

Brood-switching in Eagle Owl *Bubo bubo* fledglings

VINCENZO PENTERIANI* & MARÍA DEL MAR DELGADO

Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., Avda. de María Luisa s/n., Pabellón del Perú, Apdo 1056, 41013 Seville, Spain

Keywords: adoption, alloparental care, raptor.

Nest-switching, the (permanent or temporary) intrusion of one or several foreign young in another brood (which generally occurs when fledglings are capable of flight but are not yet completely independent of parents) and their subsequent adoption by a foster family (parents + native young), has been recorded in many bird species (Riedman 1982). These include several birds of prey (Ospreys *Pandion haliaetus*, Poole 1982, Gilson & Marzluff 2000; Eurasian Sparrowhawks *Accipiter nisus*, Wyllie 1985; American Kestrels *Falco sparverius*, Lett & Bird 1987; Egyptian Vultures *Neophron percnopterus*, Donazar & Ceballos 1990; Black Kites *Milvus migrans* and Red Kites *Milvus milvus*, Bustamante & Hiraldo 1990; Northern Goshawks *Accipiter gentilis*, Kenward *et al.* 1993; Spanish Imperial Eagles *Aquila adalberti*, Ferrer 1993; Lesser Kestrels *Falco naumanni*, Tella *et al.* 1997; Montagu's Harrier *Circus pygargus*, Arroyo & García 2002) and owls (e.g. Barn Owl *Tyto alba*, Roulin 1999).

One of the most intriguing aspects of this form of alloparental care (Riedman 1982) is the investment of resources by birds into non-genetic offspring, instead of allocating breeding effort exclusively to their own genetic contribution to future generations. Such behaviour seems incompatible with classic evolutionary theory, because it apparently violates the Darwinian principle by which selection does not act to benefit competing genotypes.

To explain adoptions in birds, several hypotheses have been invoked and tested. The potential explanations for nest-switching and alloparental care form two main groups (see reviews in Redondo *et al.* 1995, Bize *et al.* 2003). First, there may be adaptive explanations such as (1) benefit to fledglings (e.g. better care than in the natal nest, acquisition of a dominant rank within a younger brood, reduction of the ectoparasite load), and (2) kin-selected benefits

from a parental perspective when young switch to nests of related adults, diluting predation risk, or increasing breeding experience of related individuals. Secondly, there may be non-adaptive explanations such as reproductive errors or adoptions with negligible costs which do not affect reproductive success or survival of the foster parent. The different intensities of selection pressure for intruder chicks (surviving vs. dying) and foster parents (cost of investment in unrelated fledglings) can also be conceived of as an arms race (Pierotti & Murphy 1987). Under such a scenario, chicks are likely to 'win' (and consequently gain adoption) because the selection pressure is stronger than on foster parents to discriminate and reject intruders.

Here, we report detailed observations of two cases of nest-switching in radiotagged Eagle Owl *Bubo bubo* fledglings and discuss them in an evolutionary context. Because nest-switching occurred during the post-fledging dependence period (i.e. owlets were no longer in the nest because they abandon it completely), hereafter we consider it more appropriate to replace the term nest-switching with brood-switching.

METHODS

During 2003–06 we studied the post-fledging dependence period of 74 young Eagle Owls originating from 46 broods (south-western Spain; for more details see Penteriani *et al.* 2005 and Penteriani *et al.* 2007a). Chicks were sexed by molecular procedures using DNA extracted from blood.

Each individual was fitted with a teflon ribbon backpack harness that carried a 30-g radio-transmitter (Biotrack Ltd; see also Penteriani *et al.* 2007b). During the continuous radiotracking (from 1 h before sunset to 1 h after sunrise) of family units, we recorded two cases of brood-switching. In the first case (2004), due to the difficulty of simultaneously recording all the movements of a total number of seven owlets (3 switchers + 4 resident fledglings), we located owlet position once per hour.

In the second case of brood-switching (2006), because both the foster female and the switcher were radiotagged, it was possible to follow the two individuals simultaneously and continuously.

Locations of radiotagged animals were determined using biangulation with 3-element hand-held Yagi-antenna connected to an ICOM (IC-R20) portable receiver. Biangulations were generally done at a low range of distances (100–300 m), with an accuracy of $[00]x = 83.5 \pm 49.5$ m. Such a value was calculated when, after a biangulation, we needed to locate exactly the individual to manipulate it during field experiments (e.g. Penteriani *et al.* 2007b) or to record the cause of mortality if it died.

RESULTS

The brood-switching in 2004 took place after two-thirds of the post-fledging dependence period (Penteriani

*Corresponding author.
Email: penteriani@ebd.csic.es

Table 1. Characteristics of the **switcher** ($n_s = 4$) and **foster** ($n_f = 6$) Eagle Owl fledglings. In the 2004 post-fledging dependence period, three owlets switched between two neighbouring nesting territories (separated by c. 500 m; from nest C to nest Q). In the same period of 2006, one owlet switched between two nests separated by c. 3000 m (from nest T to nest S).

	Owlets									
	S_{C1}	S_{C2}	S_{C3}	F_{Q1}	F_{Q2}	F_{Q3}	F_{Q4}	S_{T1}	F_{S1}	F_{S2}
Date of brood-switching	28/06/04							29/07/06		
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
Age (days) when brood-switching occurred	119	123	125	123	125	130	132	128	137	139
Brood size when brood-switching occurred	3			4				3		
Distance (m) between natal and foster nests	535 ^a							2772 ^b		
Age (days) when dispersal starts	151	155	157	166	168	173	175	126	169	171
% post-fledging ^c at foster nests	30			30				0		
Young fate ^d	BF	UF	S	UF	UF	SA	SAR	SA	UF	SA

^aNearest neighbour nest.

^bNatal and foster nests are not neighbours, being separated by eight different territories of Eagle Owls (all of them with young when brood-switching occurred).

^cPercentage duration of the post-fledging period that switchers spent at foster nests, calculated from when the young reached the new nest site to when they started dispersal (for more information on the owlets post-fledging period see also Penteriani *et al.* 2005). Post-fledging starts when fledglings begin to move in the vicinity of the nest (i.e. when they begin to move away from the nest) and ends when they leave the parental home range to disperse.

^dBF = the transmitter battery failed approximately 12 months after dispersal, when the individual was still alive; UF = unknown fate, we lost contact with the owl just after the start of dispersal; S = shot; SA = still alive at December 2006; SAR = still alive in December 2006, and reproduced during the 2006 breeding season.

et al. 2005; Table 1). Three fledgling males (of nest C) left the parental territory and joined the nearest other occupied nest (nest Q) (see also Table 1 and Fig. 1). This nesting territory was occupied by four resident young (two males and two females), resulting in a total brood of seven fledgling owlets. Two of them were the same age as the intruders, the other two being older. The switching birds never returned to the parental territory, as shown by the home range that they explored until dispersal, which never overlapped with the territory of the male of the parental nest. From the moment at which brood-switching occurred to the start of dispersal, the switching birds moved closer to the foster nest than the home nest and occupied a smaller range than the resident fledglings. The mean distances of the three switchers ($n = 75$ locations during 6 complete nights of radiotracking) and the four resident fledglings ($n = 129$ locations during 6 complete nights of radiotracking) to the foster nest were 357 ± 207 m (range: 33–1197 m) and 415 ± 246 m (range: 60–2318 m), respectively. The mean distance between the seven owlets (the three switchers and the four residents; $n = 262$ contemporaneous locations during 6 complete nights of radiotracking) was 394 ± 267 m (range: 29–1661 m). The mean distance among the three switchers ($n = 56$ contemporaneous locations) was of 320 ± 243 m (range: 35–915 m), whereas mean distance among the four resident fledglings ($n = 164$ contemporaneous locations) was 390 ± 337 m (range: 17–2263 m). Distances among switchers, resident fledglings

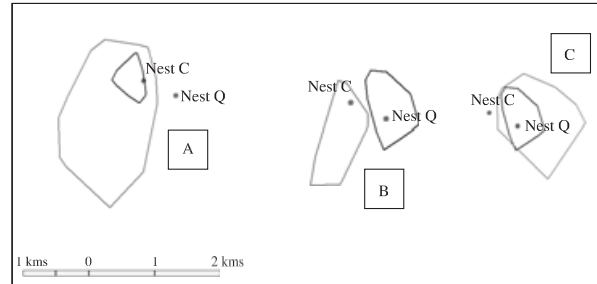


Figure 1. Home range overlaps of the male parent and the three switcher owlets during brood-switching. Areas represent the whole territory used by owlets from the beginning of fledging (A) in the natal territory (nest C; $n = 17$ complete nights of radiotracking) to the period between brood-switching to nest Q and the start of dispersal (B) ($n = 6$ complete nights of radiotracking). (A) Before brood-switching, the area explored by the three owlets (black polygon; MCP) overlaps completely with the home range of the male (grey polygon; MCP). (B) After brood-switching, the whole area prospected by the three owlets never overlapped with the male territory. (C) Representation of the whole area used by the switchers (black polygon) and the resident (grey polygon) fledglings during the whole period of adoption.

and switcher vs. resident fledglings were not significantly different ($\chi^2 = 5.68$, $df = 2$, $P = 0.06$; Kruskal-Wallis test).

The 2006 brood-switching occurred at the beginning of early attempts at dispersal (Table 1). In fact, when the

fledgling male of nest T left the parental territory, he did not come directly to the foster territory. When he established himself in the territory of the foster parents (Table 1), this territory was occupied by two resident fledglings (one male and one female), both older. This switching bird also never returned to the parental territory. The area that he explored when in the foster territory largely overlapped (in both extension and spatial location) with the home range of the foster female. During two nights of continuous radiotracking ($n = 20$ locations), we recorded a mean distance of 598 ± 307 m (range: 266–1191 m) between the adopted fledgling and the foster female; and the mean distance between the switcher and the foster nest was 788 ± 274 m (range: 269–1191 m).

In both cases of brood-switching, the switchers started dispersal before the resident fledglings ($n = 10$, $t = 3.99$, $P = 0.007$), even if they were younger than the resident owlets.

Finally, adoption did not affect the fate of both switching and resident owlets. In fact (Table 1), when excluding the four young that were lost immediately after the start of dispersal, one owlet was shot (i.e. mortality due to a stochastic event not related with brood care), another survived at least one year after fledging (when the battery of the receiver failed) and four individuals were still alive at the end of December 2006 (one of them, a female, reproduced successfully in her first year of life).

The age of dispersal of the young within the broods in which brood-switching occurred ($n = 10$, $x = 161.1 \pm 14.7$ days-old, range = 126–175; Table 1) did not differ ($t = -0.047$, $df = 67$, $P = 0.96$) from the age of mean natal dispersal of the Eagle Owl population ($n = 59$, $x = 170 \pm 20.5$, range = 131–232 days old).

DISCUSSION

Based on these two observations, brood-switching by Eagle Owl has unusual characteristics when compared with brood-switching in other raptor species. Specifically, we only recorded male switchers, and switchers joined broods with older fledglings in both cases. Adoptions were permanent (switching fledglings never came back to the parental territory and stayed with the foster family until dispersal). The amalgamation of alien fledglings with resident young appeared to be a fluent, non-aggressive event, as indirectly revealed by the small distances between the fledglings of different broods and the switcher and foster parents; and the fact that relatively young switching birds integrated with older resident fledglings; a risky strategy for switching birds if interactions with resident young are aggressive. Although we did not collect any direct observation of foster parents feeding alien owlets, the fact that switching birds stayed for so long with the resident fledglings (not overlapping with the home range of their parents at the time) implies that they were getting alloparental care from foster parents.

Brood-switching in Eagle Owls seems to be an infrequent behaviour. In fact, of a sample of 74 radiotagged young during a period of 4 years, we only recorded two cases of brood-switching involving four individuals (5.4% of all marked owlets, $n = 20$ nests). Moreover, because brood-switching generally occurs when population density is high (Poole 1982, Bustamante & Hiraldo 1990, Donazar & Ceballos 1990, Kenward *et al.* 1993), our study population should be characterized by high rates of brood-switching because it represents the highest breeding density recorded in Europe (35 breeding pairs/100 km², Delgado & Penteriani 2007). However, as also pointed out by Kenward *et al.* (1993) and Roulin (1999), in those species whose fledglings beg loudly for long periods (as in Eagle Owls, Delgado & Penteriani 2007), it should be easy for a switcher to detect potential foster families even from large distances. High density may not promote brood-switching to the same extent in all species.

The two cases of brood-switching reflect the two not-mutually-exclusive models advanced to explain facultative brood-switching in semi-altricial species (Gilson & Marzluff 2000). Thus, brood-switching may arise from: (1) a non-random, deterministic behaviour determined by the conditions experienced by the fledgling in the natal territory (as we can suppose for the 2004 brood-switching); or (2) random pre-dispersal movements of fledglings (i.e. the 2006 brood-switching).

Foster adults did not appear to benefit from adoptions. No adoptions took place in single-chick broods (where parents could gain breeding experience) and brood-switching does not lower the risk of predation of young because old owlets of > 100 days are the same size as adults and predation is virtually non-existent.

High frequencies of wandering fledglings might select for non-aggressive adults. For example, frequent chases of intruder young may not be energetically efficient for adults. This could be especially true in high density populations when adjacent pairs are so close that they are within the range of movement of young during the post-fledging dependence period. The mean net straight line distance between the whole set of owlet locations and the nest ($x = 504 \pm 266$ m, ranging up to 1500 m; Penteriani *et al.* 2005) can explain frequent encounters between strange young and foster parents in the high density of the study area.

Generally, brood-switching has been characterized by younger (and presumably subordinate) fledglings of large broods moving to a nesting territory with younger chicks (Poole 1982, Bustamante & Hiraldo 1990), in which the former become the dominant fledglings and can improve their food intake (consequently increasing their probability of survival; Hébert 1988). Moreover, they may benefit from a longer period of parental care if they establish themselves in younger broods (Pierotti & Murphy 1987). In Eagle Owls, however, brood-switching did not extend the period of parental care for switchers because they were

adopted within older broods and did not delay the start of dispersal. Intruding fledglings may simply have taken advantage of a food surplus in a situation of high prey availability, reducing or avoiding aggression by foster parents, which simply fed all the young in the nest area. As suggested by Kenward *et al.* (1993), brood-switching in raptors could be more similar to a process of brood parasitism than adoption.

We thank B. Arroyo, G.A. Sonerud, J. Wilson and two anonymous referees for the helpful comments on the first draft of the manuscript.

REFERENCES

- Arroyo, B.E. & García, J.T. 2002. Alloparental care and kleptoparasitism in the semicolonial Montagu's Harrier *Circus pygargus*. *Ibis* **144**: 676–679.
- Bize, P., Roulin, A. & Richnerl, H. 2003. Adoption as an offspring strategy to reduce ectoparasite exposure. *Proc. R. Soc. Lond. B* **270**: S114–S116.
- Bustamante, J. & Hiraldo, F. 1990. Adoptions of fledglings by black and red kites. *Anim. Behav.* **39**: 804–806.
- Delgado, M.M. & Penteriani, V. 2007. Vocal behaviour and neighbour spatial arrangement during vocal displays in eagle owl. *J. Zool., Lond.* **271**: 3–10.
- 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. Natural adoption of fledglings by Spanish Imperial Eagles *Aquila adalberti*. *J. Ornithol.* **134**: 335–337.
- Gilson, L.N. & Marzluff, J.M. 2000. Facultative nest switching by juvenile Ospreys. *Auk* **117**: 260–264.
- Hébert, P.N. 1988. Adoption behaviour in gulls: a new hypothesis. *Ibis* **130**: 216–220.
- Kenward, R.E., Marcström, V. & Karlbom, M. 1993. Post-nestling behaviour in Goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. *Anim. Behav.* **46**: 371–378.
- Lett, D.W. & Bird, D.M. 1987. Post-fledging behavior of American Kestrels in southwestern Quebec. *Wilson Bull.* **99**: 77–82.
- Penteriani, V., Delgado, M.M., Alonso-Álvarez, C. & Sergio, F. 2007a. The importance of visual cues for nocturnal species: Eagle Owls signal by badge brightness. *Behav. Ecol.* **18**: 143–147.
- Penteriani, V., Delgado, M.M., Alonso-Álvarez, C., Viqueira Pina, N., Sergio, F., Bartolommei, P. & Thompson, L.J. 2007b. The importance of visual cues for nocturnal species: Eagle Owl fledglings signal with white mouth feathers. *Ethology* **113**: 934–943.
- Penteriani, V., Delgado, M.M., Maggio, C., Aradis, A. & Sergio, F. 2005. Development of chicks and pre-dispersal behaviour of young in the Eagle Owl *Bubo bubo*. *Ibis* **147**: 155–168.
- Pierotti, R. & Murphy, E.C. 1987. Inter-generational conflicts in gulls. *Anim. Behav.* **35**: 435–444.
- Poole, A. 1982. Breeding Ospreys feed fledglings that are not their own. *Auk* **99**: 781–784.
- 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. *Q. Rev. Biol.* **57**: 405–435.
- Roulin, A. 1999. Natural and experimental nest-switching in Barn Owl *Tyto alba* fledglings. *Ardea* **87**: 237–246.
- Tella, J.L., Forero, M.G., Donazar, 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.
- Wyllie, I. 1985. Post-fledging period and dispersal of young Sparrowhawks. *Bird Study* **32**: 196–198.

Received 25 May 2007; revision accepted 31 March 2008.