



## Post-fledging behaviour of juveniles in the Little Owl (*Athene noctua*)

Pedersen, Dorthe; Thorup, Kasper; Sunde, Peter; Jacobsen, Lars Bo; Rahbek, Carsten

*Published in:*  
Ornis Fennica

*Publication date:*  
2013

*Document version*  
Publisher's PDF, also known as Version of record

*Document license:*  
[Unspecified](#)

*Citation for published version (APA):*  
Pedersen, D., Thorup, K., Sunde, P., Jacobsen, L. B., & Rahbek, C. (2013). Post-fledging behaviour of juveniles in the Little Owl (*Athene noctua*). *Ornis Fennica*, 90(2), 117-128.

## Post-fledging behaviour of juveniles in the Little Owl (*Athene noctua*)

Dorthe Pedersen, Kasper Thorup, Peter Sunde, Lars Bo Jacobsen  
& Carsten Rahbek

*D. Pedersen, K. Thorup & L. B. Jacobsen, Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark. Corresponding author: Kasper Thorup, e-mail: kthorup@snm.ku.dk*

*P. Sunde, Department of Bioscience, Aarhus University, Grenåvej 14; DK-8410 Rønne, Denmark*

*C. Rahbek, Center for Macroecology, Evolution and Climate; Department of Biology; University of Copenhagen; DK-2100 Copenhagen, Denmark*

*Received 27 April 2012, accepted 10 January 2013*

Before dispersal, social and spatial behaviour in owls has only been briefly studied. We used radio tracking to monitor age-influenced social and spatial behaviour in 10 juvenile Little Owls (*Athene noctua*) from nests in Northern Jutland, Denmark. On average, the post-fledging dependency period lasted 35 days ( $n=6$ ). Juveniles stayed on the natal territory 45 days ( $n=5$ ) from independence to dispersal. Half of the juveniles had dispersed by mid-September, and the other half remained on the natal territory until at least mid-October. The home range size (minimum convex polygons) was  $0.56 \pm 0.53$  ha (mean  $\pm$  SD) from fledging to independence and  $3.25 \pm 4.15$  ha from independence to dispersal. Within the first 40 days after fledging, the nightly distance from the nest and the distance between siblings increased, and the frequency and intensity of begging calls decreased. These results were consistent with the notion that food provided by the parents decreased as juvenile foraging skills increased.



### 1. Introduction

The offspring of altricial birds experience a period of post-fledging dependency after they have left the nest. The post-fledging parental care period might comprise over one third of the total parental investment period and includes the critical phase of transitioning to independence (Koga & Shiraishi 1994, Bustamante 1995, Wheelwright & Templeton 2003, Sunde 2008). The stage after an individual has stopped receiving parental care, but

before the bird has left the natal site, is often unrecognised in studies of post-fledging behaviour (Sunde 2008). Raptorial birds often require parental food provision for extended periods after fledging (Newton 1979). In some cases, these periods may be associated with substantial mortality (e.g., Sunde 2005).

The Little Owl (*Athene noctua*) is a small, nocturnal raptor feeding on a varied diet, including both invertebrates and small vertebrates (Van Nieuwenhuysse *et al.* 2008). Currently, the species

is declining in many European countries (Van Nieuwenhuysse *et al.* 2008). In Denmark, a high level of juvenile mortality has been observed prior to dispersal (Thorup *et al.* 2013). Basic knowledge of the social and spatial behaviour of juveniles from fledging to dispersal could prove valuable for conservation planning. Little Owls are monogamous and male and female mates share the responsibility of rearing their young (Van Nieuwenhuysse *et al.* 2008).

Vocal communication is a central characteristic of the social behaviour in owls. During the dependency period, juvenile Little Owls produce a monosyllabic begging call, a harsh “szip” or “chsiij” (Cramp 1985). The general consensus among researchers in the field is that begging calls are honest signals of hunger and body condition, directed at the parents (Hofstetter & Ritchison 1998, Quillfeldt 2002, Sacchi *et al.* 2002, Gladbach *et al.* 2009). Begging may also serve as communication between siblings (Roulin *et al.* 2000). According to Haverschmidt (1946), begging identifies the exact location of the young to the foraging parents. In some species, the post-fledging begging rate decreases with age (Holleback 1974, Nikolov & Hristova 2007).

There is an inherent difficulty in studying non-vocal behaviour in nocturnal species. Several studies on Little Owls have used radio tracking to overcome potential biases such as overrepresentation of vocal individuals (e.g. Exo 1992, Finck, 1990 Génot & Wilhelm 1993, Zuberogoitia *et al.* 2007, Grzywaczewski 2009, Framis *et al.* 2011). Here, we use radio tracking to study the patterns of juvenile, post-fledging begging and spatial behaviour in Little Owls in Denmark. We estimate home range sizes and specifically aim to investigate whether age of the juvenile influenced (1) the distances at which juveniles ventured away from the nest (roosting site), (2) inter-sibling distances, and (3) begging. Finally, we discuss whether the parents or the offspring are most likely to determine when the dependency period ends.

## 2. Material and methods

### 2.1. Study areas and field methodology

We conducted our study in an 85-km<sup>2</sup>, intensively-managed farmland area (Sunde *et al.* 2009) around

Aars in Himmerland, Northern Jutland, Denmark (N56°40', E9°20'). Ten juvenile Little Owls were radio tracked from the fledging period in mid-June to death or last dispersal in late October, 2008. We visited the nests at least once a week, from egg laying to fledging, more often around expected hatching.

The hatching date was estimated based on the length of the 8<sup>th</sup> primary feather and plumage colour (Glutz von Blotzheim & Bauer 1980). In the analyses, we included offspring from one breeding pair that was provided with supplemental food during egg incubation and nest feeding (Thorup *et al.* 2010). The supplemental feeding was discontinued at fledging, before we initiated radio tracking and this was considered unlikely to have a large effect on post-fledging behaviour.

We ringed the nestlings, on average 20 days after hatching and 14 days before fledging. In addition, on the day of ringing, we attached a VHF radio transmitter (type Ag393, leg mount tag, from BioTrack, Ltd.) to one leg of 10 nestlings from 5 nests (Appendix I). The weight of the transmitters was 3–4 g, which was maximally 4% of a nestling's body weight at the time of ringing. Radio transmitters were expected to last for 4–5 months. The maximum tracking range of the transmitter was about 600 m.

During the nestling period, we carefully checked for fledging birds. Little Owl nests are often hidden away with some space inside a building where the young can roam around before actually flying. As a result, the fledging dates are not only dependent on developmental stage but also on the specific surroundings. We define the day of fledging as the first day a young owl was observed visually or recorded by telemetry outside the nest. The term “juvenile” is used to describe the stage between fledging and the first breeding season. We use number of days after fledging as a proxy for age.

We determined the positions of the juvenile owls by detecting the transmitted signal with a handheld VHF receiver (RX-98H from Televilt Int.) and a directional antenna. Birds were located by triangulation, and by slowly homing in on the assumed location, taking care not to flush the bird. Radio tracking ended with confirmed juvenile death, or when no signal was detected within a 1-km radius from the nest. If the signal disappeared

without any sign of transmitter failure, we interpreted the loss of signal as juvenile dispersal. Signs of transmitter failure could for example be if we detected a strong frequency drift or decreasing signal strength. Random searching for owls was performed outside the 1-km radius and no birds were found in those searches. From fledging in mid-June 2008 to mid-September, we visited each study site 1–6 times per week. After that, daytime radio tracking was done at least once a month until the last juvenile had left the natal territory in late October.

We recorded nightly begging rates between the hours of 21:50 and 05:24, from the time of fledging in June until the end of August (40 days post-fledging), when all juveniles had stopped begging for food. Before beginning radio tracking at each location, the observer was positioned within hearing distance of the nest. When an owl was located, the observer would be silent and still for 5 min before recording the sound. Begging rates were calculated as the number of begging calls over a 10 min period. Each “szip” or “chsiij” call was recorded as one begging call for food, and calls from all the individuals in each brood were added together and divided by the number of individuals to calculate the “begging intensity”, begging calls per min per juvenile.

## 2.2. Data analysis

### 2.2.1. Spatial behaviour

We used the positions determined with night radio tracking to calculate the nightly distances to the nest, distance between siblings, and home ranges. Our analyses were based on data from (1) fledging to dispersal (4 individuals, identified as #105, #106, #113 and #115), (2) fledging to death after independence, but prior to dispersal (1 individual: #107) and (3) fledging to approximately one month before dispersal (no night observations over the last month; 4 individuals: #108, #110, #111 and #112). The distances from the juvenile night position to the nest were estimated with data from 9 juveniles from 5 broods (Appendix I). The distances between siblings were estimated only in broods with more than 1 juvenile; hence, 7 juveniles from 3 broods (Appendix I).

A large proportion of the data points were re-

corded from juveniles in the nest. However, all the nests were in buildings, and in several cases, birds located by telemetry closer than 10 m from the nest could not be distinguished from positions in the nest. For this reason, we analysed the effect of age (measured as number of days after fledging) on the presence or absence at the nest and the effect of days after fledging on the distance from the nest. We also investigated whether the distances between siblings were dependent on days after fledging. For practical reasons, it was not possible to track all individuals in a brood immediately after begging rates were recorded. Thus, it was not possible to analyse the relationship between the begging rate and the distance to the nest or the distance between siblings.

We used ArcView GIS 3.3 with the Animal Movement 1.1 extension (Hooge & Eichenlaub 1997) to calculate 100% minimum convex polygons (MCP) with and without zero observations (distances <1 m from the nest). The MCPs were used to estimate the home range sizes from fledging to independence, from independence to dispersal, and from fledging to dispersal. When days after fledging at independence was unknown ( $n=3$ ), the average days after fledging at independence was used. To avoid underestimating home range sizes, MCPs were only calculated for individuals that survived the entire period studied. Thus, home ranges were calculated for 9 juveniles from fledging to independence and for 8 juveniles from independence to dispersal and from fledging to dispersal. All but two home ranges were calculated with more than the 30 fixes suggested by Kenward (2001).

The dispersal date was taken as the date halfway between the last day an owl was located on the natal territory and the day of the follow up search conducted within  $\approx 1$  km of the nest site. To investigate the timing of dispersal from the nest sites and the extent of natal dispersal distances throughout the first year, we supplemented the radio tracking data with historical ring recovery data from juvenile Little Owls marked from 1920 to 1999 throughout Denmark (from Copenhagen Bird Ringing Centre's data base). To estimate the mean date/age of when the juveniles left the natal site, we fitted a logistic regression model. Here, we modelled the probability of whether a bird had moved more than 1 km away from the ringing site

Table 1. Juvenile Little Owl nightly maximum distance (m) from the nest and age (days) according to developmental stages. For each juvenile, the maximum distance recorded from fledging until independence and from independence until dispersal are given, with days after fledging in parentheses. Age at which the juvenile was located for the first time >10 meters from the nest, number of days after fledging at the last nest visit before dispersal, and number of days after fledging at dispersal, are shown. Average is given  $\pm$  SD. For individual #110, #111 and #112 where there is no record of independence date, the average age of independence found in this study is used. The number of telemetry positions for each individual in the periods fledging to independence and independence to dispersal are given in Table 2.

Owl ID	Maximum distance, dependent (m, days after fledging)	Maximum distance, independent (m, days after fledging)	Days after fledging at first departure from nest (days)	Days after fledging at last nest visit before dispersal (days)	Days after fledging at estimated dispersal (days)
105	85 (40)	268 (79)	29	80	82
106	103 (31)	112 (59)	29	75	77
107	45 (30)	190 (66)	1	43	–
108	67 (32)	341 (86)	2	43	118
110	246 (19)	225 (67)	0	33	98
111	83 (2)	150 (59)	0	39	98
112	89 (16)	191 (57)	0	21	96
113	42 (26)	144 (31)	17	59	63
115	230 (22)	291 (29)	0	0	57
Average	110 $\pm$ 75	212 $\pm$ 75	9 $\pm$ 13	44 $\pm$ 25	86 $\pm$ 20
Min	42	112	0	0	57
Max	246	341	29	80	118

as a function of the log number of days after ringing (logit-link and binomial error distribution, where the ringing year was included as a random effect). The average day of ringing was 18 June, when the nestlings were 12–25 days old.

### 2.2.2. Begging behaviour

We analysed begging behaviour based on data only from broods that exhibited begging calls with a known total number of juveniles. Six juveniles from 3 broods fulfilled these criteria (Appendix I). The analysis of begging patterns was restricted to the period of time between the first and last begging calls recorded at a given location.

When begging calls were recorded, it was not possible to determine the number of juveniles begging. For this reason, the begging rate per individual was estimated as the total observed begging rate (calls/min) divided by the number of known juveniles in the brood at the time of begging. We expected variations in begging rates among broods, due to differences in brood size (Roulin *et al.* 2000). As a result, begging rates were not di-

rectly comparable among broods; thus, we chose to stratify the analyses, with brood as a random variable.

The analysis of begging rates was based on nightly begging rates, with a maximum of one rate per night per brood. We performed two analyses. In the first analysis, the response variable was the presence or absence of begging calls. In some cases, begging ceased when the young were still present on the natal territory. For this reason, we included only the period of time between the first and last begging calls recorded for each brood. In the second analysis, the response variable was the “begging intensity”; i.e., the number of begging calls per min per juvenile in each brood. Here, the purpose was to analyse only the intensity of begging when juveniles were actually heard begging; thus, observations were excluded when no begging occurred.

### 2.2.3. Statistical models

To test for effects of days after fledging, we fitted generalised linear mixed models in the Proc

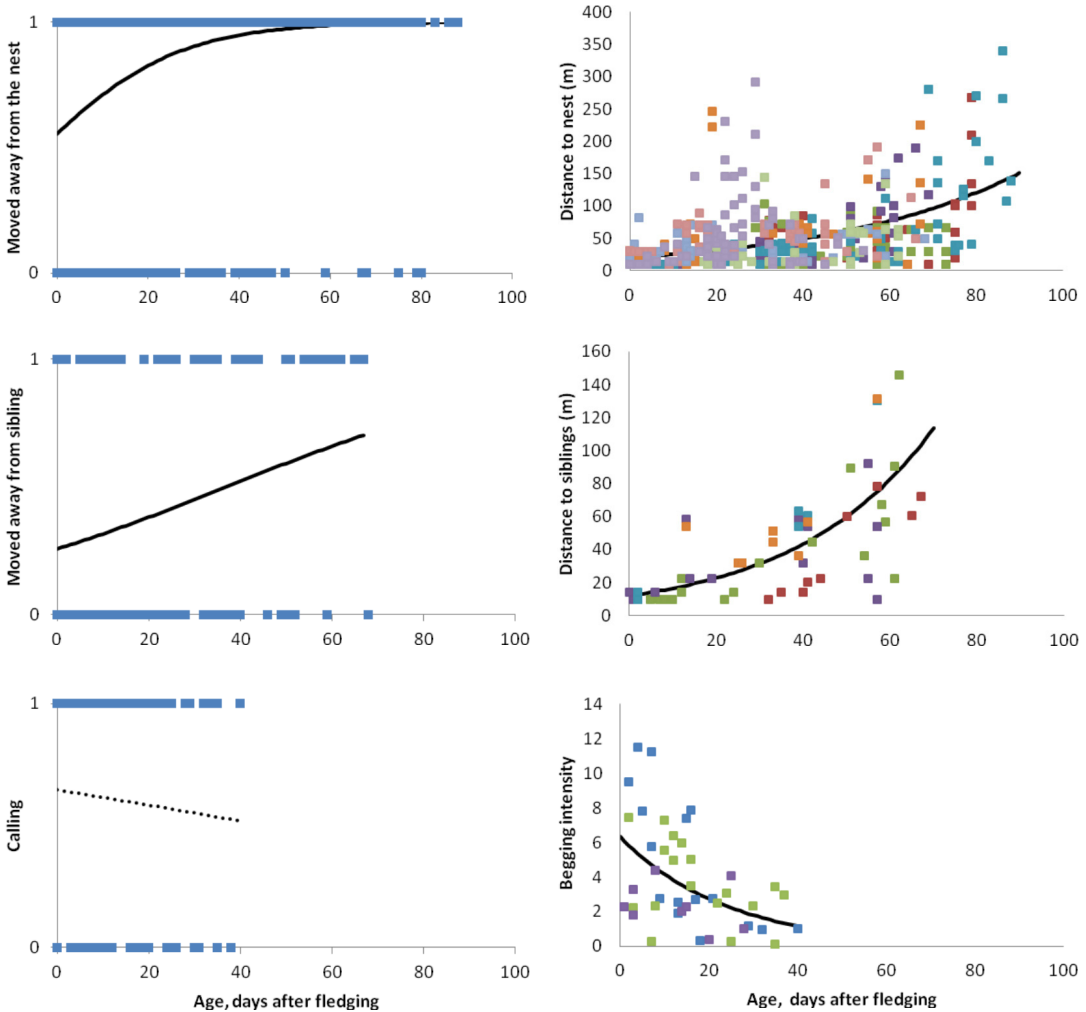


Fig. 1. Changes in behaviour with age after fledging in the Little Owl. Changes with days after fledging are shown for movement away from the nest (upper row), distance between siblings (middle row), and begging (lower row). Zero values are not shown in the right-hand panels. In the right-hand panels, upper and middle graphs show individual birds in different colours; in the lower graph, different nest sites are indicated with different colours (symbols are coloured only in PDF version). Black lines show fitted functions.

GLIMMIX in SAS 9.1. To control for differences among broods when modelling the distance from the nest, we included the owl ID nested within the brood ID as random effects. To allow for differences among broods in their responses to age-related changes, we also included the owl ID nested within the brood ID as random effects in an interaction term with days after fledging. When modelling the distances between siblings and the begging characteristics, owl ID could not be modelled. These models included the brood ID as a

random effect both alone and in the interaction term, brood ID\*days after fledging.

We tested for a relationship between days after fledging and movement away from the nest with a logistic regression model (logit-link and binomial error distribution). A relationship between days after fledging and the distance moved from the nest was tested with a model that included a log-link and a gamma error distribution (to account for the skewed distribution). Similarly, we used a model with logit-link and binomial error distribution for

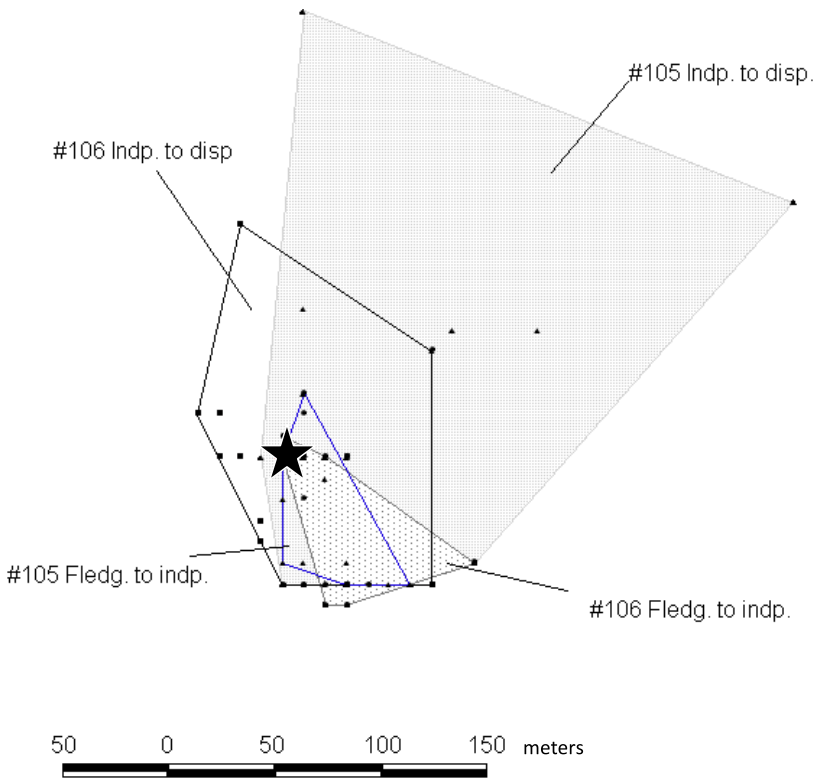


Fig. 2. Locations of nocturnal observations of two radio-tagged Little Owls (# 105 and 106) from the same brood. Distances from the nest were surveyed from fledging to independence (Fledg. to indep.), and from independence to the initiation of natal dispersal (Indp. to disp.). The total areas covered during the different phases are indicated with 100% minimum convex polygons. The location of the nest is marked with a star.

the effect of days after fledging on whether an owl had moved away from its siblings, and for the effect of days after fledging on the presence/absence of begging. The effects of days after fledging on the distance between siblings and on the begging rate were modelled with a log-link and gamma error distribution.

### 3. Results

The radio-tagged Little Owls were  $34 \pm 9$  days old (mean  $\pm$  SD) at fledging (range 22–46 days;  $N = 10$ ). They begged until  $35 \pm 6$  days post fledging (range: 26–40 days;  $N = 6$ ). Owls dispersed at  $86 \pm 20$  days after fledging (range: 57–118 days,  $N = 8$ ). Half of the radio-tracked juveniles had dispersed by mid-September. The other half remained on the natal territory until late October. Hence, the interval between independence and dispersal was  $45 \pm 20$  days (range 31–81;  $N = 5$ ).

#### 3.1. Spatial behaviour

Juveniles were first observed moving away from

the nest location at  $9 \pm 13$  days after fledging (range 0–29,  $N = 9$ ; Table 1). The last time juveniles were observed at the nest location was  $44 \pm 25$  days after fledging (range 0–80,  $N = 9$ ).

Juveniles were located  $110 \pm 75$  m from the nest at night during the post-fledging dependency period and  $212 \pm 75$  m from the nest in the independence to pre-dispersal period. As juveniles became older, they were more likely to move away from the nest (days after fledging:  $F_{1,720} = 79.86$ ,  $P < 0.0001$ ; owl ID nested within brood ID:  $F_{8,720} = 11.89$ ,  $P < 0.0001$ ; and  $P > 0.05$  for the interaction term); also, the distance moved increased with age (days after fledging:  $F_{1,582} = 113.70$ ,  $P < 0.0001$ ; owl ID nested within brood ID:  $F_{8,582} = 15.63$ ,  $P < 0.0001$ ; owl ID nested within a brood ID\*days after fledging:  $F_{8,582} = 8.27$ ,  $P < 0.0001$ ; Fig. 1, upper row). Both the tendency to move away from siblings (days after fledging:  $F_{1,96,89} = 11.69$ ,  $P = 0.0009$ ; brood ID\*age:  $F_{2,86,61} = 4.93$ ,  $P = 0.009$ ) and the distance between siblings (days after fledging:  $F_{1,39,04} = 84.76$ ,  $P < 0.0001$ ; brood ID\*days after fledging:  $F_{2,35,4} = 2.49$ ,  $P = 0.1$ ) also increased as a function of age (Fig. 1, middle row).

Table 2. Home range estimates for juvenile Little Owls. Area in ha (100% Minimum Convex Polygons) is given for each juvenile, from fledging to dispersal, and for the two periods: fledging to independence and independence to dispersal. Number of nocturnal telemetry observations is given in parentheses. Values are mean ± SD. \* marks home ranges calculated with less than 30 fixes. Owls #108, #110, #111 and #112 did not disperse until after 16 October; however, last night observation and thereby last observation used in home range estimate is 16 September.

Owl ID	Fledging to independence (ha, n)	Independence to dispersal (ha, n)	Fledging to dispersal (ha, n)
105	0.29 (54)	4.02 (48)	4.04 (102)
106	0.34 (46)	1.35 (42)	1.50 (88)
107	0.22 (44)	–	–
108	0.28 (50)	13.19 (57)	13.19 (107)
110	1.21 (41)	2.2 (37)*	3.05 (78)
111	0.49 (38)	0.45 (23)*	0.79 (61)
112	0.34 (39)	1.63 (27)	1.91 (66)
113	0.14 (35)	1.13 (40)	1.13 (75)
115	1.69 (46)	2.01 (30)	3.48 (76)
Mean±SD (ha)	0.56±0.53	3.25±4.15	3.64±4.03
Range	0.14–1.69	0.45–13.29	0.79–13.19

The home-range sizes (100% MCPs) increased 6-fold from the post-fledging dependency period (0.56 ha) to the independence-pre-dispersal period (3.3 ha; Fig. 2, Table 2; Wilcoxon signed-rank test,  $P < 0.05$ ). The 22 ring recoveries of birds marked from 1920 to 1999 also indicate that some juveniles remained on the natal territory well into late autumn (Fig. 3). The mean ring recovery dis-

tance within one year after the ringing of owls that had dispersed ( $> 1$  km from nest site) was  $18 \pm 11$  km (range 6–39).

### 3.2. Begging behaviour

Fledged Little Owls vocalised at least once in 60% of the individual 10-min scanning sessions ( $N =$

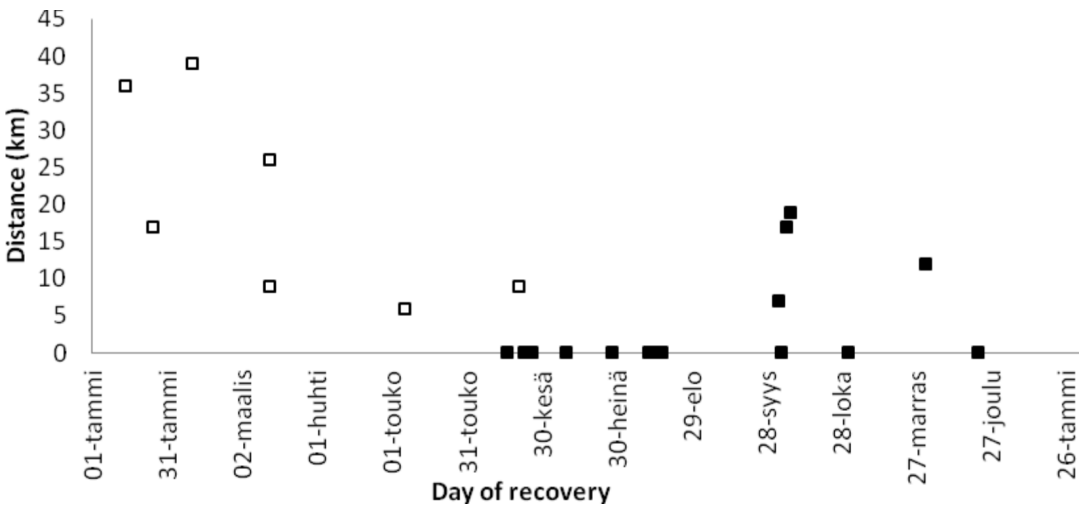


Fig. 3. Distance from the ring-recovery site to the ringing site as a function of the date of ring recovery. Filled symbols represent rings recovered in the individual's hatching year. Open symbols represent rings recovered after the hatching year.



72) performed before begging ceased entirely. The probability of begging did not change during the period that the young were begging (days after fledging:  $F_{1,66.57} = 0.52$ ,  $P = 0.47$ ; brood ID\*days after fledging:  $F_{2,1} = 0.16$ ,  $P = 0.87$ ). The begging intensities ranged from 0.1 to 11.5  $\text{min}^{-1}$  (Fig. 1, lower right). The begging intensity decreased with the number of days after fledging (Fig. 1, lower right; age:  $F_{1,37.91} = 17.61$ ,  $P = 0.0002$ ; brood ID\*days after fledging:  $F_{2,33.72} = 2.47$ ,  $P = 0.10$ ).

## 4. Discussion

### 4.1. Duration of the post-fledging dependency period and beginning of dispersal

The duration of the begging period indicated that the radio-tagged juvenile Little Owls received parental care for up to 40 days after fledging. Telemetry data (supported by ring recovery data) showed that natal dispersal commenced at 2–3 months post fledging. Hence, all birds remained for at least 4 weeks and some remained up to 11 weeks on the natal territory after cessation of parental care. There was considerable individual variation in the duration of post-fledging dependence and independence before dispersal. Our study is based on a relatively small sample of individuals as is naturally the case when dealing with a small population. Thus, care must be taken when interpreting the results and extrapolating to other populations. Nevertheless, this variation indicates that behavioural strategies are subject to considerable plasticity.

Our estimates of the duration of the post-fledging dependency period and the onset and ending of dispersal were similar to those previously reported from field observations (Haverschmidt 1946), ringing data (Exo & Hennes 1980), and radio telemetry analyses (Van Nieuwenhuysse *et al.* 2008). Our estimate of the period from independence to dispersal was longer than the 4–5 weeks observed by Glue and Scott (1980). Additionally, the ring recovery data within the first year of life indicated that juveniles remained at or near the natal territory for an extended period after independence.

In our study, all the young remained on the parental territory for several weeks before commencing natal dispersal. This behaviour indicated that

juvenile fitness, at least in this Little Owl population, was not strongly dependent on “winning a race” for territory vacancies, as may be the case for other terrestrial bird species (e.g., Nilsson & Smith 1988). In this study, other concerns, like building up body reserves before dispersal (Perrins 1965, Gaston 1997, Overskaug *et al.* 1999) and possibly improving foraging skills in a familiar hunting area, appeared to outweigh any advantage of early dispersal. A similar pattern was reported for juvenile Tawny Owls (*Strix aluco*) which also often postponed dispersal for several weeks after independence (Sunde 2008). In comparison, most young Barn Owls (*Tyto alba*), ringed in Denmark from 1921 to 2009, dispersed from their breeding areas within a few weeks after ringing (Huffeldt *et al.* 2012). This behaviour suggested that Barn Owl offspring did not receive prolonged parental care, and they did not feel any strong affiliation to the natal area after fledging. Hence, different owl species in similar habitats and with relatively similar ecology appear to express great differences in parental post-fledging investment. The reasons for these differences remain unclear.

### 4.2. Spatial behaviour

The young Little Owls became increasingly mobile as they aged, and they frequented increasingly larger areas. Similarly, age after fledging in Eagle Owls (*Bubo bubo*; Penteriani *et al.* 2005), Tawny Owls (Overskaug *et al.* 1999), and Spanish Imperial Eagles (*Aquila adalberti*; Donazar & Ceballos 1990) was correlated with distance from the nest. Previously, Eick (2003; cited in Van Nieuwenhuysse *et al.* 2008) has also noted that home-range size increases with age after fledging in juvenile Little Owls.

The sibling association in Little Owls gradually decreased before independence. This behaviour contrasted with that of other species, including the Tawny Owls, where the young showed strong associations, calling nearly continuously, until the last day of dependence (Muir 1954, Sunde & Markussen 2005). The potential benefits of sibling association in the early phases after fledging include enhanced feeding opportunities, because parents must visit only one place to deliver food, and improved anti-predator defence

from the mother (Cresswell 1994). In the Woodchat Shrike (*Lanius senator*), as juveniles grow older, they spend less time near other juveniles (Nikolov & Hristova 2007).

Juvenile home ranges increased considerably from dependence to independence, also reported previously in a different Little Owl population (Eick 2003). However, the juvenile home ranges found in the present study were much smaller than those previously reported (Eick 2003), and slightly smaller or similar to that of the juvenile Tawny Owls (Southern *et al.* 1954, Petty & Thirgood 1989). The home ranges of juveniles were much smaller than those of adult Little Owls. Adults had 100% MCP sizes greater than 100 ha during the same time period (Sunde *et al.* 2009).

### 4.3. Begging behaviour

The negative relationship between begging intensity and age after fledging indicated that the individual benefit of investing in begging decreased with age after fledging. Hunger levels either decreased with age after fledging, as expected when begging is considered an honest signal that indicates hunger (e.g., Quillfeldt 2002), or the parents provided food less frequently with increasing owlet age. It was not possible to observe whether non-vocalising owlets were foraging for themselves. Little Owls largely feed on a wide array of invertebrate prey during the summer (Van Nieuwenhuysse *et al.* 2008). It is probable that the young began to hunt on their own to fulfil part of their needs within a few weeks after fledging. This explanation was supported in a study by Ille (1983), who found gradual improvement in the prey-handling skills of captive Little Owls. Ille (1983) also found that they were able to catch prey by 62–76 days after hatching, which corresponds to their age at independence. An alternative, but not mutually exclusive explanation could be that parents gradually reduced the frequency and amount of food provided to the offspring (Koga & Shiraishi 1994) to ensure that begging was less profitable than independent feeding. In this view, the parents' actions would effectively force the juveniles to forage on their own (Wheelwright & Templeton 2003).

Sunde and Markussen (2005) found that the

begging intensity of juvenile Tawny Owls appeared to increase at the end of the post-fledging period. On the other hand, Koga and Shiraishi (1994) and Roulin (2001) showed that the begging intensity did not vary significantly with age after fledging in the Black Kite (*Milvus migrans*) and Barn Owl. These species mainly feed on vertebrate prey. This means that the young of these species have greater difficulty in capturing prey than for example Little Owls that largely forage on (presumably easier caught) invertebrates in summer and early autumn (Van Nieuwenhuysse *et al.* 2008). These actions may explain the apparent differences among species in age-related begging patterns. In all circumstances, the gradual decrease in begging rates indicates that there is no strong parent-offspring conflict (Trivers 1974) over parental food provisioning towards the end of the dependency period. This finding contrasts with the recognised behaviour in some vertebrate-predating raptors, which exhibit prolonged parental care periods (e.g., Bustamante 1994, 1995, Sunde 2008).

### Nuorten minervanpöllöjen lentokyvyn saavuttamisen jälkeinen käyttäytyminen

Pöllöjen sosiaalinen ja tilakäyttäytyminen ennen nuoruusiän levittäytymistä on vähän tutkittu aihe. Seurasimme minervanpöllön (*Athene noctua*) sosiaalista ja tilakäyttäytymistä sekä iän vaikutusta näihin Tanskassa radioseurantamenetelmällä. Seurannassa oli kymmenen pesästä lähtenytä poikasta viidestä pesyeestä. Lentokyvyn saavuttamisen jälkeinen riippuvuusjakso oli keskimäärin 35 päivää ( $n = 6$ ). Nuoret yksilöt pysyttelivät syntymäreivilläään 45 vuorokautta ( $n = 5$ ) lentokyvyn saavuttamisen ja levittäytymisen välillä. Puolet nuorista levittäytyi syyskuun puoleenväliin mennessä, mutta puolet pysytteli syntymäreivilläään ainakin lokakuun puoleenväliin.

Pienimmän konveksin polygonin perusteella arvioitu elinpiiri oli lentokyvyn saavuttamisen ja riippumattomuuden välillä  $0,56 \pm 0,53$  ha (keskiarvo ja SD) sekä riippumattomuuden ja levittäytymisen välillä  $3,25 \pm 4,15$  ha. Lentokyvyn saavuttamisen jälkeisinä ensimmäisinä 40 vuorokausina nuorten yksilöiden etäisyys pesästä kasvoi samalla kun kerjuuäänten toistuvuus ja intensiteetti vähenivät. Havainnot sopivat siihen, että vanhemmat

vähentävät jalkikasvun ruokkimista saalistuskyy-  
vyn kehittymisen myötä.

## References

- 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. 1995: The duration of the post-fledging dependence period of ospreys *Pandion haliaetus* at Loch Garten, Scotland. — *Bird Study* 42: 31–36.
- Cramp, S. (ed.) 1985: Handbook of the Birds of Europe, the Middle East and North Africa. Vol. IV: Terns to Woodpeckers. — Oxford University Press, New York.
- Cresswell, W. 1994: Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. — *Animal Behaviour* 47: 433–442.
- Donazar, J.A. & Ceballos, O. 1990: Post-fledging dependence period and development of flight and foraging behaviour in the Egyptian vulture *Neophron percnopterus*. — *Ardea* 78: 387–394.
- Eick, M. 2003: Habitatnutzung und Dismigration des Steinkauzes *Athene noctua*. — Master's thesis, Universität Hohenheim. (In German)
- Exo, K.-M. 1992: Population ecology of Little Owls *Athene noctua* in Central Europe: a review. In The ecology and conservation of European owls (ed. Galbraith, C.A., Tailor, I.R. & Percival, S.): 64–75. — Joint Nature Conservation Committee, Peterborough.
- Exo, K.-M. & Hennes, R. 1980: Beitrag zur Populationsökologie des Steinkauzes (*Athene noctua*) — eine Analyse deutscher und niederländischer Ringfunde. — *Die Vogelwarte* 30: 162–179. (In German)
- Finck, P. 1990: Seasonal variation of territory size with the Little Owl (*Athene noctua*). — *Oecologia* 83: 68–75.
- Framis, H., Holroyd, G.L., Mañosa, S. 2011: Home range and habitat use of little owl (*Athene noctua*) in an agricultural landscape in coastal Catalonia, Spain. — *Animal Biodiversity and Conservation* 34: 369–378.
- Gaston, A. J. 1997: Mass and date at departure affect the survival of ancient murrelet *Synthliboramphus antiquus* chicks after leaving the colony. — *Ibis* 139: 673–678.
- Génot, J.-C. & Wilhelm, J.-L. 1993: Occupation et utilisation de l'espace par la Chouette chevêche, *Athene noctua*, en bordure des Vosges du Nord. — *Alauda* 61: 181–194. (In French)
- Gladbach, A., Büßer, C., Mundry, R. & Quillfeldt, P. 2009: Acoustic parameters of begging calls indicate chick body condition in Wilson's storm-petrels *Oceanites oceanicus*. — *Journal of Ethology* 27: 267–274.
- Glue, D. & Scott, D. 1980: Breeding biology of the Little Owl. — *British Birds* 73: 167–180.
- Glutz von Blotzheim, U.N. & Bauer, K.M. 1980: Handbuch der Vögel Mitteleuropas. Vol.9. — Akademische Verlag, Weisbaden. (In German)
- Grzywaczewski, G. 2009: Home range size and habitat use of the Little Owl *Athene noctua* (Scopoli 1769) in Lublin Region (East Poland). — *Ardea* 97: 541–545
- Haverschmidt, F. 1946: Observations on the breeding habits of the Little Owl. — *Ardea* 34: 214–246.
- Hofstetter, S.H. & Ritchison, G. 1998: The begging behavior of nestling eastern screech-owls. — *The Wilson Bulletin* 110: 86–92.
- Holleback, M. 1974: Behavioral interactions and the dispersal of the family in black-capped chickadees. — *The Wilson Bulletin* 86: 466–468.
- Hooge, P.N. & Eichenlaub, B. 1997: Animal movement extension to ArcView. Version 1.1. — Alaska Biological Science Center, U.S. Geological Survey, Anchorage.
- Huffeldt, N.P., Aggerholm, I.N., Brandtberg, N.H., Jørgensen, J.H., Dichmann, K. & Sunde, P. 2012: Compounding effects on nest-site dispersal of Barn Owls *Tyto alba*. — *Bird Study* 59: 175–181.
- Ille, R. 1983: Ontogenese des Beutefangverhaltens beim Steinkauz (*Athene noctua*). — *Journal für Ornithologie* 124: 133–146. (In German)
- Kenward, R.E. 2001: A Manual for Radio Tagging. — Academic Press, London.
- Koga, K. & Shiraiishi, S. 1994: Parent-offspring relations during the post-fledging dependency period in the black kite (*Milvus migrans*) in Japan. — *Journal of Raptor Research* 28: 171–177.
- Muir, R.C. 1954: Calling and feeding rates of fledged tawny owls. — *Bird Study* 1: 111–117.
- Newton, I. 1979: Population ecology of raptors. — T. & AD Poyser, Berkhamsted, UK.
- Nikolov, B.P. & Hristova, I.P. 2007: Time-activity budgets of juvenile woodchat shrikes *Lanius senator* during the post-fledging period. — *Ardea* 95: 235–241.
- Nilsson, J.Å. & Smith, H.G. 1988: Effects of dispersal date on winter flock establishment and social dominance in marsh tits *Parus palustris*. — *Journal of Animal Ecology* 57: 917–928.
- Overskaug, K., Bolstad, J.P., Sunde, P. & Øien, I.J. 1999: Fledging behavior and survival in northern tawny owls. — *The Condor* 101: 169–174.
- Penteriani, V., Delgado, M.M., Maggio, C., Aradis, A. & Sergio, F. 2005: Development of chicks and dispersal behaviour of young in the eagle owl *Bubo bubo*. — *Ibis* 147: 155–168.
- Perrins, C.M. 1965: Population fluctuations and clutch-size in the great tit, *Parus major* L. — *Journal of Animal Ecology* 34: 601–647.
- Petty, S.J. & Thirgood, S.J. 1989: A radio tracking study of post-fledging mortality and movements of tawny owls in Argyll. — *Ring and Migration* 10: 75–82.
- Quillfeldt, P. 2002: Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. — *Animal Behaviour* 64: 579–587.
- Roulin, A. 2001: Food supply differentially affects sibling negotiation and competition in the barn owl (*Tyto al-*

- ba). — Behavioural Ecology and Sociobiology 49: 514–519.
- Roulin, A., Kölliker, M. & Richner, H. 2000: Barn owl (*Tyto alba*) siblings vocally negotiate resources. — Proceedings of the Royal Society B: Biological Science 267: 459–463.
- Sacchi, R., Saino, N. & Galeotti, P. 2002: Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. — Behavioral Ecology 13: 268–273.
- Southern, H.N., Vaughan, R. & Muir, R.C. 1954: The behaviour of young tawny owls after fledging. — Bird Study 1: 101–111.
- Sunde, P. 2005: Predators control post-fledging mortality in tawny owls, *Strix aluco*. — Oikos 110: 461–472.
- Sunde, P. 2008: Parent-offspring conflict over duration of parental care and its consequences in tawny owls *Strix aluco*. — Journal of Avian Biology 39: 242–246.
- Sunde, P. & Markussen, B.E.N. 2005: Using counts of begging young to estimate post-fledging survival in tawny owls *Strix aluco*. — Bird Study 52: 343–345.
- Sunde, P., Thorup, K., Jacobsen, L.B., Holsegård-Rasmussen, M.H., Ottesen, N., Svénné, S. & Rahbek, C. 2009: Spatial behaviour of Little Owls (*Athene noctua*) in a declining low-density population in Denmark. — Journal of Ornithology 150: 537–548.
- Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. 2010: Breeding season food limitation drives population decline of Little Owl *Athene noctua* in Denmark. — Ibis 152: 803–814.
- Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. 2013: Survival and causes of mortality in Danish Little Owls. — Journal of Ornithology (in press).
- Trivers, R.L. 1974: Parent-offspring conflict. — American Zoology 14: 249–264.
- Van Nieuwenhuysse, D., Génot, J.-C. & Johnson, D.H. 2008: The Little Owl: Conservation, Ecology and Behaviour of *Athene noctua*. — Cambridge University Press, New York.
- Wheelwright, N.T. & Templeton, J.T. 2003: Development of foraging skills and the transition to independence in juvenile savannah sparrows. — Condor 105: 279–287.
- Zuberogoitia, I., Zabala, J., Martínez, J.A., Hidalgo, S., Martínez, J.E., Azkona, A. & Castillo, I. 2007: Seasonal dynamics in social behaviour and spacing patterns of the Little Owl *Athene noctua*. — Ornis Fennica 84: 173–180.

Appendix I. Radio-tracking data for juvenile Little Owls in 2008. The date of dispersal is an estimate calculated as halfway between the date of last contact and the date of the first unsuccessful search. Age is given in days after hatching, with days after fledging in parentheses. The last column shows the different analyses performed with data from each individual. The different types of analyses are: B=Analysis of begging rate; N=Analysis of distance to the nest; S=Analysis of the distance between siblings, and H=Calculation of home ranges. At Herredsvej, two individuals from four eggs fledged; at Vester Hornumvej, three individuals from four eggs fledged; at Løgstørvej, three individuals from six eggs fledged; at Kathrinevej, one individual from four eggs fledged; at Rodhøjvej, one individual from three eggs fledged; and at Kjemtrupvej, three individuals fledged from an unknown number of eggs. Nestlings from Løgstørvej received supplemental food.

Owl ID	Location	Suppl. food	Hatch date	Fledging date	Age: fledging last begging	Last contact	Age: last contact	Search date	Age: search	Disper- sal date	Age: disper- sal	Reason	Analysis
105	Herredsvej	-	1-6-08	23-6-08	22	62 (40)	11-9-08	14-9-08	105 (83)	13-9-08	104 (82)	Dispersed	B, N, S, H
106	Herredsvej	-	1-6-08	23-6-08	22	62 (40)	6-9-08	10-9-08	101 (79)	8-9-08	99 (77)	Dispersed	B, N, S, H
107	Vester Hornumvej	-	21-5-08	20-6-08	30	67 (37)	29-8-08	-	-	-	-	Died between independence and dispersal	B, N, S, H
108	Vester Hornumvej	-	21-5-08	20-6-08	30	67 (37)	8-10-08	24-10-08	156 (126)	16-10-08	148 (118)	Dispersed	B, N, S, H
109	Vester Hornumvej	-	21-5-08	20-6-08	30	-	8-7-08	-	-	-	-	Dead before independence	B
110	Løgstørvej	+	27-5-08	10-7-08	44	-	8-10-08	24-10-08	150 (106)	16-10-08	142 (98)	Lost signal	N, S, H
111	Løgstørvej	+	27-5-08	10-7-08	44	-	8-10-08	24-10-08	150 (106)	16-10-08	142 (98)	Dispersed	N, S, H
112	Løgstørvej	+	27-5-08	12-7-08	46	-	8-10-08	24-10-08	150 (104)	16-10-08	142 (96)	Dispersed	N, S, H
113	Rodhøjvej	-	17-5-08	28-6-08	42	70 (28)	29-8-08	31-8-08	106 (64)	30-8-08	105 (63)	Dispersed	B, N, H
115	Kjemtrupvej	-	28-5-08	27-6-08	30	56 (26)	20-8-08	25-8-08	89 (59)	23-8-08	87 (57)	Dispersed	N, H
Mean					34	64 (35)			126 (91)		121 (86)		
Min					22	56 (26)			89 (59)		87 (57)		
Max					46	70 (40)			156 (126)		148 (118)		