

until one had 15 attacks, may mask the real meaning of 'winning' when contesting resources. Under laboratory conditions, individuals with high expectations may be 'motivated' to attack first (as in nature), but as a contest progresses, information on such things as 'fighting ability' and other 'intrinsic' factors may affect the probability of winning a prolonged encounter (Parker & Rubenstein 1981).

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References

- Beacham, J. 1988. The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish. *Anim. Behav.*, **36**, 623–624.
- Dowd, B. & Elwood, R. 1985. Shell wars II: the influence of relative size on decisions made during hermit crab shell fights. *Anim. Behav.*, **33**, 649–657.
- Ewald, P. 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Anim. Behav.*, **33**, 705–719.
- Parker, G. 1974. Assessment strategy and the evolution of fighting behaviour. *J. theor. Biol.*, **47**, 223–243.
- Parker, G. & Rubenstein, D. I. 1981. Role assessment, reserve strategy and acquisition of information in asymmetric animal contests. *Anim. Behav.*, **29**, 221–240.
- Verrell, P. 1986. Wrestling in the red-spotted newt: resource value and contestant asymmetry determine contest duration and outcome. *Anim. Behav.*, **34**, 398–402.
- (Received 16 June 1989; initial acceptance 17 July 1989; final acceptance 7 August 1989; MS. number: AS-634)

Adoptions of Fledglings by Black and Red Kites

Adoptions in nidifugous birds (Pierotti & Murphy 1987) are known to be frequent. In nidicolous species adoptions are also possible, especially during the post-fledging dependence period. Black kite, *Milvus migrans*, and red kite, *M. milvus*, fledglings are dependent on their parents for about 4 weeks so those from different nests could intermingle and recognition errors might arise. Here we document the occurrence of adoption in kites and try to identify the factors that promote it.

We studied the post-fledging dependence period of 90 black kite juveniles from 47 breeding pairs from 1985 to 1988 and of 37 red kite juveniles from

21 breeding pairs from 1987 to 1988, in the Doñana Biological Reserve, south-west Spain. All juveniles were individually marked with plastic wing-tags a week before their first flight. Eleven black kite and six red kite juveniles were also equipped with a transmitter fixed with a back-pack harness. We checked nests in a 2-h period after sunrise or before sunset at least every 2 days (but almost daily when adoptions were detected) and recorded the location of all juveniles. Observations started when the eldest chick was 40 days old and ended when no fledgling roosted near the nest on 3 consecutive observation days. All nests had been previously monitored so hatching dates were known or could be estimated. Thirteen of the black kite nests and five of the red kite nests were also continuously monitored during 5–9 complete observation days, regularly distributed over the post-fledging dependence period. Complete observation days and radio-tagged fledglings showed that dependent fledglings always roosted near their nest, so that age of independence and identity of fledglings dependent on a particular adult pair could be estimated with reasonable accuracy from short daily observations and for individuals that were only wing-tagged.

During the first 2 weeks after fledging four marked red kite fledglings (10.8%) and one black kite fledgling (1.1%) abandoned their nests and were adopted by neighbouring breeding pairs of the same species. Five monitored red kite pairs (23.8%) permanently adopted unrelated fledglings but only one black kite pair did so (2.1%). The proportion of fledglings adopted and of pairs that adopted differed significantly between the two species ($\chi^2 = 4.59$, $df = 1$, $P < 0.05$ and $\chi^2 = 6.00$, $df = 1$, $P < 0.05$, respectively).

We never observed the exact moment of adoption but could estimate the age at adoption within 1–2 days (Table 1). Adopted red kite fledglings were older than the oldest fledgling of the adopting pair. In the single observed black kite adoption, the original fledgling had disappeared a few days before the adoption took place, and the adopted fledgling was of the same age. In both species adopted fledglings changed their home ranges so that the adoptive nest became its centre. They were never seen to be attacked by adoptive parents or by the latter's offspring and fed on prey brought to the nest by the adults.

Two weeks after fledging, kite juveniles wander further from the nest, regularly visiting nests in the vicinity, pirating food if possible. At least three red kite and 12 black kite fledglings (not those that had been adopted) were seen switching nests but returning to roost at their nest until they became independent.

Table I. Characteristics of adoptions observed

	Fledgling					
	BKJ1	RKJ2*	RKJ1*	RKJ2*	RK?	RKJ1
Year	1987	1987	1987	1987	1987	1988
Number of fledglings at natal nest	2	3	2	3	1?	3
Number of fledglings at foster nest	1	3	2	1	1	3
Distance moved (m)	500	725	690	1300	575?	725
Age at adoption (days)	65	60	73	69	?	58
Ages and fate of siblings at foster brood	†	57	62	50‡	50‡	47
		56	60			46
		54‡				44
Age of independence of adopted chick from foster parents	80	87	85	82	?	83
% Of post-fledging spent at foster nest	44.0	84.4	44.4	43.3	?	75.8

BK: black kite; RK: red kite; J1 and J2 are respectively first and second hatched chick at the natal nest. RK? probably came from a nearby nest with only one fledgling, which was not monitored.

*Equipped with transmitter.

†Disappeared 2 days before adoption (62 days old), probably died.

‡Died before independence.

Although a slightly larger proportion of red kite fledglings from broods of three (three from 15 fledglings) abandoned their nest than those from broods of two (1/12) or one (0/10), they were never the smaller last-hatched sibling (Table I), and so would not have been suffering food stress. The mean number of feeds per day ($\bar{X} \pm \text{SD} = 3.4 \pm 2.6$, $N = 10$) and minutes spent by an adult near the nest ($\bar{X} \pm \text{SD} = 343.2 \pm 172.2$, $N = 10$) at nests that lost fledglings were similar to those at nests that adopted ($\bar{X} \pm \text{SD} = 2.5 \pm 2.4$ feeds and $\bar{X} \pm \text{SD} = 374 \pm 173.5$ min, $N = 6$).

The younger offspring of three red kite pairs that adopted fledglings ($N = 5$) died during post-fledging while this happened to only two pairs that did not adopt ($N = 16$; Fisher test, $P = 0.0137$). Also, if parental investment was adjusted to brood size, the adoption of an intruder would increase parental effort and might decrease future adult survival or reproduction.

Risks for juveniles seeking food or adoption are low, as attacks by adults of both species rarely injure the intruder. Adopted fledglings could benefit in three ways. (1) They might be adopted by a pair that invests more in feeding or defence against predators. However, none of the adopted kite fledglings got into nests where feeding rate or vigilance was greater than at their nests of origin. (2) They might enter a brood with younger fledglings in which they would compete for feedings more successfully. All adopted red kite fledglings were older than the oldest offspring of the adopting pair. In this species competition for food among

siblings seems to be important as suggested by the high mortality of the younger siblings in broods increased by adoption. (3) Fledglings might prolong the period of parental care. This was not the case in our study, however, as the age of independence did not differ for adopted fledglings ($\bar{X} \pm \text{SD} = 84.3 \pm 2.2$ days, $N = 4$) and their original siblings ($\bar{X} \pm \text{SD} = 82.2 \pm 6.7$ days, $N = 6$; $t = 0.59$, $df = 8$, ns).

Adoption may be a result of altruism (Pierotti 1980, 1982), kin selection (Waltz 1981; Poole 1982), intergenerational conflict (Pierotti & Murphy 1987; Pierotti et al. 1988) or a maladaptive behaviour (Bitterbaum & Brown 1981; Holley 1981, 1988). The reduction in fitness that adoption causes in adopting adults makes it unlikely that this behaviour evolved by means of altruism or reciprocal altruism. Kin selection cannot be totally excluded as, due to the philopatric behaviour of both kites (J. Bustamante & F. Hiraldo, unpublished data), neighbouring breeding pairs could be closely related. The single black kite adoption could fit this model as the adopted pair seemed to have lost their offspring 1–2 days before the adoption took place and might have increased their inclusive fitness by helping to raise a fledgling of a related pair. Unless the degree of relatedness among neighbouring breeding pairs in the two species differs, however, kin selection cannot explain why red kite adoptions are more frequent. Intergenerational conflict may explain why fledglings switch nests at the end of post-fledging when parental investment is starting to decrease and why adult black kites chase away

juvenile intruders when they are detected. Red kite adults, however, should be just as aggressive towards intruders as their fledglings are also able to change nests.

We suggest that the relatively low nearest-neighbour distance between red kite nests in our study area (\bar{X} = 893.1 m, range = 690–2250, N = 21; elsewhere in Europe 4–5 km; Davies & Davis 1973; Valet 1975) is the proximate cause for the high frequency of adoptions observed. Red kite fledglings fly up to 400 m from the nest during the first 2 weeks after fledging (J. Bustamante & F. Hiraldo, unpublished data). With a nearest neighbour at 4–5 km a still dependent fledgling is unlikely to enter another territory.

Although in Doñana black kites nest even closer to each other than red kites (\bar{X} = 205.7 m, range = 30–630, N = 47) there are fewer black kite adoptions. Colonial species may be better at recognizing offspring than closely related solitary ones as has been demonstrated for hirundines (Stoddard & Beecher 1983). Black kites, which habitually nest in loose groups, behave aggressively towards intruding fledglings and never towards their offspring (Bustamante & Hiraldo, in press a) while the more solitary red kites never attack any fledglings coming near their nests (Bustamante & Hiraldo, in press c). This aggressive behaviour of black kites probably prevents frequent permanent adoptions, as fledglings of both species develop flying skills at a similar rate (Bustamante & Hiraldo in press b, unpublished data) and frequently visit close neighbouring kite nests. We therefore suggest that the higher frequency of adoption by red kites is due to a maladaptation to breed at high density.

Funding was provided by CSIC-CAICYT and a Predoctoral Fellowship of the PFPI to J.B. We thank M. Hiraldo, G. Doval, F. Domínguez, F. Martínez, J. Jañez, M. Aragonese, J. Viñuela, J. Chan, G. Vilchez and P. Ferreras for assistance in the field and E. Aguilera, J. Aguilar-Amat, A. J. F. Holley, and R. Pierotti for helpful suggestions on a first version of this paper.

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References

- Bitterbaum, E. J. & Brown, C. R. 1981. A martin house is not a home. *Nat. Hist.*, **90**, 64–67.
- Bustamante, J. & Hiraldo, F. In press a. Factors influencing family rupture and parent-offspring conflict in the black kite (*Milvus migrans*). *Ibis*.
- Bustamante, J. & Hiraldo, F. In press b. Post-fledging dependence period and maturation of flight skills in the black kite *Milvus migrans*. *Bird Study*.
- Bustamante, J. & Hiraldo, F. In press c. Parental investment in nest-defence by kites *Milvus milvus* and *M. migrans*, during the post-fledging dependence period. *Behav. Ecol. Sociobiol.*
- Davies, P. W. & Davis, P. E. 1973. The ecology and conservation of the red kite in Wales. *Br. Birds*, **66**, 183–224.
- Holley, A. J. F. 1981. Naturally arising adoption in herring gulls. *Anim. Behav.*, **29**, 302–303.
- Holley, A. J. F. 1988. Intergenerational conflict in gulls. *Anim. Behav.*, **36**, 619–620.
- Pierotti, R. 1980. Spite and altruism in gulls. *Am. Nat.*, **115**, 290–300.
- Pierotti, R. 1982. Spite, altruism and semantics: a reply to Waltz. *Am. Nat.*, **119**, 116–130.
- Pierotti, R., Brunton, D. & Murphy, E. C. 1988. Parent-offspring and sibling-sibling recognition in gulls. *Anim. Behav.*, **36**, 620–621.
- Pierotti, R. & Murphy, E. C. 1987. Intergenerational conflicts in gulls. *Anim. Behav.*, **35**, 435–444.
- Poole, A. 1982. Breeding ospreys feed fledglings that are not their own. *Auk*, **99**, 781–785.
- Stoddard, P. K. & Beecher, M. D. 1983. Parental recognition of offspring in the cliff swallow. *Auk*, **100**, 795–799.
- Valet, G. 1975. La sedentarisation du milan royal *Milvus milvus* en Auxois. *Alauda*, **43**, 263–269.
- Waltz, E. C. 1981. Reciprocal altruism and spite in gulls: a comment. *Am. Nat.*, **118**, 588–592.

(Received 24 April 1989; initial acceptance 27 June 1989;
final acceptance 14 August 1989;
MS. number: sc-514)

Similarity of Songs Within Songbird Repertoires: Analytic Problems

According to several hypotheses, song repertoires are an adaptation that reduces habituation of listening birds (see references in Whitney 1981). These hypotheses predict that repertoires should be composed of dissimilar songs: listening birds will generalize little between these songs and therefore will habituate more slowly than to repertoires of more similar songs.

Results consistent with this prediction have been obtained for two species, great tits, *Parus major*, and varied thrushes, *Zoothera naevia*. The phrase length of great tit songs is more variable within repertoires than among repertoires (Krebs 1976). The dominant frequency (Hz) and modulation rate of varied thrush songs are each more variable within repertoires than would be expected if the songs were drawn at random from all the songs in the population (Whitney 1981).