J Ornithol (2017) 158:185–191
DOI 10.1007/s10336-016-1381-z

ORIGINAL ARTICLE

Alloparental care and adoption in Tengmalm's Owl (*Aegolius funereus*)

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Received: 23 May 2016 / Revised: 23 June 2016 / Accepted: 25 July 2016 / Published online: 4 August 2016

Abstract Few cases of adoption have been reported in solitary breeding raptors, and in owls adoption has only been reported in two species. Here we report four cases of brood-switching of juvenile Tengmalm's Owls (*Aegolius funereus*), recorded during and after the post-fledging dependence period using radio-telemetry, and a case of three orphaned siblings (one nestling and two fledglings) originally from one nestbox successfully fostered to another one. A possible evolutionary context of the brood-switching is discussed.

Keywords Nestling phase · Post-fledging dependence period · Radio-telemetry · Adoption · Alloparental care · Brood-switching

Zusammenfassung

Alloparentale Brutpflege und „Adoption" beim Raufußkauz (*Aegolius funereus*)

Fälle von Adoption bei solitär brütenden Greifvögeln sind nur selten beschrieben worden und bei den Eulen bisher auch nur für zwei Arten. Wir berichten hier von vier Fällen von Brut-Vertauschens bei jungen Raufußkäuzen (*Aegolius funereus*), die während und nach des Ausfliegens per Radiotelemetrie verfolgt wurden. Ferner beschreiben wir den Fall von drei verlassenen Jungen (eines noch im Nest, die anderen beiden gerade flügge geworden), die erfolgreich von einem Nistkasten in einen anderen umgesetzt und weiter gefüttert worden wurden. Mögliche evolutionsbiologische Zusammenhänge des Brutvertauschens werden diskutiert.

Introduction

Adult individuals providing parental care for young which are not genetically related to them are referred to as alloparents (Wilson 1975). The alloparental care (temporary or permanent adoption) of non-related juveniles has been reported in many bird species (Riedman 1982), even though such altruistic behaviour (Hamilton 1964) essentially violates Darwinian theory that individuals are selected not to expend resources in the propagation of competing genotypes (Wilson 1975; Dawkins 1976; Riedman 1982). Several possible explanations have been offered to account for this apparent inconsistency between theory and observation (see reviews in Redondo et al. 1995; Avital et al. 1998; Bize et al. 2003). These include non-adaptive explanations, such as maladaptive behaviour, reproductive errors and adoptions with no or negligible costs in term of fitness for foster parents, and adaptive explanations, such as kin-selected benefits for alloparents (genetic relatedness, reciprocal altruism, predation dilution and better predator detection, gain of breeding experience). There may also be direct benefits for juveniles (better parental care, higher food intake, higher rank in the foster brood, reduction of parasite load, match-making

Communicated by F. Bairlein.

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hypothesis). The validity of these explanations and the emphasis which can be placed on them vary in relation to the developmental stage of the young of that particular species at hatching (precocial, semi-precocial and altricial), the breeding system (solitary, semi-colonial and colonial) and breeding phase during which adoptive behaviours occur (early or late nestling or post-fledging period) (see, for example, Bustamante and Hiraldo 1990; Williams 1994; Brown et al. 1995; Larsson et al. 1995; Redondo et al. 1995; Roulin 1999; Bukacinski et al. 2000; Bize and Roulin 2006; Penteriani and Delgado 2008).

Few cases of adoption in solitary breeding raptors have been described (see reviews in Arroyo and García 2002; Penteriani and Delgado 2008; Anctil and Franke 2013), and in owls adoption has only been reported in two species, namely, the Barn Owl (*Tyto alba*; Roulin 1999) and the Eagle Owl (*Bubo* bubo; Penteriani and Delgado 2008). All reported observations of adoption in birds of prey took place at the end of nestling period or during post-fledging dependence period (hereafter PFDP). Such examples in predatory bird species could therefore be described as post-fledging brood parasitism rather than adoption (Kenward et al. 1993) and possibly result from an effort by the juveniles to receive extra food, facilitated only in situations of high breeding densities and/or where there is a potential for a failure of offspring recognition by foster parents (e.g. Bustamante and Hiraldo 1990; Donazar and Ceballos 1990; Tella et al. 1997; Arroyo and García 2002; Penteriani and Delgado 2008).

Tengmalm's Owl (*Aegolius funereus*) is a solitary breeder, nesting in natural cavities or artificial nestboxes (Mikkola 1983; Cramp 1985; Kouba et al. 2014b). Juveniles hatch asynchronously over a 2-day timespan and stay in the nest for 27–38 days after hatching (Korpimäki 1981; Kouba et al. 2015), thus fledging at different times and reaching independence between 5 and 9 weeks after fledging (Eldegard and Sonerud 2009, 2010, 2012; Kouba et al. 2013). By far the majority of prey brought to the young throughout the late nestling phase and the PFDP is delivered by the male of this species (Zárybnická 2009; Eldegard and Sonerud 2010, 2012). During this time, the offspring vocalize to solicit food from parents with short, hissing cheet calls (König and Weick 2008; Kouba et al. 2014a). The coloration of young during late nestling and PFDP is distinctly different from that of adults and thus the former can be distinguished by an observer (Korpimäki and Hakkarainen 2012).

The results of experiments involving the manipulation of brood size and cross-fostering of newly hatched Tengmalm's Owl chicks have demonstrated that survival of the transferred nestlings can equal that of the resident young, suggesting that breeding adults do not discriminate effectively between their own chicks and fostered ones (Korpimäki 1987, 1988; Thomson et al. 2014).

We report here our observations of cases of nest- and brood-switching undertaken and recorded during radio-tracking of juvenile Tengmalm's Owls throughout the PFDP. We also report possible alloparenting of unrelated fledglings by wild owls, as well as the results of a deliberate manipulation in which we relocated three siblings into a different nest. This latter intervention was performed to rescue these three young birds when it became obvious that their own father had—for undetermined reasons (possibly death)—stopped providing them with food.

Methods

Duration of the PFDP in Tengmalm's Owl was studied over four breeding seasons in the Czech Republic (2010–2012 and 2015) using radio-tracking. The study area is situated in the Ore Mountains (50°N, 13°E; 730–960 m a.s.l.) and covers about 70 km^2 (for detailed description of the study area, see Kouba et al. 2013). As compensation for the lack of natural tree cavities, wooden nestboxes lined with wood chips have been installed gradually in the area since 1999, and the majority of owls now breed in these artificial nestboxes. During the study period all nestboxes (n = 120–170) within the study area were visited regularly at intervals of 2–3 weeks from early March to July. Nests identified were then checked sufficiently often to assess the number of eggs, time of hatching and number of hatchlings. Nestlings were sexed by molecular procedures using DNA extracted from blood (for details, see Kouba et al. 2014a).

Several days before fledging 76 fledglings from 19 nestboxes were equipped with leg-mount transmitters (Biotrack Ltd., Wareham, UK) (2010: 6 nests, 29 nestlings; 2011: 5 nests, 10 nestlings; 2012: 2 nests, 10 nestlings; 2015: 6 nests, 27 nestlings). After fledging, the young were located by radio-tracking once every night (2010–2012) and every day (2012 and 2015) until the fledglings became independent [58 individuals which survived until independence were located throughout the PFDP for a mean of 49 ± 6 days (mean ± standard deviation)] using a MVT-9000 receiver (Yupiteru Industries Co. Ltd., Tokyo, Japan) and 3-element Yagi antenna and following the 'homing-in' method (Kenward 2001; Kouba et al. 2013, 2014a). Once spotted, the fledgling's position was recorded using the GPS receiver (GPSmap 60CSx; Garmin Ltd., Schaffhausen, Switzerland).

As in the previous studies (see Kouba et al. 2013, 2014a), prey availability in the study area was assessed by using snap-traps at the beginning of June in each year of the study. The snap-traps were set up in squares (with 10-m spacing), left out for 3 days and checked daily. Thus, the total trapping effort was 1089 trap-nights ($n = 3$ locations). The number of captured mammals per 100 trap-nights was then calculated.

Results

We observed four ‘natural’ cases of possible alloparental care. The first two cases (A1 and A2, in 2011 and 2012, respectively) involved one newly independent fledgling each; these were observed to be begging by calling together with fledglings from another nest. That we identified only these two cases of possible alloparental care from the 326 possible opportunities during 3 years of nocturnal radio-tracking aimed at discovering individual brood-switching after PFDP demonstrates the negligible low frequency of this behaviour (0.6 %). In 2011 (case A1; Table 1; Figs. 1, 2) a male fledgling left his natal area and was seen begging for food together with a female who had fledged from the nestbox actually associated with that new area. In 2012 (case A2; Table 1; Fig. 1, 2) a female fledgling left her natal area and was observed begging for food within a group of five fledglings resident within that new area. Both individuals were considered to be brood-switchers (sensu Penteriani and Delgado 2008).

The third and fourth cases of possible ‘natural’ alloparental care (B1 and B2; both in 2015) involved five unknown and non-tagged fledglings repeatedly observed to be roosting with resident fledglings from two different nests. These two cases were recorded over a 4-year period during which time a total of 19 nests/sibling groups were monitored. The data suggest a frequency of 11 % brood-switching during the PFDP.

In case B1 (Table 1; Fig. 1) five nestlings were known to have fledged from the ‘home’ nestbox within a given area of which four were radio-tagged (the first/oldest young fledged before tagging). Later, one to four non-tagged fledglings were observed roosting close together with four resident young on a total of 32 occasions. The scenario was similar in case B2 (Table 1; Fig. 1) where two unknown fledglings were observed roosting close together with three radio-tagged resident fledglings on 17 occasions in total (recorded near the nestbox where the orphaned juveniles were fostered—case report C described below). In this case, four nestlings fledged from the resident’s nestbox, among which three survived up to independence and one was most probably lost to predation (Table 1). In both cases, unknown individuals were also considered to be brood-switchers.

The last case (C; Table 1; Fig. 1) involved the fate of three siblings (1 nestling and 2 fledglings, 29, 31 and 33 days from hatching, respectively) from one nestbox which were fostered to another nestbox. One resident young with no stored prey was in the host nestbox at the time when the three unrelated young were added. On the following day (30 May) the resident chick had fledged and the nestbox contained only the three fostered young, together with eight fresh prey items [7× yellow-necked mouse (*Apodemus flavicollis*) and 1× field vole (*Microtus agrestis*)]. Fresh prey was found in the host’s nestbox during each of the following days until the fostered young had fledged. Thereafter, two fostered and the one resident juvenile from the host nestbox survived until independence (being radio-located every day from fledging to dispersion). These three individuals stayed close together throughout the PFDP and behaved like true siblings. Daily inter-individual distances (mean ± standard deviation) between the resident young (female R_f) and the two adopted young (male A_m; female A_f) were calculated to be 62 ± 74 m ($n = 52$ days), with $R_f - A_m = 73 \pm 101$ m, $R_f - A_f = 46 \pm 65$ m and $A_m - A_f = 67 \pm 92$ m.

Discussion

The brood-switches recorded in our study in 2011 and 2012 (A1 and A2) seem to be very similar to those observed in 2006 by Penteriani and Delgado (2008) in Eagle Owls. Both of the Tengmalm’s Owl brood-switches observed in our study coincided more or less with the end of PFDP and were thus associated with the random predispersal movements of fledglings; specifically, both brood-switches occurred shortly before the end of the PFDP of the broods, which the switchers joined. Brood-switching in this way might be more common because of the high breeding density of Tengmalm’s Owl in our study area (10–37 breeding pairs/100 km^2 over a 16-year period) and because the young of this bird species beg loudly for food, especially at the end of PFDP (Kouba et al. 2014a). These factors suggest the possibility of promoting brood-switching in several other birds of prey, such as the Red Kite (*Milvus milvus*), Egyptian Vulture (*Neophron percnopterus*), Spanish Imperial Eagle (*Aquila adalberti*), Goshawk (*Accipiter gentilis*), Barn and Eagle Owl (Bustamante and Hiraldo 1990; Donazar and Ceballos 1990; Ferrer 1993; Kenward et al. 1993; Roulin 1999; Penteriani and Delgado 2008). We suggest that after cessation of their own parental care, these two brood-switchers tried to obtain extra food during predispersal movements. We did not observe if they received any real alloparental care; however, one of them was begging together with the residents during two consecutive nights, suggesting that alloparental care was likely.

Cases B1 and B2 (recorded in 2015; 10 km between the two involved nestboxes) seem to be very similar to the brood-switches recorded in 2004 in Eagle Owls (Penteriani and Delgado 2008). However, in both of these latter cases it is possible that brood-switching and possible alloparenting might be explained based on theories of kin

Table 1 Details of nestboxes/individuals involved in the five described case reports

Details on nestboxes/individuals	Case							
	A1		A2		B1	B2	C	
Year	2011		2012		2015	2015	2015	
Nestbox no.	406	44	409	623	1431	1385[d]	1383	1385
Label	Brood-switchers	Residents	Brood-switchers	Residents	Residents	Residents	Fostered-switchers	Residents
No. of involved young	1	1	1	5	5	3	3[e]	1[g]
No. of days from fledging before brood-switching event occurred	62	55	49	44–53	14–22	24–28	–	–
Date of observations when brood-switching event occurred	1–2 August		3–4 and 4–5 August		6–27 July	27 June–24 July	29 May–1 August	
No. of days until independence after brood-switching event occurred	–	2	–	2–9	2–6	2–10	–	–
No. of days from hatching when brood-switching event occurred	99	87	82–83	76–85	45–72	56–88	27–31	32
Sex (male:female)	Male	Female	Female	2:3	3:2	1:2	1:2	Female
Distance from nestbox, in m (mean ± standard deviation)	2356	733	1369 ± 72	737 ± 53	654 ± 170 ($n = 32$)	188 ± 78 ($n = 17$)	174 ± 102 ($n = 177$)	
Between-nestbox distance (m)	1803		1470		–	–	4192	
No. of eggs[a]	5	4	6	6	7	5	5	5
Date of hatching	25 April	5 May	12 April	10, 12, 14, 16, 18 April	16, 17, 20, 21, 22 May	27, 28 April, 2 May	24, 26, 28, 30 April, 2 May[f]	27 April
No. of hatchlings[a]	5	3	5	6	6	2	5	2
Date of fledging	1 June	7 June	15 May	12, 13, 14, 17, 20 May	14, 15, 18, 18, 22 June	30, 31 May, 3 June	25, 26, 27, 28 May[f]	30 May
No. of fledglings[a]	4	2	5	5	5	4	4	2
No. of nestlings equipped with radio-transmitter	4	2	5	5	4	4	5	2
Date of reaching independence	1 August	3 August	1 July	5, 6, 9, 11, 11 July	29, 30, 31 July, 2 August	26, 26 July, 3 August	–	26 July
No. of young surviving the post-fledging dependence period[a]	2	1	5	5	4 (5)[c]	3	0	1
Prey availability[b]	0.6		4.9		2.5		2.5	

[a] Number of eggs, hatchlings, fledglings and individuals surviving until independence from the specific nestboxes involved in the case studies reported

[b] Prey availability within the study area during particular breeding seasons calculated as the number of captured individuals per 100 trap-nights

[c] Confirmation of whether the non-tagged resident young survived up to independence was not possible

[d] The three fostered and adopted young were considered to be residents in this case

[e] Two other fledged siblings were found dead on 29 May near nestbox no. 1383, and the third fostered young was found dying in the resident's nestbox on 31 May (subsequent autopsy revealed starvation as a cause of their deaths)

[f] Dates of hatching in and fledging from original nestbox before fostering

[g] The older resident female nestling fledged on 28 May and disappeared on 3 June, most probably due to predation

selection and kinship altruism (Hamilton 1964); it is possible the individuals in mixed broods were genetically related since polygyny has been regularly reported in Tengmalm's Owl (Korpimäki and Hakkarainen 2012) and has been repeatedly recorded in our study area as well (K. Šťastný, unpublished data). If this were to be true, it might explain the two cases of brood-switching (by unmarked individuals) in terms of brood unification for a single male caring for a double brood. On the other hand, it is equally possible that the situation is analogous to that described for

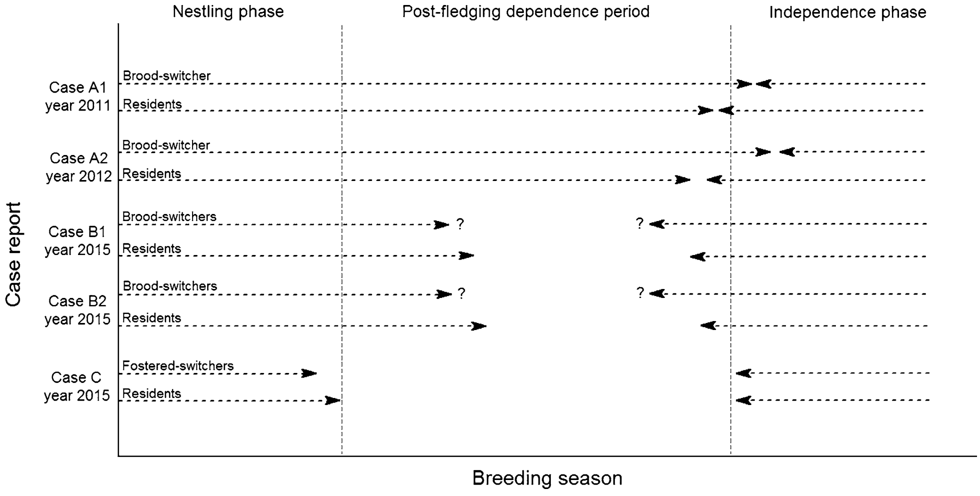

Fig. 1 Simple graphic timeline of the occurrence of the reported cases of brood-switching (*A1*, *A2*, *B1*, *B2*, *C*) during the breeding seasons of 3 different years. *Arrowheads* illustrate the approximate time of the beginning and the end of the cases reported, *distance between arrows* denotes the approximate duration of each particular observation of brood-switching

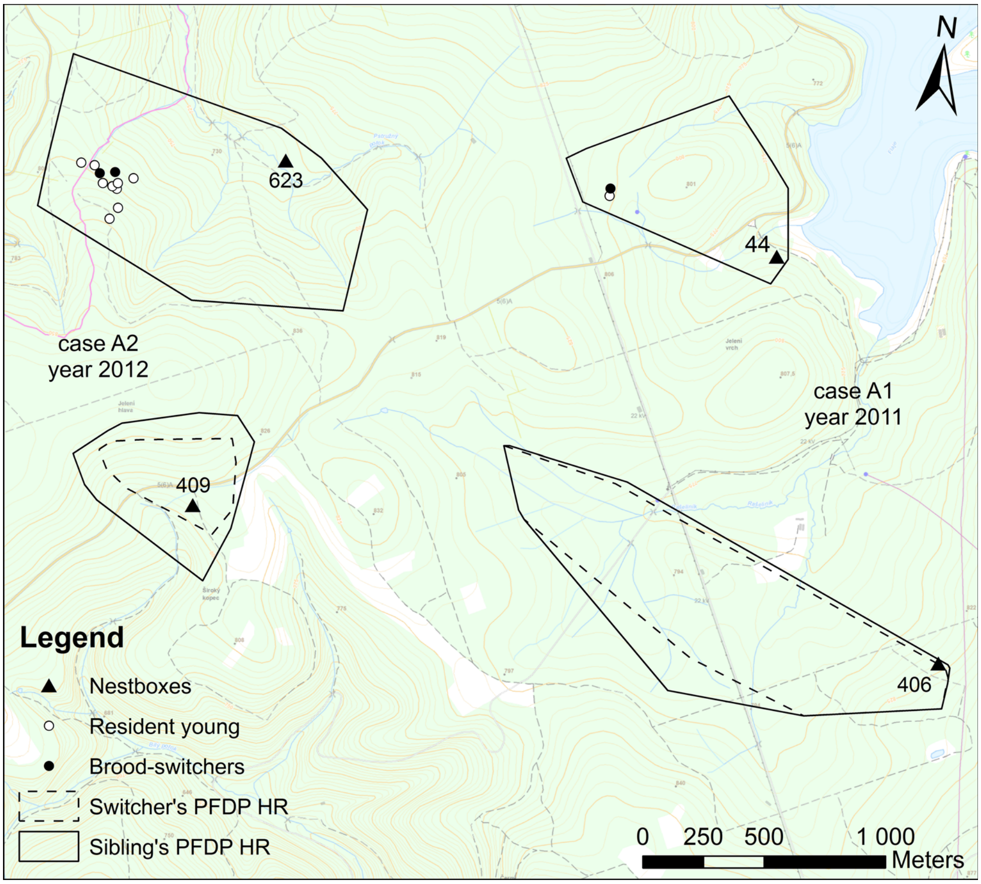

Fig. 2 Siblings' post-fledging dependence period (*PFDP*) home ranges (*HR*) (*solid lines*) and individual switchers' PFDP HR (*dashed lines*) based on each nocturnal location (2011) and nocturnal and diurnal location (2012) recorded by radio-tracking throughout the PFDP and established by the 100 % minimum convex polygon method (Hayne 1949). Locations of resident young (*open circles*) and brood-switchers (*black circles*) within the residents' HR, as described in case report A1 (nestboxes no. 406 and 44) and A2 (nestboxes no. 409 and 623). Both case reports are shown in reverse because the map illustrates the actual spatial arrangement of the home ranges within the study area

Eagle Owls by Penteriani and Delgado (2008): alien fledglings establish themselves in foster broods during the later part of PFDP and simply take advantage of a food surplus in an area/year of high prey availability and adults may not be able to accurately distinguish between progeny and simply feed all the young in the vicinity of their nest area.

This notion of an inability of a parent to discriminate between juveniles is further supported by the case of adoption after fostering, which certainly would suggest that Tengmalm's Owl parents were not able to recognize offspring even during the late nestling and fledging phase. If brood-switching was a relatively common event in Tengmalm's Owl, then we might expect a selection pressure on the parents to reject genetically unrelated young (Dawkins and Krebs 1979). Our successful fostering took place during a year in which the food supply was moderate to plentiful, suggesting that Tengmalm's Owl adults (or at least males) were not able to recognize their own chicks even at the fledging age since the fostered young did not show any signs of starvation after fostering. This state of well-being was maintained over the 64-day period until the end of PFDP. It seems quite possible the Tengmalm's Owl adults are not even able to count and remember how many chicks there were initially in the nest. Similarly, Roulin (1999) reported that foster Barn Owl families tolerated alien fledglings. Likewise, Eagle Owl families adopted and cared for fledgling intruders without any hostility against them (Penteriani and Delgado 2008).

To conclude, based on our observations we speculate that the brood-switching (at least A1 and A2) and artificial fostering (C) which took place in our study area could be explained by the inability of adult owls to discriminate between their own and unrelated, offspring even at the fledging age. We suggest that this inability to distinguish between offspring can be used for conservation purposes and rehabilitation projects in the case of abandoned, orphaned and/or injured nestlings, as has already been suggested for other raptors (Postupalsky and Holt 1975; Di Vittorio 2006). The same explanation may also account for the brood-switches observed in 2015 (B1 and B2), although here we may alternatively speculate some involvement of kinship and inclusive fitness (Hamilton 1964). This area of research is clearly interesting, and more studies on bird species with established polygyny are needed.

Acknowledgements We are grateful to Alessandro Fantoni and Petr Kouba for their help in the field, and to Lucie Brejšková and Markéta Zárybnická for DNA analysis and sexing the nestlings. We also acknowledge Rory Putman for valuable comments on the early draft of the manuscript and for improving the English. Last but not least, we would like to thank Peter Sunde and two anonymous reviewers for their comments and suggestions on an earlier draft of the manuscript. This work has been supported by grants from the Czech University of Life Sciences Prague (CIGA ČZU 20104205 and 20144203), the Ministry of Education, Youth and Sports of the Czech Republic (MŠMT 1321/213205), Ministry of Agriculture of the Czech Republic (MZERO 0716), and by grant EHP-CZ02-OV-1-024-2015 from Iceland, Liechtenstein and Norway.

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