

Short communication

Alloparental care and kleptoparasitism in the semicolonial Montagu's Harrier *Circus pygargus*

BEATRIZ E. ARROYO^{1,2*} & JESUS T. GARCÍA³

¹Centre d'Etudes Biologiques de Chizé, CNRS,
79360 Villiers en Bois, France

²Centre for Ecology and Hydrology, Hill of Brathens,
Banchory AB31 4BY, Scotland

³Departamento de Biología Animal I, Facultad de
Ciencias Biológicas, Universidad Complutense,
28040 Madrid, Spain

Alloparental care, where foster parents feed or defend foreign nestlings, has been reported in many bird species (Riedman 1982). This seemingly altruistic behaviour does not show a uniform pattern among bird groups, and has different interpretations according to when the adoption takes place, and whether the young are precocial, semi-precocial or altricial (e.g. Pierrotti 1991, Choudhury *et al.* 1993, Redondo *et al.* 1995, Brown 1998).

In the case of raptors, temporary or permanent adoptions have been reported in several species, mainly in the post-fledging period (e.g. Poole 1982, Simmons 1992, Bustamante & Hiraldo 1993b). In these cases, alloparental behaviour is apparently initiated by the demand for food from fledglings, and may be forced (the result of kleptoparasitism) or arise through the parents' inability to discriminate. Bustamante and Hiraldo (1993b) observed that fledgling adoptions were more frequent in the territorial Red Kite *Milvus milvus* than in the colonial Black Kite *M. migrans*. They suggested that colonial species may be better at recognizing offspring than solitary ones, given that fledgling intrusions are potentially more frequent in colonial contexts (see also Simmons *et al.* 1987), and that alloparental feeding may happen maladaptively in territorial species when breeding at high densities. However, this hypothesis has never been explored further.

We report on the occurrence of alloparental feeding of fledglings in the semicolonial Montagu's Harrier *Circus pygargus*. We also examine, through the acceptance of introduced nestlings and fledglings and the agonistic behaviour of parents, whether Montagu's Harriers can recognize their own offspring. Finally, we discuss these data together with those published in other raptor species to evaluate whether misdirected feeding is more common in territorial than colonial raptors.

*Corresponding author.
Email: bea@ceh.ac.uk

METHODS

From 1993 to 1995, we monitored 89 individually identifiable wing-tagged Montagu's Harrier fledglings from 29 nests in north-eastern Madrid province (central Spain, 40°38'N, 3°30'W). All nests in the study area were in cereal fields. Most (85%) pairs bred in clumps of 2–16 nests. The average nearest-neighbour distance in colonies was 220 ± 141 m ($n = 331$). We defined the number of neighbours as the number of nests within 600 m. Nests were monitored twice a week for 2–3 h. Adults from the monitored nests were identified by wing-tags and plumage characteristics. The main aim of that study was to evaluate feeding rates (Arroyo 1995), and agonistic interactions between adults and fledglings were rarely quantified. Detailed data on parent-offspring behaviour during the post-fledging period were obtained in 1996 in Marais de Rochefort (Charente-Maritime, western France, 45°57'N, 0°55'W), when a colony of 10 pairs (where 60% adults were wing-tagged) with 29 wing-tagged fledglings was observed every 2 days. In addition to prey deliveries, agonistic interactions (chases followed by diving or talon presentation) were quantified, whether they were initiated by the adults or by the fledglings and, if the former, whether they were directed towards a fledgling of their own or another brood.

When nesting in cereal crops, unfledged Montagu's Harrier chicks may be killed at harvest time, and conservation measures have been implemented in many areas. In Madrid, we occasionally introduced nestlings into foster nests when no other conservation measures were possible. Foster nests were chosen so that the age of the nestlings was similar (within 4 days) to that of the introduced nestlings. We introduced one chick at each nest ($n = 14$), except in two cases when part of the foster brood had died due to harvesting activities, and where we introduced two nestlings in each nest.

RESULTS

In Madrid, fledglings followed and solicited food from food-carrying adults that were not their parents in 12 out of 58 prey deliveries, primarily in large colonies: this was never observed for prey deliveries in nests with 0–1 neighbours ($n = 8$), only once in a nest with two or three neighbours ($n = 9$), but it happened in 25% of prey deliveries at nests with more than four neighbours ($n = 41$). Such behaviour was also observed in Rochefort, but it was not quantified. In some cases (three in Madrid, seven in Rochefort) soliciting by unrelated fledglings was accompanied by chases and dives on the adult to try and steal the food. Four of these kleptoparasitic attempts were successful (two in Madrid, two in Rochefort). Only on three occasions did we observe non-pirated prey deliveries from adults to unrelated fledglings. Two of these observations (at Rochefort) involved two males whose own fledglings had already left the breeding area. Each of these males was seen once

delivering food to a different dependent fledgling from the same brood. The third observation (in Madrid) represented a case of permanent adoption. The foster pair nested in a large colony with 13 other pairs. They lost their own nestlings (aged 26–28 days old, just pre fledging age) when the field where the nest was located was harvested. A fledgling from a nearby nest (second from a brood of four) was seen 2 days later in the nest area of the foster pair, 400 m away from its own nest area. Both male and female from the foster nest were seen feeding the adopted fledgling 15 days after the adoption.

Parents were apparently able to recognize their fledged offspring. First, adults in Rochefort attacked unrelated fledglings twice as frequently as their own fledglings (0.015 ± 0.01 vs. 0.070 ± 0.05 attacks per hour, paired *t*-test, $t = 4.01$, $n = 10$, $P = 0.005$). Secondly, Montagu's Harriers in Madrid accepted foster nestlings introduced into their nests, but not fledglings: from 1991 to 1996, we introduced 15 nestlings aged 15–20 days into 14 nests. All of these introductions were successful: parents fed the introduced nestlings, and behaved similarly towards them and their own offspring after fledging. In contrast, we introduced three nestlings aged 27–29 days to two nests where some of the foster nestlings were already making their first flights. In both of these occasions, introduced nestlings were not accepted, i.e. they were not fed and were attacked by the adults if they solicited food, and had to be retrieved two days after introduction for their own welfare.

DISCUSSION

Alloparental care may be adaptive if foster parents gain benefits from their behaviour. Simmons (1992) described how a male African Marsh Harrier *Circus ranivorus* adopted the brood of a female that had recently lost her mate. Its breeding performance in subsequent years suggested that young adults may gain experience, a territory or a mate for future breeding through such behaviour. Such an explanation probably does not apply to the cases of alloparental care observed in the Montagu's Harrier, given that they occurred when neither parent was missing, and that mate fidelity is extremely low in this species (A. Leroux & V. Bretagnolle unpublished results). In the Montagu's Harrier, an important component of alloparental provisioning after fledging was the result of kleptoparasitism, and occurred mainly in large colonies (see also Pandolfi & Giacchini 1990). That the frequency of kleptoparasitic attempts increased with colony size indicates that they might represent some cost of coloniality. Nevertheless, successful attempts were rare (< 2%), so this cost is probably low. When not forced, alloparental feeding was only performed by breeding adults no longer engaged in feeding their nestlings. The only observed case of permanent adoption involved a pair that had lost their brood just before the adoption, as in the only case of adoption

observed in the Black Kite (Bustamante & Hiraldo 1993b). Parent Montagu's Harriers have been observed bringing food to the nest a few days after the brood died. This maintenance of parental investment after failure or fledgling departure might result from endocrinological mechanisms, which might be exploited by intruding fledglings in the same way that penguin chicks exploit failed breeders (Jouventin *et al.* 1995).

In any case, fledgling adoptions and misdirected feeding behaviour were relatively rare in the semicolonial Montagu's Harrier, as in other colonial species. Temporary or permanent adoptions involved more than 10% of the nestlings and nests in only one out of five colonial species, whereas such values were reached or exceeded in four out of five solitary species (Table 1). Bustamante and Hiraldo (1993b) stated that adoptions or allofeeding are a maladaptation for normally solitary species breeding at high densities. The latter implies that only species that are adapted to clumped nesting might have developed mechanisms preventing misdirected investment, such as fledgling recognition. The rejection of introduced fledglings and the higher aggression towards foreign fledglings observed in this study suggest that Montagu's Harriers were able to recognize their own fledglings (as observed in Northern Harriers *Circus hudsonii* by Simmons *et al.* 1987), although maybe not nestlings. Breeding raptors do not seem to discriminate against foreign chicks during the nestling period, and will raise nestlings that are not their own (review in Postupalsky & Holt 1975). Selection for nestling discrimination mechanisms in raptors has probably never occurred, given that nest switches by nestlings are extremely rare. They have only been described in the Lesser Kestrel *Falco naumanni* nesting colonially in buildings (Tella *et al.* 1997), where nestlings can walk between nests. In contrast, the benefits of fledgling discrimination are higher, as the probability of fledgling intrusions and kleptoparasitism is high in colonial contexts (e.g. this study). The latter might have selected for offspring discrimination at the fledgling stage in colonial raptors. In the four colonial species with low levels of fledgling adoption, adults frequently attacked unrelated fledglings approaching their nest area (Bustamante & Hiraldo 1993a, Bustamante & Negro 1994, Simmons 2000, this study). In contrast, such behaviour was rare in solitary species such as the Red Kite or the Common Kestrel *Falco tinnunculus* (Bustamante & Hiraldo 1993a, Bustamante 1994). However, a different behaviour towards foreign fledglings was also observed in the Egyptian Vulture *Neophron percnopterus* (Donazar & Ceballos 1990) and the Spanish Imperial Eagle *Aquila adalberti* (Ferrer 1993) suggesting that these species also had discriminating abilities, but that they were not efficient in avoiding misdirected behaviour when at very high density. In other words, offspring recognition alone might not prevent misdirected feeding behaviour.

Finally, mechanisms of offspring recognition in raptors are still unknown, and the question of how fledglings but

Table 1. Reported frequency of fledglings adopted (temporary or permanently) and percentage of foster nests involved, in raptors, according to their breeding system. S = solitary, C = colonial or semicolonial. Sample sizes in parentheses.

Species	Percentage of adoptions	Breeding system		Reference
		fledglings	nests	
Egyptian Vulture	25 (8)	33 (6)	S	Donazar and Ceballos (1990)
Goshawk	10 (70)	28 (77)	S	Kenward <i>et al.</i> (1993)
Sparrowhawk	17 (36)	–	S	Frumkin (1994)
Red Kite	11 (37)	24 (21)	S	Bustamante and Hiraldo (1993b)
Imperial Eagle	5 (36)	10 (19)	S	Ferrer (1993)
Average	13.6 ± 8	23.7 ± 10		
Osprey	23 (13)	40 (5)	C	Poole (1982)
African Marsh Harrier	10 (31)	8 (12)	C	Simmons (1992)
Montagu's Harrier	7 (29)	10 (10)	C	This study, Rochefort
Montagu's Harrier	1 (83)	3 (29)	C	This study, Madrid
Black Kite	1 (90)	2 (47)	C	Bustamante and Hiraldo (1993b)
Lesser Kestrel	0 (15)	0 (5)	C	Bustamante and Negro (1994)
Average	7.0 ± 8	10.5 ± 13		

not nestlings are recognized is also unclear. Parent-offspring or sibling recognition is based in acoustic signals in many bird species (e.g. Wanker *et al.* 1998, Jouventin *et al.* 1999). In many raptor species, chick calls change prior to, or after, fledging (Cramp & Simmons 1980), and the structure of chick calls and the information contained may also change with age (BrittanPowell *et al.* 1997). A potential explanation for fledgling but not nestling recognition in raptors could thus be that chick call structure changes prior to fledging to include individual characteristics. Further research would be needed to identify the costs and benefits of discrimination and aggressive behaviour at different nesting densities, the mechanisms of fledgling recognition, and when these mechanisms are developed during the rearing period.

We thank Luis Palomares, Sergio Ródenas and Elena Bellas for help with fieldwork in Madrid. Observations at Rochefort were made by Lionel Courmont. Work at Rochefort was part of a programme funded by a grant from the Région Poitou Charente and CNRS to P. Duncan and V. Bretagnolle. Javier Bustamante, Massimo Pandolfi, Steve Redpath, Rob Simmons and Pierre Jouventin commented constructively on the manuscript.

REFERENCES

- Arroyo, B.E. 1995. *Breeding ecology and nest dispersion of Montagu's Harrier Circus pygargus in central Spain*. DPhil thesis. University of Oxford, UK.
- BrittanPowell, E.F., Dooling, R.J. & Farabaugh, S.M. 1997. Vocal development in budgerigars (*Melopsittacus undulatus*): contact calls. *J. Comp. Psych.* **111**: 226–241.
- Brown, K.M. 1998. Proximate and ultimate causes of adoption in ring-billed gulls. *Anim. Behav.* **56**: 1529–1543.
- Bustamante, J. 1994. Family break-up in Black and Red Kites *Milvus migrans* and *M. milvus*: is time of independence an offspring decision? *Ibis* **136**: 176–184.

- Bustamante, J. & Hiraldo, F. 1993a. The function of aggressive chases by breeding Black and Red Kites *Milvus migrans* and *M. milvus* during the post-fledging dependence period. *Ibis* **135**: 139–147.
- Bustamante, J. & Hiraldo, F. 1993b. Adoptions of fledglings by black and red kites. *Anim. Behav.* **39**: 805–806.
- Bustamante, J. & Negro, J.J. 1994. The post-fledging dependence period of the Lesser Kestrel (*Falco naumanni*) in southwestern Spain. *J. Raptor Res.* **28**: 158–163.
- Choudhury, S., Jones, C.S., Black, J.M. & Prop, J. 1993. Adoption of young and intraspecific nest parasitism in Barnacle Geese. *Condor* **95**: 860–868.
- Cramp, S. & Simmons, K.E.L. (eds) 1980. *The Birds of the Western Palearctic*, Vol. 2. Oxford: Oxford University Press.
- Donazar, J.A. & Ceballos, O. 1990. Acquisition of food by fledgling Egyptian Vultures *Neophron percnopterus* by nest-switching and acceptance by foster adults. *Ibis* **132**: 603–617.
- Ferrer, M. 1993. *El Aguila Imperial Ibérica*. Madrid: Quercus.
- Frumkin, R. 1994. Intraspecific brood-parasitism and dispersal in fledgling Sparrowhawks *Accipiter nisus*. *Ibis* **136**: 426–433.
- Jouventin, P., Aubin, T. & Lengagne, T. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Anim. Behav.* **57**: 1175–1183.
- Jouventin, P., Barbraud, C. & Rubin, M. 1995. Adoption in the emperor penguin, *Aptenodytes forsteri*. *Anim. Behav.* **50**: 1023–1029.
- Kenward, R.E., Marcstrom, V. & Karlbom, M. 1993. Post-nestling behaviour in goshawks, *Accipiter gentilis*. II. Sex differences in sociality and nest-switching. *Anim. Behav.* **46**: 371–378.
- Pandolfi, M. & Giacchini, P. 1990. Cleptoparasitismo di juvenes su juvenes in albanella minore *Circus pygargus*. *Avocetta* **14**: 74–75.
- Pierrotti, R. 1991. Infanticide versus adoption: an intergenerational conflict. *Am. Nat.* **138**: 1140–1158.
- Poole, A. 1982. Breeding ospreys feed fledglings that are not their own. *Auk* **99**: 781–785.

- Postupalsky, S. & Holt, J.B.** 1975. Adoption of nestlings by breeding bald eagles. *J. Raptor Res.* **9**: 18–20.
- Redondo, T., Tortosa, F.S. & Arias de Reyna, L.** 1995. Nest switching and alloparental care in colonial white storks. *Anim. Behav.* **49**: 1097–1110.
- Riedman, M.L.** 1982. The evolution of alloparental care and adoption in mammals and birds. *Quart. Rev. Biol.* **57**: 405–435.
- Simmons, R.** 1992. Brood adoption and deceit among African Marsh Harriers *Circus ranivorus*. *Ibis* **134**: 32–34.
- Simmons, R.E.** 2000. *Harriers of the World. Their Behaviour and Ecology*. Oxford: Oxford University Press.
- Simmons, R., Barnard, P. & Smith, P.C.** 1987. Reproductive behaviour of *Circus cyaneus*. North America and Europe: a comparison. *Ornis Scand.* **18**: 33–41.
- Tella, J.L., Forero, M.G., Donázar, J.A., Negro, J.J. & Hiraldo, F.** 1997. Non-adaptive adoptions of nestlings in the colonial lesser kestrel: proximate causes and fitness consequences. *Behav. Ecol. Sociobiol.* **40**: 253–260.
- Wanker, R., Apcin, J., Jennerjahn, B. & Waibel, B.** 1998. Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behav. Ecol. Sociobiol.* **43**: 197–202.

Received 23 November 2000,
revised manuscript accepted 22 May 2001