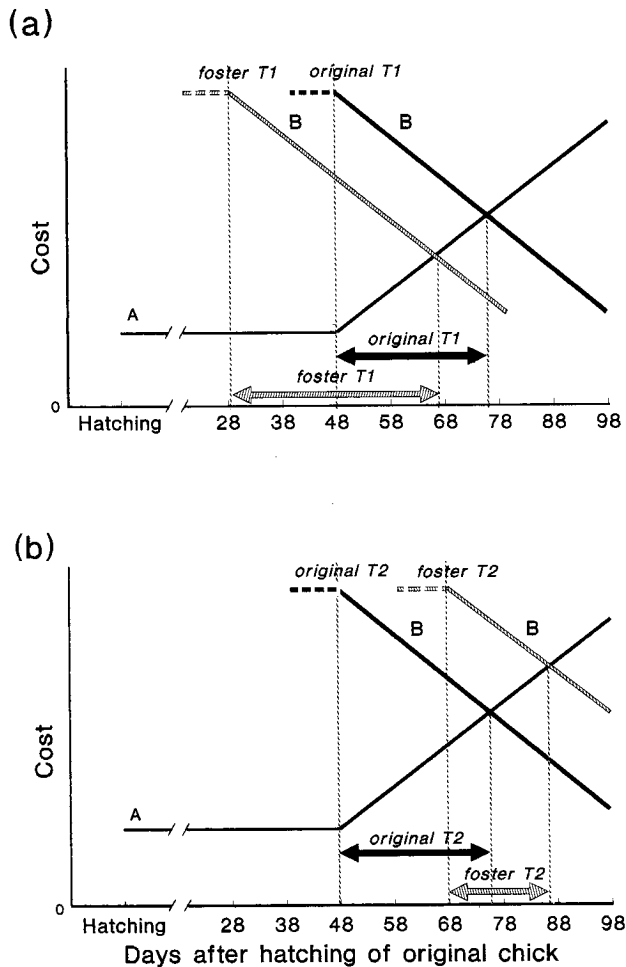


Figure 1. (a) Represents a two-chick brood in which the first-hatched chick has been replaced by a chick 20 days older (Experiment 2, treatment 1). The introduced chick is *foster T1* and the original second-hatched chick is *original T1*; (b) Represents a two-chick brood in which the second-hatched chick has been replaced by a foster chick 20 days younger (experiment 2, treatment 2). The introduced chick is *foster T2* and the original first-hatched chick is *original T2*. The hatching asynchrony between the first- and second-hatched chick in the original brood (0–5 days) is ignored, and both *original T1* and *original T2* fledge 48 days after hatching, the average fledging age for Black Kites (Bustamante & Hiraldo 1989). 'A' represents a curve of increasing cost for the chicks to obtain food from the adults and is assumed to be the inverse of the total adult feeding rate and equal for both chicks (adults do not feed chicks separately during post-fledging). Only one of the possible alternatives is represented, which is when adults follow a fixed rule "feed chicks for 48 days after hatching and then decrease feeding rate" (see Methods, experiment 2). 'B' represents the decreasing cost for the chicks to obtain food by themselves after they fledge (based on the gradual improvement of their flying skill with age). 'B' is different for each chick, *foster T1* will fledge 20 days earlier than the original chick and *foster T2* will fledge 20 days later than the original chick. Once the cost of obtaining food by itself falls below the cost of obtaining it from the adults, the chick should become independent. The arrows represent the expected duration of the post-fledging period of the foster and of the original chick (fledging to independence). According

where young were killed by a predator 21 days after the exchange, and this was excluded from the sample.

The experiment assumes that parents decrease their investment during the post-fledging period (Davies 1978) so that the cost of obtaining parental investment increases gradually for fledglings. If parents followed a fixed rule (e.g. "feed chicks for X days after hatching and then decrease or stop feeding them"), foster chicks in treatment 1 (*foster T1*) would find themselves with adoptive parents that would feed them for a longer period of time and should extend their post-fledging dependence period, while foster chicks in treatment 2 (*foster T2*) would find themselves with parents less willing to invest and should shorten their post-fledging period (Fig. 1). The duration of the post-fledging dependence period should follow $foster T1 > foster C > foster T2$, while all original chicks should have a post-fledging period of a similar duration to that of *foster C*.

Parents could have a flexible rule and modify their investment according to chick development. One rule could be "start decreasing the feeding rate as soon as the first chick fledges". Then we would expect no differences in durations of the post-fledging period among the first chicks to fledge in the brood (*foster 1*, *original 2* and control chicks), but these should have a post-fledging period longer than that of chicks which fledge 20 days later (*original 1* and *foster 2*). An alternative rule for the parents could be "maintain feeding rate while a chick has not fledged and start decreasing thereafter". Then we would expect no differences among the last fledged chicks in the brood (*original 1*, *foster 2* and control chicks), but those that fledge 20 days earlier (*foster 1* and *original 2*) should have a longer post-fledging period.

Black Kite adults bring food to the nest but do not feed the chicks separately during the post-fledging period. This implies that the level of food supplied is the same for the two chicks at the nest (original and foster). Then, whatever the rule that the adults follow, if the duration of the post-fledging period is affected by parental investment, there should be differences in duration among some of the six groups of chicks considered (*original T1*, *foster T1*, *original T2*, *foster T2*, *original C* and *foster C*). The null hypothesis is that if the duration of the post-fledging period in the Black Kite is not influenced by parental investment, all chicks should have a post-fledging period of similar duration.

Fledglings in experiments 1 and 2 were individually marked with coloured wing-tags. All nests were checked every 2 days to estimate the chick's age at first flight. Two weeks after the first flight of the eldest chick, nests were visited again every 2 days to determine the date of independence of each fledgling. Nests were visited until there were no fledglings seen in the vicinity of the nest for three consecutive days (for more details on the procedures, see Bustamante 1993).

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to this model, the duration of the post-fledging period should follow $foster T1 > original T1 = original T2 > foster T2$.

Data analysis

In the observational study, I divided the post-fledging period into two parts: (A) the first 20 days after the first flight of the eldest chick and (B) from 20 days after the first flight of the eldest chick to independence of the last chick. Black and Red Kites become independent on average 28 and 26 days, respectively, after the first flight (Bustamante & Hiraldo 1989, Bustamante 1993), so it should be during the second period, nearing the time of independence, that any signs of parent-offspring conflict are shown. I considered each kite brood to be an independent unit and estimated the daily mean values of all variables (Appendix) in each period for each brood. I compared the mean values between these two periods and between the Red and the Black Kite broods with two-way ANOVAS for unbalanced designs (Proc. GLM, SAS Institute Inc. 1987). Following Zar (1984), variables were transformed when their distribution departed from a normal distribution. FEEDS, PREY, FLIGHTS TOWARDS OFFSPRING, BEGGING INSTANCES, NUMBER OF FLIGHTS TOWARDS ADULTS, COST 2 and COST 3 are counts or variables derived from counts; follow a Poisson distribution and were square root transformed; TIME BEGGING and COST 1 that had log-normal distributions were log-transformed and PROPORTION OF FLIGHTS TOWARDS ADULTS, being a proportion, was arcsin square root transformed.

In experiment 1, I also considered each brood to be a unit and used the average duration of the post-fledging dependence period in each brood. I performed a three-way ANOVA for unbalanced designs, with species, treatment and year as factors. I tested *a posteriori* within species for an increase in the duration of the post-fledging dependence period in supplemented broods with a Dunnett's one-tailed *t*-test (SAS Institute Inc. 1987).

In experiment 2, I considered each fledgling to be an independent unit. I then tested if there were any differences in the duration of the post-fledging dependence period among the six different categories of chicks (foster and original chick in control nests, foster and original chick in treatment 1 and foster and original chick in treatment 2) with a one-way ANOVA. As there were differences in average fledgling date among chick categories and fledgling dates affect the duration of the post-fledging period (Bustamante & Hiraldo 1990a), post-fledging duration was corrected previously for fledgling date.

RESULTS

Observational work

I tested for differences in all the variables by measuring (1) parental investment, (2) parental interest in the offspring, (3) level of offspring demand and (4) amount of parental care obtained by offspring in relation to demand (Appendix) between Black and Red Kites and between the two parts of the post-fledging period. The parent-offspring conflict theory predicts that parental investment and parental interest

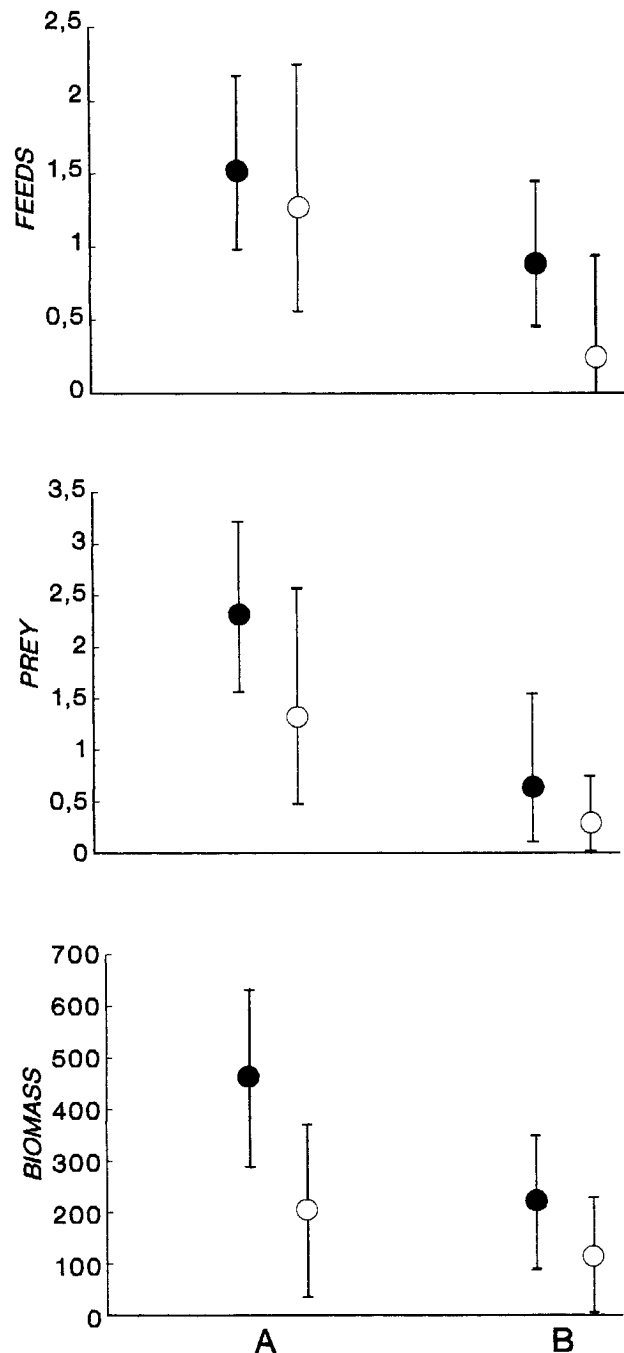


Figure 2. Changes in food brought to the offspring during the post-fledging period in the Black (solid circle) and in the Red Kite (open circle). Means and 95% confidence intervals are given for the variables FEEDS, PREY and BIOMASS (Appendix) during the first part (A) and during the end of the post-fledging period (B). Two-way ANOVAS for unbalanced designs (PROC GLM, SAS Institute Inc. 1987), type III sum of squares, testing the differences between species and time periods during the post-fledging: FEEDS: species $F_{1,26} = 2.66$, n.s.; time $F_{1,26} = 7.42$, $P < 0.02$; species * time $F_{1,26} = 1.02$, n.s.; PREY: species $F_{1,34} = 3.14$, n.s.; time $F_{1,34} = 13.5$, $P < 0.001$; species * time $F_{1,34} = 0.04$, n.s.; BIOMASS: species $F_{1,34} = 5.65$, $P < 0.03$; time $F_{1,34} = 4.74$, $P < 0.05$; species * time $F_{1,34} = 1.05$, n.s.

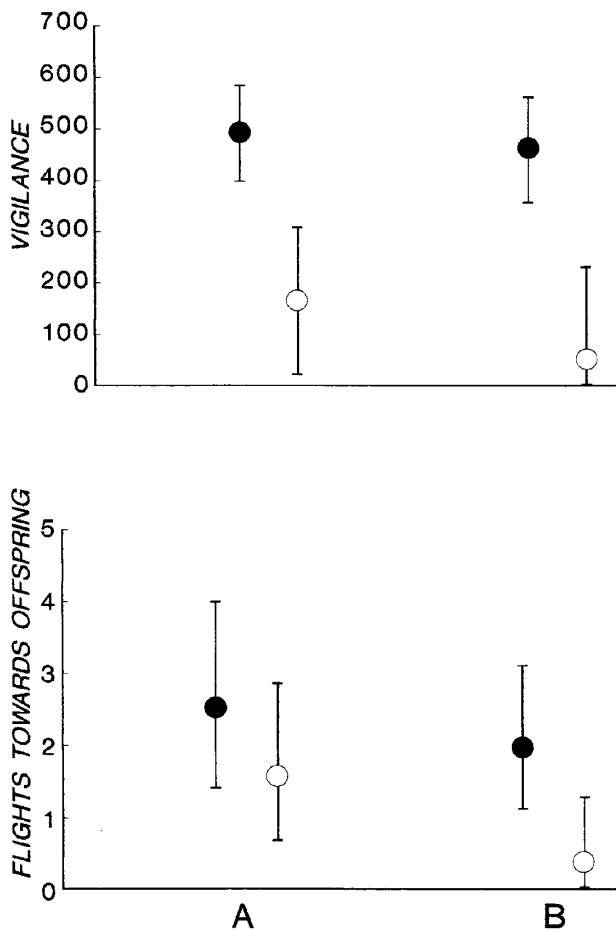


Figure 3. Changes in parental interest in the offspring during the post-fledging period in the Black (solid circle) and in the Red Kite (open circle). Means and 95% confidence intervals are given for the variables *VIGILANCE* and *FLIGHTS TOWARDS OFFSPRING* (Appendix) during the first part (A) and during the end of the post-fledging period (B). Two-way ANOVAs for unbalanced designs (PROC GLM, SAS Institute Inc. 1987), type III sum of squares, testing the differences between species and time periods during the post-fledging: *VIGILANCE*: species $F_{1,26} = 31.6$, $P < 0.001$; time $F_{1,26} = 1.33$, n.s.; species * time $F_{1,26} = 0.44$, n.s.; *FLIGHTS TOWARDS OFFSPRING*: species $F_{1,26} = 5.12$, $P < 0.05$; time $F_{1,26} = 2.84$, n.s.; species * time $F_{1,26} = 0.98$, n.s.

in the offspring should decrease, offspring demand should increase and the ratio of offspring demand to parental investment—cost to the offspring—should increase during the post-fledging dependence period.

Both species of kites decreased the number of prey items they brought to their offspring at the end of the post-fledging period (Fig. 2). Common prey items at both kite nests were crayfish, fish, wildfowl and wader fledglings, small rabbits and carrion, ranging from 20 to 800 g. The number of prey items per fledgling brought by the parents (*FEEDS*) in broods that were monitored the complete day decreased ($P < 0.02$), as did the amount of prey remains (*PREY*) and the estimated

biomass of prey (*BIOMASS*) in nests that were checked every 2 days ($P < 0.001$ and $P < 0.05$, respectively). The Black Kite tended to bring more food to its offspring during the post-fledging period than did the Red Kite. This difference was not significant in *FEEDS* or *PREY* but was significant in *BIOMASS* ($P < 0.05$).

Neither the reduction in time that adults spent close to the nest (*VIGILANCE*) during the post-fledging period nor the reduction in the number of instances parents approached their offspring (*FLIGHTS TOWARDS OFFSPRING*) was significant. Black Kite adults, however, invested significantly more in *VIGILANCE* than did Red Kites ($P < 0.001$) and seemed to be more attached to their offspring, flying significantly more frequently towards them ($P < 0.05$) (Fig. 3).

Fledglings of both Black and Red Kites increased their demands during the post-fledging period as was shown by an increase in *TIME BEGGING* ($P < 0.05$) (Fig. 4), but the increases in *BEGGING INSTANCES* and *NUMBER OF FLIGHTS TOWARDS ADULTS* were not significant. Black Kite fledglings were not more demanding but seemed to approach their parents more often than did Red Kite fledglings, especially when measured by the *PROPORTION OF FLIGHTS TOWARDS ADULTS* ($P < 0.03$).

The amount of parental care in relation to offspring demand decreased during the post-fledging period, and therefore the cost for the offspring of obtaining parental care increased. The increase in cost was significant when the food obtained in relation to time begging (*COST 1*) ($P < 0.01$) or to begging instances (*COST 2*) ($P < 0.02$) was considered, but it was not significant in relation to flights towards parents (*COST 3*) (Fig. 5). There were no significant differences in costs for the offspring between Black and Red Kites.

Experiment 1

The experiment of supplementing nests with food significantly extended the time fledglings remained attached to their nests in the Red Kite but not in the Black Kite (Fig. 6). There was no significant interaction between species and treatment, suggesting that the effect of the treatment may be similar in both species although stronger in the Red Kite.

Experiment 2

As post-fledging duration in the Black Kite decreased significantly with fledging date ($r_{95} = 0.34$, $P < 0.001$), I first corrected for date the post-fledging duration of all experimental chicks, calculating the residual post-fledging duration (observed duration – expected duration) from a least squares regression (post-fledging duration = $36.87 - 0.153$ fledging date¹) obtained from Black Kite fledglings not used in experimental treatments ($n = 43$).

The experiment of transferring Black Kite chicks to nests in which the foster chick was 20 days older or younger than the original chicks had no appreciable effect on the subse-

¹ Measured as days since the first of May.

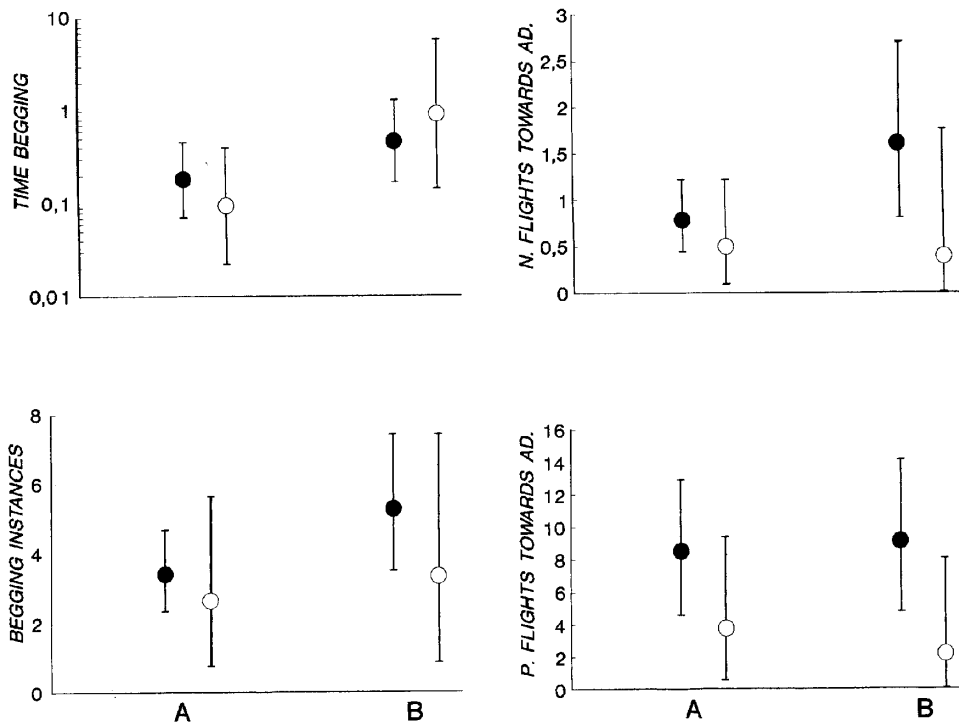


Figure 4. Changes in offspring demand during the post-fledging period in the Black (solid circle) and in the Red Kite (open circle). Means and 95% confidence intervals are given for the variables *TIME BEGGING*, *BEGGING INSTANCES*, *NUMBER OF FLIGHTS TOWARDS ADULTS* and *PROPORTION OF FLIGHTS TOWARDS ADULTS* (Appendix) during the first part (A) and during the end of the post-fledging period (B). Two-way ANOVAS for unbalanced designs (PROC GLM, SAS Institute Inc. 1987), type III sum of squares, testing differences between species and time periods in the post-fledging: *TIME BEGGING*: species $F_{1,26} = 0.00$, n.s.; time $F_{1,26} = 5.93$, $P < 0.03$; species * time $F_{1,26} = 0.99$, n.s.; *BEGGING INSTANCES*: species $F_{1,26} = 1.48$, n.s.; time $F_{1,26} = 1.33$, n.s.; species * time $F_{1,26} = 0.20$, n.s.; *NUMBER OF FLIGHTS TOWARDS ADULTS*: species $F_{1,26} = 3.77$, n.s.; time $F_{1,26} = 0.55$, n.s.; species * time $F_{1,26} = 1.19$, n.s.; *PROPORTION OF FLIGHTS TOWARDS ADULTS*: species $F_{1,26} = 6.01$, $P < 0.03$; time $F_{1,26} = 0.18$, n.s.; species * time $F_{1,26} = 0.40$, n.s.

quent duration of the post-fledging period of the different groups of chicks considered (Fig. 7). Chicks introduced in less advanced broods (*foster T1*) did not prolong their post-fledging period, nor did they affect the post-fledging duration of the original younger chick (*original T1*). Chicks introduced in more advanced broods (*foster T2*) did not have shorter post-fledging periods, nor did they prolong the post-fledging of the original older chick (*original T2*).

DISCUSSION

The observational study showed a pattern that agrees with the predictions of the parent-offspring conflict theory for the post-fledging period (Trivers 1974, 1985). Parents reduced their investment and offspring increased their demands, with the consequence that the cost of parental investment for the offspring increased during the post-fledging period.

There are some differences between the two species of kites. Black Kite parents invested more in food and in vigilance and seemed to be more attached to their offspring during the post-fledging period. They also invested more than Red Kites in nest defence during the post-fledging pe-

riod (Bustamante & Hiraldo 1993). Black Kite fledglings may demand more from their parents than Red Kite fledglings, although this could be a bias caused by the fact that Red Kite parents spent comparatively less time near their offspring.

Experiment 1 showed that the artificial increase in parental investment created by supplementing the nest with food increased significantly the duration of the post-fledging period in the Red Kite. Similar experiments with the Sparrowhawk *Accipiter nisus* (I. Newton, pers. comm.) and the Goshawk *Accipiter gentilis* (Kenward *et al.* in press) have also shown that food supplements in the nest increase the time juveniles are attached to it.

There is no clear reason for the lack of an effect in Red Kites in 1991. This was a dry year with a poor food supply during the nestling period that caused a heavy mortality rate in both species of kites. In all, 36% of Red Kite chicks and 33% of Black Kite chicks initially marked for experiments died before independence ($n = 25$ and $n = 24$, respectively), compared with only 14% of Red Kite chicks and 7% of Black Kite chicks in 1987 and 1988 ($n = 37$ and $n = 75$, respectively). This mortality rate could have caused a bias towards better quality parents in the 1991 sample. The Red Kite

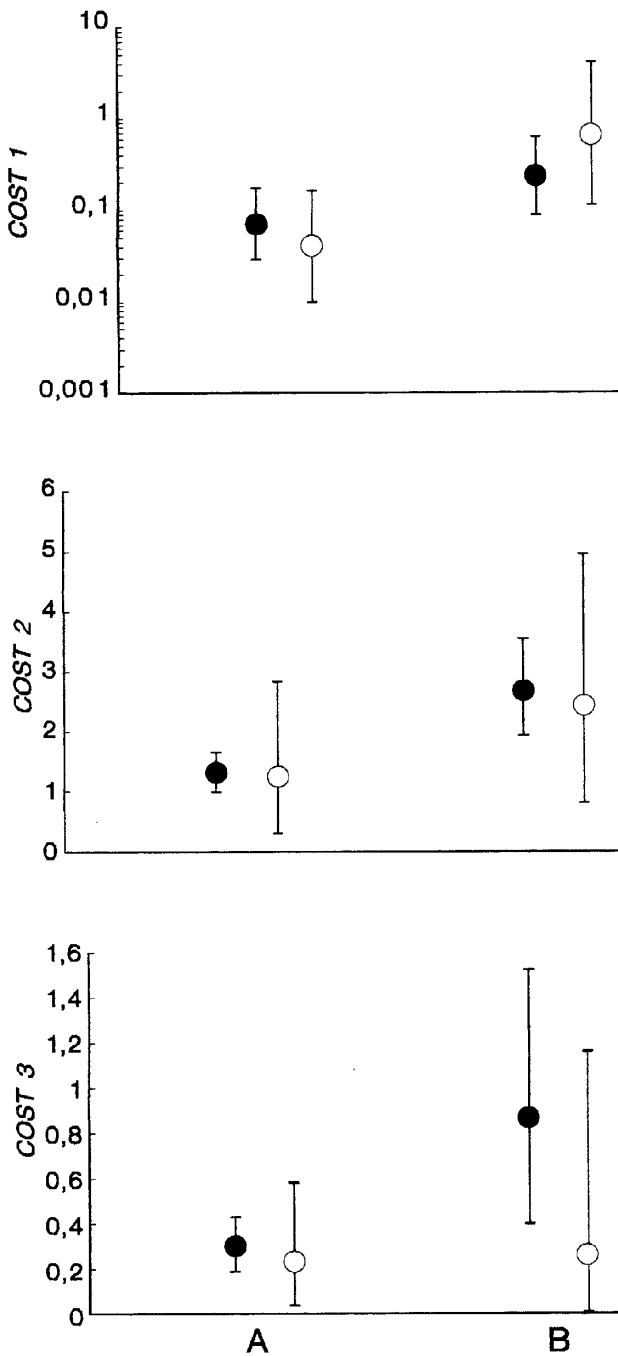


Figure 5. Changes in the cost of parental investment for the offspring during the post-fledging period in the Black (solid circle) and in the Red Kite (open circle). Means and 95% confidence intervals are given for the variables *COST 1*, *COST 2* and *COST 3* (Appendix) during the first part (A) and during end of the post-fledging period (B). Two-way ANOVAS for unbalanced designs (PROC GLM, SAS Institute Inc. 1987), type III sum of squares, testing the differences between species and time periods in the post-fledging: *COST 1*: species $F_{1,26} = 0.16$, n.s.; time $F_{1,26} = 9.75$, $P < 0.005$; species * time $F_{1,26} = 1.55$, n.s.; *COST 2*: species $F_{1,26} = 0.07$, n.s.; time $F_{1,26} = 7.06$, $P < 0.02$; species * time $F_{1,26} = 0.02$, n.s.; *COST 3*: species $F_{1,26} = 2.45$, n.s.; time $F_{1,26} = 1.83$, n.s.; species * time $F_{1,26} = 1.33$, n.s.

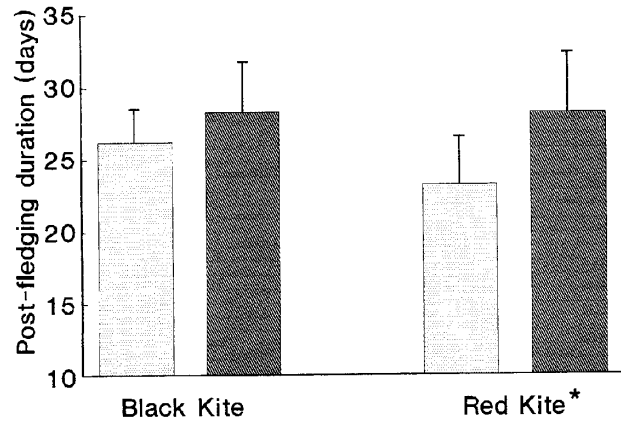


Figure 6. Mean and 95% confidence interval of durations of the post-fledging period in control broods □ and broods supplemented with food ▨ in the Black and in the Red Kite. Three-way ANOVA for unbalanced designs (PROC GLM, SAS Institute, Inc. 1987), type III sum of squares, testing differences between species, experimental treatment and year of study: species $F_{1,38} = 0.44$, n.s.; treatment $F_{1,38} = 6.85$, $P < 0.02$; year $F_{2,38} = 0.42$, n.s.; species * treatment $F_{1,38} = 0.22$, n.s.; treatment * year $F_{2,38} = 2.56$, n.s. I tested *a posteriori* for an increase in the duration of the post-fledging period in supplemented broods within species with Dunnett's one-tailed *t*-test, * $P < 0.05$.

nest visited during the post-fledging period in 1991 had significantly more food than those in 1988 (difference in *BIOMASS*, $F_{1,14} = 9.73$, $P < 0.01$). If Red Kite parents in the 1991 sample were investing more than the average, this could have diluted the effect of the food supplements.

In the Black Kite, food supplements slightly increased the duration of the post-fledging period, but this increase was not significant. A higher level of intruders eating the food supplements at Black Kite nests cannot be the reason for the lack of effect because food piracy at Black Kite nests is lower than at Red Kite nests (Bustamante & Hiraldo 1990b, 1993).

The results of experiment 2 showed similar durations of the post-fledging period in all categories of Black Kite juveniles (Fig. 7). Black Kite adults had to extend the period of post-fledging parental care by 15–20 days to cope with a younger chick that was introduced into their nest (treatment 2), but this had no effect on the duration of the post-fledging period of the original chick left at the nest. In addition, chicks did not extend their post-fledging period when they were introduced into less advanced nests (treatment 1) in which adults naturally provided a longer period of post-fledging parental investment.

There was some parent–offspring conflict over the amount of parental investment during the post-fledging period in both Black and Red Kites, since juveniles increased their begging and adults reduced the feeding rate. In the case of the Red Kite, there was also conflict over the duration of the post-fledging period. Adults forced juveniles to become independent earlier than juveniles would have preferred, as

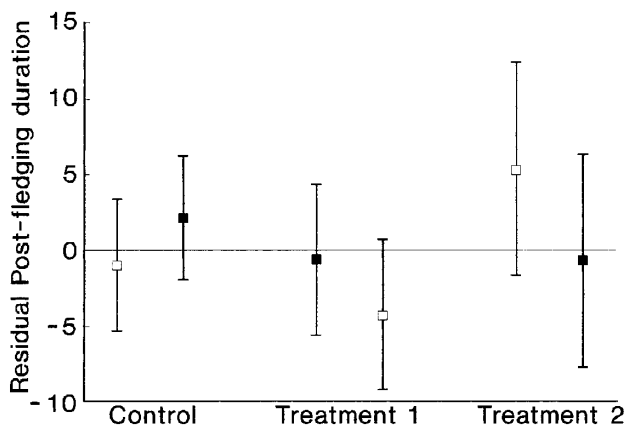


Figure 7. Mean and 95% confidence interval residual durations of the post-fledging period, after correcting for fledging date, of Black Kite chicks in experiment 2. Foster chick (solid square), original chick (open square). One-way ANOVA for differences in the residual duration among the six juvenile categories: $F_{5,29} = 1.39$, n.s.

the parent-offspring conflict theory predicts (Trivers 1974, 1985). But in the Black Kite, juveniles were not forced by their parents to become independent, and there was no parent-offspring conflict over when the post-fledging dependence period should come to an end.

Red Kite adults are 12% heavier than Black Kites, and although energy requirements by Red Kite fledglings must be greater than those of Black Kites, Black Kites bring more food than do Red Kites to their fledglings (Fig. 2). A general model for the duration of the post-fledging dependence period in diurnal raptors (J. Bustamante, unpubl.) predicts that the post-fledging period in the Black Kite should be 30% shorter than that of the Red Kite because of the smaller body mass and migratory habits of the Black Kite, but the average post-fledging duration of the Black Kite is 8% longer than that of the Red Kite. This would explain why food supplements in the nest had a greater effect in the Red than in the Black Kite and why, during the year in which Red Kites invested more, our food supplements had no effect.

Black Kite fledglings seem to 'decide' when to become independent. The level of investment they are still receiving from their parents, which is relatively high, has little effect on that 'decision'. As suggested previously (Bustamante & Hiraldo 1989), the later Black Kite juveniles fledge the shorter their post-fledging period, suggesting that the need for early migration might play a major role in the break-up of family links. When Red Kites, a sedentary species, were supplemented with food, fledglings increased the duration of their post-fledging period to that of the average Black Kite post-fledging period.

Other factors also support this difference between Black and Red Kites. The family break-up is more clearly defined in the Black Kite, with juveniles leaving the nesting area and starting migration as soon as they become independent (Bustamante & Hiraldo 1989). In the Red Kite, the break-up is more gradual, and juveniles continue to return to the

nesting area even if they are no longer fed by their parents (Bustamante 1993).

In conclusion, there are differences between the Black and the Red Kite in the way family break-up takes place. In the Black Kite, it is more an offspring decision, and there is no parent-offspring conflict over how long the post-fledging dependence period should last. In the Red Kite, family break-up seems to be forced by the parents, and parent-offspring conflict over the duration of the post-fledging period is more clearly present.

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APPENDIX

Variables used in the observational study

Indicators of parental investment

FEEDS = Mean number of prey brought daily to the nest by parents, corrected for the number of juveniles present.

*PREY*¹ = Minimum number of prey items identified per visit from prey remains found every 2 days at the nest.

*BIOMASS*¹ = Minimum biomass of prey identified per visit from prey remains found every 2 days at the nest.

Indicators of parental interest in the offspring

VIGILANCE = Daily total time in minutes at least one parent was in the vicinity of the nest.

FLIGHTS TOWARDS OFFSPRING = Number of times daily parents approached their offspring flying, excluding when food was brought.

Indicators of level of offspring demand

BEGGING INSTANCES = Daily mean number of instances in which one juvenile was heard begging, corrected for the number of juveniles present.

TIME BEGGING = Daily total time in seconds that juveniles at the nest were begging, corrected for the total time in minutes that juveniles were present.

NUMBER OF FLIGHTS TOWARDS ADULTS = Daily mean number of flights in which offspring approached their parents, corrected for the number of juveniles present.

PROPORTION OF FLIGHTS TOWARDS ADULTS = Mean proportion of juvenile flights in which they approached their parents.

Indicators of the ratio of parental care to offspring demand

$COST\ 1 = (TIME\ BEGGING + 1)/(FEEDS + 1).$

$COST\ 2 = (BEGGING\ INSTANCES + 1)/(FEEDS + 1).$

$COST\ 3 = (NUMBER\ OF\ FLIGHTS\ TOWARDS\ ADULTS + 1)/(FEEDS + 1).$

¹ *PREY* and *BIOMASS* were estimated at a different set of nests (see Methods).