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EFFECT OF GROWTH AND HATCHING ASYNCHRONY ON THE FLEDGING AGE OF BLACK AND RED KITES

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ABSTRACT.—We studied the effect of growth rate, final size, hatching sequence, hatching asynchrony, and fledging asynchrony on the fledging age of Black and Red kites (*Milvus migrans* and *M. milvus*). Feather growth explained 43% and 38% of the variance in fledging age of Black and Red kites, respectively. Fledging age increased with hatching sequence and increased fledging asynchrony in relation to initial hatching asynchrony of both species, especially in broods of three chicks. Once the effect of growth was removed, no differences in fledging age related to hatching sequence were found in the Red Kite, but there was still a delay in fledging of third-hatched Black Kite chicks. Synchronous fledging of first- and second-hatched Black Kite chicks seemed to occur when both chicks had grown at a similar rate, and was caused by a delay in the fledging of the first-hatched chick. First-hatched Black Kite chicks did not delay fledging if second-hatched chicks experienced reduced growth. Differences between the two species in the third-hatched-chick fledging delay could be due to differences in nest provisioning by adults during the postfledging dependence period. Red Kites reduced provisioning to the nest as soon as the first chick fledged, while Black Kites maintained nest provisioning longer. No evidence was found supporting the idea that parents may reduce feedings to hasten first flight of their offspring. *Received 20 May 1991, accepted 10 February 1992.*

THE LENGTH of the nestling period in birds is thought to be correlated with growth rate (Ricklefs 1968, Skutch 1976, Zach 1982b, Poole 1989). Thus, it has been used in comparative studies of growth (e.g. Bortolotti 1986a) because growth rates are more difficult to obtain. However, species with similar rates of development may have nestling periods of different length, suggesting that selective factors affecting growth rate are not the only ones acting on fledging age (Maher 1964, Skutch 1976, Zach 1982a, Freed 1988). Some studies have explored the effect of growth rates on the length of the nestling period and the extent to which growth and fledging age are related (Zach 1982a, b, Bortolotti 1984, 1986b).

Hatching asynchrony within a clutch is a widespread trait in birds that may result in the development of feeding hierarchies promoting differences in growth rates (Bryant 1978, O'Connor 1984) that can influence fledging age (Clark and Wilson 1981). There also may be a parent-offspring conflict over fledging age (Trivers 1974, 1985), the chicks trying to extend the nestling period and the parents trying to force the first flight of their chicks by a reduction in feeding rates, or by means of special behavioral mechanisms (Rowan 1955, Brown and Amadon 1968, Walker 1972, Skutch 1976, O'Connor 1984, Poole 1989). A prolonged nestling period would give extra parental care (food and defense against predators) to the chicks, increasing their survival expectancy, but also could increase the rearing costs beyond the optimum for parents.

Some studies on fledging of species in the Passeriformes have shown a trend for synchronizing the date of first flight among siblings, but it is not clear if fledging synchrony is obtained by a delay in first flight of the oldest chicks (Freed 1988), by an earlier fledging of the youngest (Gibb 1950, Skutch 1976, Zach 1982a), or by both phenomena (Lemel 1989).

Raptors follow the general trend of interspecific increase of fledging age with body size (Newton 1979, Bortolotti 1986a). Also, the smaller males fledge at a younger age than the females in size-dimorphic species (Scharf and Balfour 1971, Sherrod 1983, Wyllie 1985, Bortolotti 1986b, Poole and Bromley 1988, Delannoy and Cruz 1988), and this has been related to differences in growth rates and final size between sexes (Newton 1979, Bortolotti 1984). Hatching sequence in the asynchronous hatching Black Kite (*Milvus migrans*) has been said to affect fledging age (Bustamante and Hiraldo 1989) following the observed differences in growth rates related to hatching sequence (Hiraldo et al. 1990).

In the present study, we address the following questions: (1) To what extent do differences in hatching asynchrony and growth among individuals explain observed differences in length of the nestling period in the Black Kite and the Red Kite (*M. milvus*)? (2) Are other factors independent of growth affecting fledging age? (3) Do siblings synchronize fledging? (4) Can the parent's behavior affect the age of first flight of their offspring?

STUDY AREA AND METHODS

Research was carried out in southwestern Spain at Doñana National Park (37°00'N, 6°30'W), where the two species coexist. The three main habitats in the area are: "marisma," or seasonally drying marshland; Mediterranean scrubland with scattered cork oaks (*Quercus suber*); and coastal sand dunes with stone pine (*Pinus pinea*) stands. For more detailed descriptions of the area, see Valverde (1958, 1960), Allier et al. (1974) and Rogers and Myers (1980). Both species nest in trees in the Mediterranean scrubland and coastal sand dunes, but most nests are found close to the marisma. Red Kites were studied during 1987 and 1988 in the Doñana Biological Reserve (west of the park) and Black Kites during 1988 and 1989 in "Matas Gordas" (north of the park); the areas are physiographically similar, but differ in relative breeding densities of both species.

We studied 10 one-chick, 5 two-chick, and 5 three-chick broods of Red Kites, and 33 one-chick, 25 two-chick, and 6 three-chick broods of Black Kites. We considered only those nests where at least one chick survived until fledging. Fledging age was not known for two second-hatched Black Kite chicks in broods of two chicks and were excluded from the analysis. There was high mortality in the first two weeks of the nestling period, so we considered brood size when chicks were 15 days old. All nests were found during or before laying, and were visited daily when hatching was expected, so that exact hatching date and sequence were known for each chick.

Chicks were marked shortly after hatching with indelible color ink, banded with metal bands and individually numbered plastic bands when they were about 25 days old, and marked with different combinations of Saflag colored wing tags (Kochert et al. 1983) when about 30 days old. Individual chicks could be recognized at all times during the nestling period and from a distance during and after fledging.

After hatching, nests were visited every four to six days, and all nestlings were measured. Body mass was measured in grams with Pesola balances with an error of less than 1%, tarsus length with Vernier callipers to the nearest 0.1 mm, and seventh-primary length flattened with a ruler to the nearest millimeter. Growth-rate constants K for weight (K_w) and tarsus (K_t) and asymptotes (A_w and A_t) were estimated for each individual fitting the data to a logistic curve following Ricklefs (1967). Data for seventh-primary length were fitted to a least-squares linear regression for each individual. Growth of flight feathers is not finished when the chicks fledge; therefore, a linear model affords a better adjustment, as has been shown for other species of birds (Haftorn 1978, Richter 1983) and also for kites (Hiraldo et al. 1990). The intercept of the regression line was assumed to be the age at which the feather started growing (S_f), the slope equivalent to the feather growth rate (K_f), and we also estimated the feather length at fledging (L_f).

Nests were visited daily once the oldest chick of a brood was 45 days in the Red Kite and 40 days in the Black Kite. We made these daily visits until all the chicks of the brood had fledged; fledging date and age for each individual were recorded. The observer approached the nest tree at its base and recorded whether any chicks flew from the nest or remained perched on it or nearby branches. If chicks were not at the nest, the observer inspected the trees near the nest for 10 to 20 min and tried to locate chicks perched or flying in the vicinity. Fledging date for an individual was the first day that: (1) it was observed to fly when the observer approached the nest tree or was observed flying during the visit; (2) it was not located on the nest or nest tree, and was found alive in subsequent visits; or (3) it was on a perch that the chick could not have reached without flying from the nest. It did not seem that observer interference hastened first flights, as fledging ages obtained by this method did not differ from those obtained monitoring other kite nests from a distance from dawn to dusk every two to three days (Bustamante 1990).

Hatching asynchrony (*HA*) for second-hatched chicks was defined as the number of days between hatching of the first and second chicks in the brood. We considered *HA* for third-hatched chicks to be the number of days between hatching of the first and third chick in the brood. Fledging asynchrony (*FA*) was the number of days between the fledging of first- and second-hatched chicks, and between first- and third-hatched chicks. In those cases when second-hatched chicks flew earlier than the first-hatched sibling, a negative value of fledging asynchrony was obtained.

To determine whether adults could reduce food provisioning to the nest to hasten first flight, we recorded for 13 other pairs of Black Kites the food remains found in the nest every one to two days, from the time the eldest chick was 35 days old—13 days before average fledging age according to previous estimates (Bustamante and Hiraldo 1989)—until it fledged. For each visit we recorded the number of

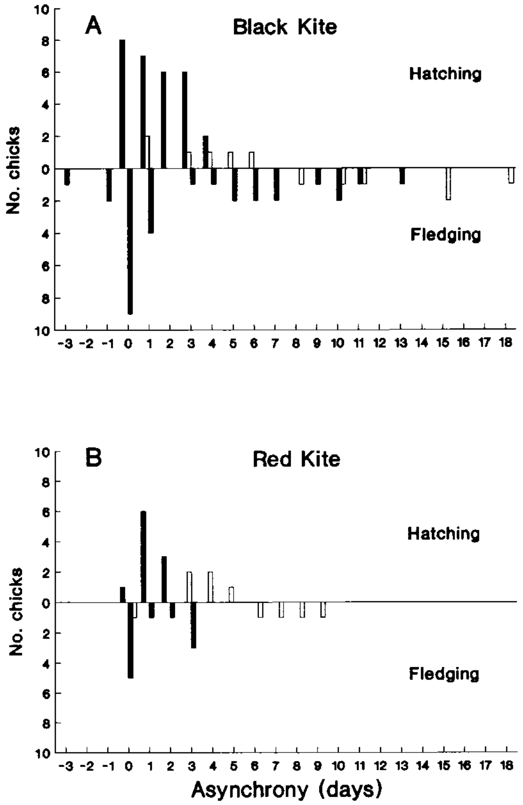

Fig. 1. Frequency distribution of hatching and fledging asynchronies of second- and third-hatched chicks in Black and Red kites. Black bars represent number of second-hatched chicks and white bars number of third-hatched chicks.

new prey items at the nest and estimated their biomass. Data from each nest were correlated with chick age to detect trends in numbers of prey and biomass brought to the nest. We also estimated average number of prey per chick-day, and average biomass per chick-day brought to each nest, and correlated it with fledging age of the eldest chick.

RESULTS

We did not find any difference between years in fledging age in the Black Kite (t = 0.680, df = 97, P = 0.498) or the Red Kite (t = 0.969, df = 33, P = 0.340), so years were pooled for all analyses. In Black Kites, hatching was asynchronous for 72.4% of second-hatched (n = 29) and all third-hatched (n = 6) chicks. Fledging was asynchronous for 70% of second-hatched and all third-hatched chicks (Fig. 1A). In second-hatched chicks, the median increase in fledging asynchrony (*FA*-*HA*) was 1 day (range −5 to 13 days, n = 29); however, differences between *FA* and *HA* were not statistically significant (median *HA* = 1 day, median *FA* = 1 day, n = 29; Wilcoxon signed rank test Z = 1.56, P = 0.12). In third-hatched chicks, fledging asynchrony was always greater than hatching asynchrony (median *HA* = 3.5 days, median *FA* = 13 days, n = 6; Z = 2.09, P = 0.036) and the median increase in FA was 9 days. *HA* and *FA* were not significantly correlated in Black Kites (Spearman rank correlation; second-hatched chicks, $r_s = -0.4$, P = 0.83; third-hatched chicks, $r_s = -0.094$, P = 0.82).

In Red Kites, hatching was asynchronous for 90% of second-hatched (n = 10) and all third-hatched (n = 5) chicks. Fledging was asynchronous for 50% of second-hatched and 80% of third-hatched chicks (Fig. 1B). *FA* in second-hatched chicks was not greater than the initial *HA* (median *FA*-*HA* was 0 days). *FA* tended to increase in relation to *HA* in third-hatched chicks (median increase in *FA* was 8 days), but it was not significant (Z = 1.62, P = 0.11). *HA* and *FA* were not significantly correlated in Red Kites (second-hatched chicks, r_s = 0.43, P = 0.19; third-hatched chicks, r_s = 0.43, P = 0.19).

Fledging age was affected by hatching sequence in Black Kites (Table 1); third-hatched chicks fledged at a significantly older age than their first- and second-hatched siblings (Tukey range test, $P < 0.05$). Differences in fledging age were not significant in Red Kites (Table 1), although third-hatched chicks also fledged at an older age than their first- and second-hatched siblings. Chicks of single broods in both species do not differ significantly from first-hatched chicks of multiple broods.

Fledging age could be affected by sex, as has been found in other species of raptors. Black and Red kites show only slight reversed sexual size dimorphism (Cramp and Simmons 1980). As a result, nestlings cannot be sexed accurately. As the effect of sex on fledging age corresponds with differences in size between males and females (Bortolotti 1984, 1986b), we used the estimated mass and tarsus asymptotes for each individual (A_m and A_t) to test for differences in fledging age related to sex. Neither A_m or A_t had a significant effect on fledging age of either species (Table 2). As indicated by the negative correlation coefficients, neither in the Black Kite nor in the Red Kite did bigger individuals tend to fledge at older ages.

TABLE 1. Fledging age and seventh-primary growth rate (K_f) in relation to hatching sequence in Black and Red kites ($\bar{x}$ ± SD). Means with same superscript are not significantly different.

		Multiple-brood chicks			ANOVA	
	Single-brood chicks	First-hatched	Second-hatched	Third-hatched	*F*	*P*
			Black Kite			
n	33	31	29	6		
Fledging age	46.9^{a} ± 0.74	47.6^{a} ± 0.69	49.2^{a} ± 0.79	54.2^{b} ± 2.12	5.99	0.0009
K_f	7.01^{ab} ± 0.09	7.09^{a} ± 0.07	6.71^{bc} ± 0.08	6.37^{c} ± 0.17	5.99	0.0008
			Red Kite			
n	10	10	10	5		
Fledging age	56.4 ± 2.67	55.5 ± 2.38	54.4 ± 1.48	58.0 ± 1.87	0.35	0.79
K_f	7.22 ± 0.26	7.09 ± 0.11	7.02 ± 0.22	7.21 ± 0.36	0.18	0.91

We used stepwise multiple regression analysis (James and McCulloch, 1990), considering as predictors the growth variables K_m, K_t, K_f, S_f, A_m and A_t to study whether growth and/or size influenced fledging age. For both species, the best regression model was the one including the two variables related to primary feather growth, K_f and S_f, explaining 43% of the variance in fledging age in the Black Kite and 38% in the Red Kite (Table 3). No other growth variable explained a significant portion of the remaining variance. Even though K_f and S_f were obtained from the least-squares regression line adjusted to seventh-primary measures for each individual, these variables were not correlated (Black Kite, $r = -0.188$, $n = 99$, $P = 0.07$; Red Kite, $r = 0.071$, $n = 35$, $P = 0.68$).

Red Kites seem to be more variable than Black Kites in growth rates and fledging age. For all variables studied, coefficients of variation were 14 to 32% higher in the Red Kites, although A_m was an exception, being more variable in Black Kites (Table 4). This greater variability for Red Kites was the case, whether we considered only first-hatched chicks or chicks hatched the same year (1988). Growth rates of seventh primary, K_f, varied with hatching sequence in Black Kites (Table 1). First-hatched chicks of multiple broods had faster growth of primaries than second-hatched chicks, which had higher growth rates than third-hatched chicks (Tukey range test, $P < 0.05$). Single-brood chicks had faster feather growth than third-hatched chicks, but did not differ from first- and second-hatched chicks. We did not find this to be the case in Red Kites (Table 1).

The residuals of the multiple regression of fledging age on K_f and S_f were significantly different among hatching order classes for Black Kites ($F = 4.25$, df = 3 and 98, $P = 0.007$), but not for Red Kites ($F = 0.83$, df = 3 and 34, $P = 0.48$; Fig. 2). Also L_f varied significantly with hatching order in Black Kites ($F = 4.5$, df = 3 and 98, $P = 0.005$), but differences could not be detected in Red Kites ($F = 1.06$, df = 3 and 34, $P = 0.38$; Fig. 3). In both species second-hatched chicks tended to fledge at a younger age than that predicted by feather growth, relative to their first-hatched siblings (Fig. 2). Also, the predicted L_f of second-hatched chicks was slightly shorter than in first-hatched chicks, although differences were not significant (Fig. 3). Single-brood chicks of Black Kites fledged with primaries that were shorter than those of first-hatched chicks of multiple broods (Tukey range test, $P < 0.05$; Fig. 3), and the fledging age was slightly lower than predicted by feather growth (Fig. 2). Results for third-hatched Red Kite chicks were similar to those for second-hatched chicks. They fledged at a slightly younger age than that predicted by feather growth (Fig. 2) and with slightly shorter feathers (Fig. 3) than their first-

TABLE 2. ANOVA of linear-regression models for fledging age on tarsus and mass asymptotes (A_t and A_m) to detect possible effects of fledgling final size in Black and Red kites (r = Pearson product-moment correlation coefficient).

Variable	R^2	*r*	*F*	*P*
		Black Kite (n = 99)		
A_t	0.044	−0.21	4.50	0.04
A_m	0.028	−0.17	2.80	0.09
		Red Kite (n = 35)		
A_t	0.008	0.09	0.27	0.61
A_m	0.024	−0.156	0.82	0.37

TABLE 3. Best multiple-regression model for fledging age on growth variables in Black and Red kites. Seventh-primary growth rate (K_f) and age of emergence (S_f) were best predictors in both species.

	Coefficient	Student-*t*	*P*	*F*	*P*
			Black Kite		
Constant	65.77	12.17	<0.0001		
K_f	−4.03	−5.99	<0.0001	50.38	<0.0001
S_f	0.79	5.16	<0.0001	26.69	<0.0001
Model				38.53	<0.0001
			Red Kite		
Constant	76.74	7.38	<0.0001		
K_f	−4.96	−3.63	0.001	11.53	0.002
S_f	0.95	3.41	0.002	11.65	0.002
Model				11.59	0.0002

hatched siblings. The pattern of third-hatched Black Kite chicks seemed to be different. They flew for the first time at an age older than that predicted by feather development (Fig. 2) and with longer seventh-primary feathers (Fig. 3) than was the case for first- and second-hatched Black Kite chicks, although, probably due to the small sample size, these differences were not significant (Tukey range test).

To explore how synchronous fledging could be attained by second-hatched Black Kite chicks, we divided the sample of multiple broods in two halves: those in which fledging of second-hatched chick was synchronous ($FA < 2$ days); and those in which it was asynchronous ($FA > 2$ days). There were no cases of two days of fledging asynchrony, and the median of fledging asynchrony frequency distribution was one day (Fig. 1A). Also, two days was the midpoint between the two groups of fledging asynchronies observed in the frequency distribution (see Fig. 1A). Feather growth rates were similar for first-hatched chicks in both kinds of broods and for second-hatched chicks of synchronous fledging broods, but they were significantly lower in second-hatched chicks of asynchronous fledging broods (Fig. 4C; $F = 7.24$, df = 3 and 57, $P = 0.0004$; Tukey range test). First-hatched chicks in synchronous broods fledged at an age older than predicted by feather growth (residuals of regression on K_f and S_f were significantly greater) and with longer primaries than first-hatched chicks in asynchronous fledging broods (ANOVA of residuals, $F = 4.59$, df = 3 and 57, $P = 0.006$; ANOVA of L_f, $F = 4.14$, df = 3 and 57, $P = 0.01$, Tukey range test; Fig. 4A and 4B). There were no significant differences in the residuals or in L_f among second-hatched chicks in both kinds of broods and first-hatched chicks in asynchronous broods.

There was not a clear reduction in food brought to the nest before the first flight of the oldest chick in the Black Kite. In only 7 of 13 Black Kite nests in which food was monitored did biomass brought to the nest decrease slightly before the first flight of the oldest chick; the proportion of nests decreasing was not significantly greater than the proportion increasing ($X^2 = 0.39$, df = 1, $P = 0.84$; Table 5). For the seven nests in which food was reduced, fledg-

TABLE 4. Mean, standard deviation (SD) and coefficient of variation (CV) of growth variables in Black and Red kites.

	Black Kite ($n = 99$)		Red Kite ($n = 35$)	
	$\bar{x} \pm$ SD	CV	$\bar{x} \pm$ SD	CV
Fledging age (days)	48.2 ± 4.5	9.3%	55.8 ± 6.6	11.8%
S_f (days)	13.0 ± 2.3	17.5%	15.1 ± 3.2	21.0%
K_f	6.91 ± 0.52	7.5%	7.13 ± 0.65	9.1%
L_f (mm)	242.9 ± 23.9	9.9%	287.8 ± 33.1	11.5%
K_t	0.139 ± 0.022	16.1%	0.124 ± 0.026	21.3%
A_t (mm)	58.5 ± 2.6	4.4%	57.6 ± 3.2	5.6%
K_m	0.167 ± 0.028	16.8%	0.154 ± 0.032	20.8%
A_m (g)	778.6 ± 106.4	13.7%	953.1 ± 104.3	10.9%

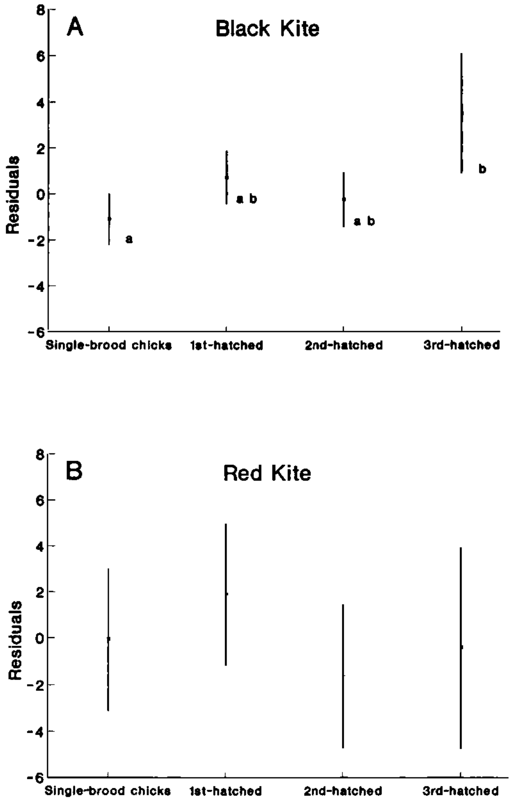

Fig. 2. Means ± 95% confidence intervals of residuals of multiple regression of fledging age on K_f and S_f in relation to hatching sequence in Black and Red kites. For the Black Kite, means with same letters not significantly different (Tukey range test, $P < 0.05$).

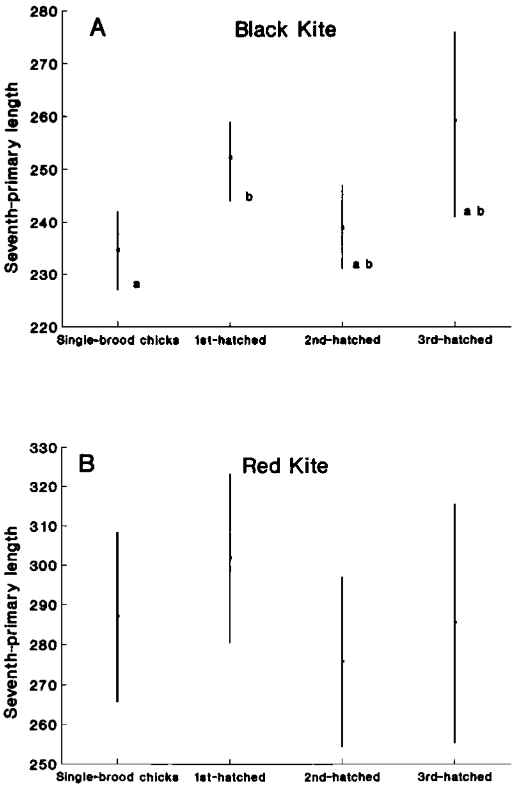

Fig. 3. Means ± 95% confidence intervals of the seventh-primary length at fledging in relation to hatching sequence in Black and Red kites. For the Black Kite, means with same letter not significantly different (Tukey range test, $P < 0.05$).

ing age was not significantly less than that of the remaining six nests ($t = 1.29$, $P = 0.224$). We did not find a significant positive correlation between fledging age and prey biomass per chick-day brought to the nest before fledging ($r_s = 0.04$, $n = 13$, $P = 0.90$), or with the number of prey per chick-day ($r_s = 0.48$, $n = 13$, $P = 0.09$).

DISCUSSION

In the few instances when hatching and fledging asynchrony both have been recorded for the same broods, either similar asynchrony (Oilbird, *Steatornis caripensis*, Snow 1961 *in* Skutch 1976; European Bee-eater, *Merops apiaster*, Lessells and Avery 1989) or reduced asynchrony at fledging (Common Tern, *Sterna hirundo*, Le Croy and Le Croy 1974; Tree Swallow, *Iridoprocne bicolor*, Zach 1982a; House Wren, *Troglodytes aedon*, Freed 1988) has been found. Detailed data on raptors are lacking, but information on hatching and fledging asynchrony in the Peregrine Falcon (*Falco peregrinus*) and Sparrowhawk (*Accipiter nisus*) suggest that hatching asynchrony usually is maintained or reduced at fledging (Ratcliffe 1980, Newton 1986). The increase in fledging asynchrony in relation to initial hatching asynchrony in third-hatched kite chicks is the first clearly recorded case of increased asynchrony at fledging. We did not find a significant correlation between hatching and fledging asynchronies. The frequency distribution of fledging asynchrony among second-hatched chicks of both kites (Fig. 1) shows that in some broods initial hatching asynchrony is reduced, while in others it is greatly increased.

Sex, as related to final body size, does not seem to have a significant effect on fledging age in Black and Red kites, at least in the way pre-

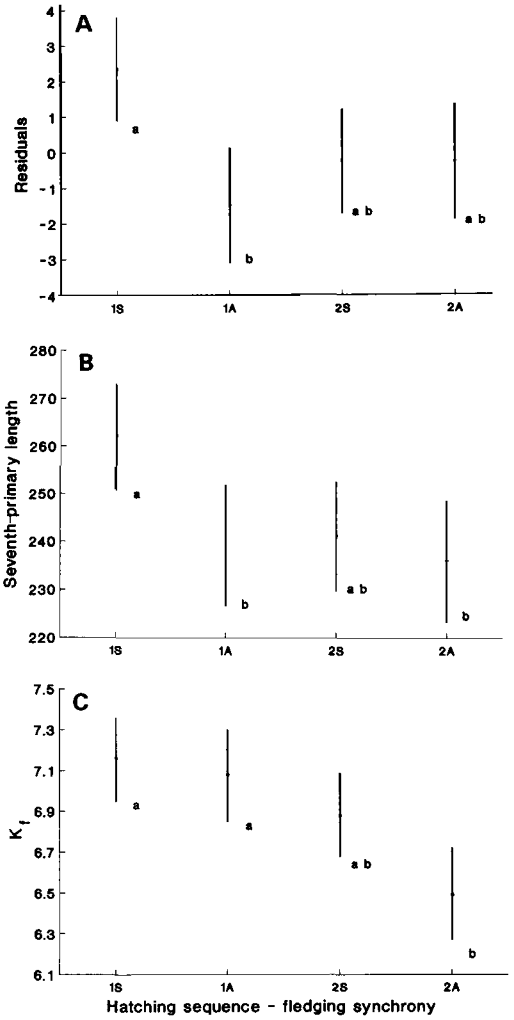

Fig. 4. Means ± 95% confidence intervals of (A) residuals of multiple regression of fledging age on K_f and S_f, (B) seventh-primary length at fledging, and (C) feather growth rate (K_f) in relation to hatching sequence and fledging asynchrony in Black Kites. The 1S and 2S are first- and second-hatched chicks of synchronous fledging broods, and 1A and 2A are first- and second-hatched chicks of asynchronous fledging broods. Means with same letter not significantly different (Tukey range test, $P < 0.05$).

dicted by previous work. We found a weak tendency in the Black Kite for birds with greater final size fledging at lower ages, a result opposite to that found previously (greater females fledging later than smaller males). However, this result could be more a consequence of the relationship between growth and fledging age (A_t and A_m were positively correlated with K_f, see below), than a reflection of sex-related fledging ages, especially taking into account that both species are only slightly dimorphic.

Growth, a highly variable trait in kites (Veiga and Hiraldo 1990, Hiraldo et al. 1990), is an important factor in determining fledging age. Variations in growth rate seem to explain better than hatching asynchrony variations in fledging age of both species. The initial size asymmetries created by hatching asynchrony may be increased or reduced during the nestling period (Viñuela unpubl. data), and this would explain why growth is a more important factor on fledging age, and why hatching asynchrony can be either increased or decreased at fledging. Variables introduced in the regression model for fledging age summarize growth in the first part (S_f) and second part (K_f) of the nestling period, and no other growth variable explains a significant part of the remaining variance. Once the effect of growth on fledging age is statistically removed, some of the unexplained variance of the model is explained in Black Kites by hatching sequence and fledging asynchrony.

In Black Kites, synchronization of the second-hatched chick with its older sibling at fledging, whenever it happens, is the result of a slight delay in the fledging of the first-hatched chick. Figure 4 shows second-hatched chicks that synchronize fledging with their older siblings have grown both at a similar fast rate, and the older sibling tends to delay fledging. Asynchronously fledging second-hatched chicks grow slower than their first-hatched siblings, and the latter do not delay fledging. Our results on growth agree with those of Hiraldo et al. (1990), who found that growth of first-hatched chicks in Black Kites shows little variation, while growth of second-hatched birds can be as fast as first-hatched, or as slow as third-hatched chicks.

It could be that the first-hatched chicks are able to modify their fledging date based on the condition of their younger siblings. Behavior of younger siblings could serve as an indicator of condition to their older sibling. The frequently executed behaviors of wing flapping and jumping vertically at the nest (Brown and Amadon 1968) develop when the chick is healthy and in an advanced stage of feather growth. Perhaps, this could stimulate the synchronized fledging of siblings. On the contrary, if the older sibling is ready to fly, but its younger sibling has not developed these behaviors, first flight might not be delayed.

TABLE 5. Mean number of prey items per chick and mean biomass of prey per chick (±SD) found at Black Kite nests at regular visits every one to two days after oldest chick was 35 days old and until it fledged (*r* = Pearson product-moment correlation coefficient of daily biomass with eldest chick age).

Nest	No. siblings	No. visits	No. prey	Biomass (g)	*r*	Fledging age[a]
A144	1	4	1.75 ± 1.26	280 ± 271	0.81	44
A191	1	6	3.33 ± 1.21	737 ∓ 238	0.44	48
B15	1	12	1.5 ± 1.09	164 ± 132	0.11	47
I2	1	12	4.92 ± 4.19	381 ± 325	−0.73	51
I6	1	9	1.0 ± 0.7	200 ∓ 208	−0.06	44
I8	1	11	1.9 ± 1.2	193 ± 186	0.04	48
A211	2	7	1.14 ± 0.48	185 ± 75	0.37	50
H4	2	8	1.25 ± 0.8	123 ± 121	−0.73	46
N39	2	12	1.45 ± 1.03	159 ± 78	−0.13	46
B2	2	8	1.18 ± 0.59	232 ± 187	−0.70	43
B16	2	14	1.89 ± 1.32	242 ± 183	−0.29	49
I9	2	9	0.72 ± 0.51	133 ± 75	−0.09	44
I11	3	18	1.44 ± 0.63	127 ± 67	0.20	52

[a] Fledging age of oldest chick in brood.

What is the advantage obtained by the first chick by delaying fledging? Fledging synchrony has been observed in some passeriforms (Zach 1982a, Freed 1988, Lemel 1989). It has been said that parents reduce their efficiency if they have to feed fledglings and nestlings simultaneously and, if fledglings are favored over nestlings during feedings, this would stimulate fledging synchrony. The senior chick delays its fledging to attain kin-selection-related advantages, or last-hatched chicks advance their fledging, trying to counteract disadvantages imposed by parental feeding behavior (see Freed 1988 and Lemel 1989). In our study, fledging synchrony would not be necessary, since adults continue to bring food mostly to the nest during the postfledging dependence period (Bustamante 1990). Nestlings would be favored over fledglings during feedings, because fledglings progressively spend more and more time away from the nest and adults seldom feed their young away from the nest. Moreover, late in the nestling period, feeding hierarchies are not so clear because size asymmetries among siblings are reduced (Newton 1979, Bortolotti 1986b). Perhaps, by synchronizing fledging, the first chick may prevent the second chick obtaining feeding advantages at the nest.

It seems that first chicks do not delay fledging when growth differences with their younger siblings are too large. Thus, although more research is needed, it is possible that a more delayed first flight is associated with other costs, perhaps related to the need to train flight muscles. Similar arguments relative to feeding hierarchies may be used; if size differences are substantial, the first chick might maintain its feeding advantages even being outside of the nest and, when the second chick reaches the size of the first chick, the latter could have learned to live more independently from its parents.

We did not find any similar effect for Red Kites, but the sample size for this species was much smaller. This fact, along with the greater variability in the parameters considered for Red Kites, could be masking some relationship with hatching order. However, feather growth does not show variation with hatching order in Red Kites (Table 1), fledging asynchrony is never as large as in Black Kites (Fig. 1), and perhaps Black Kite nestlings have more capacity to reduce growth (Veiga and Hiraldo 1990). Hence, it is possible that such marked size asymmetries do not exist in Red Kites.

Third-hatched chicks of both kites always have slower growth rates (Hiraldo et al. 1990, Veiga and Hiraldo 1990) and, for them, fledging asynchrony was greater than hatching asynchrony (Fig. 1). Red Kite third-hatched chicks fledge at an age closer to that predicted by their feather growth, while Black Kite third-hatched chicks fledge at an older age than that predicted by feather growth and with longer primary feathers. Black Kites continue bringing food to the nest for a long period during the postfledging dependence period and do not seem to reduce the amount of food brought (Bustamante and Hiraldo 1990, Bustamante 1990). The Red Kite reduces quickly the amount of food brought to the nest during the postfledging dependence period (Bustamante 1990). Under such circumstances, Black Kite third-hatched nestlings probably obtain feeding advantages when their older siblings fledge, and could probably delay fledging (there is no stimulation by siblings and the amount of food they receive is maintained or even increased). On the contrary, in Red Kite nests, feeding improvement is not clear for third-hatched chicks and, probably, hunger would hasten first flight.

Although Bustamante and Hiraldo (1990) proposed that Black Kites could reduce feedings before fledging to promote the first flight by the young, we have not been able to find a clear reduction in feedings. Sometimes, starving nestlings of Black and Red kites jump or fall from the nests before they are able to fly (pers. observ.). Similar behavior has been observed in other raptors like Lesser Kestrels (*Falco naumanni*) when feeding conditions are poor (J. Negro and J. Bustamante unpubl. data). Nevertheless, the amount of food brought to the nest at the end of the nestling period has no clear effect on the fledging age in healthy chicks, and a reduction in feeding rates is not a general phenomenon in this species. The food brought to the chicks by Black Kites has a great seasonal and daily variation (Veiga and Hiraldo 1990, Viñuela unpubl. data), and it is doubtful that only slight variations in feeding frequency could affect fledging ages.

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