How Fledglings Explore Surroundings from Fledging to Dispersal. A Case Study with Eagle Owls Bubo bubo

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Source: Ardea, 97(1) : 7-15

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0102

How fledglings explore surroundings from fledging to dispersal. A case study with Eagle Owls *Bubo bubo*

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Delgado M.M., Penteriani V. & Nams V.O. 2009. How fledglings explore surroundings from fledging to dispersal. A case study with Eagle Owls *Bubo bubo*. Ardea 97(1): 7–15.

Movement strategies are one of the primary mechanisms underlying animal survival. Despite the impressive amount of studies on animal movement during successive stages in the life history in birds, little is known about the characteristics of movements during the post-fledging dependence period. Such a period represents a crucial phase of the life history during which individuals can show important displacements around the natal nest. Here we present path search strategies employed by radio-tagged fledgling Eagle Owls *Bubo bubo* during the post-fledging dependence period (1962 locations from 41 tagged owlets). During the post-fledging dependence period, individuals show dynamic movement behaviours that might be related to the development of individuals' mobility and cognitive abilities. Immediately after leaving the nest, individuals focused their activities close to the nest, but after a few weeks individuals travelled further and faster, up to the moment that they started to disperse. At the time that the mobility of owlets was highest, their movements described straighter paths. Movement patterns were not affected by morphological- or physiological parameters of body condition. Between-sibling distances showed a significant interaction between sex and time: until 20 days after owlets left the nest, siblings were closer together, independently of the sex. Between-sibling distances increased with time as individuals became increasingly mobile; just before the start of dispersal, family units seemed to dissolve.

Key words: *Bubo bubo,* fractal analysis, path search strategies, perceptual range, post-fledging dependence period

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INTRODUCTION

The study of animal movement patterns allows us to understand ecological processes at various spatial and temporal scales (Kareiva & Shigesada 1983, Wiens *et al.* 1995, Blackwell 1997). At small spatial scales, animals rely on movements for finding food, mates, cover and avoiding predators (e.g. Vásquez *et al.* 2002). The way in which animals move around affects the fate of individuals and, consequently, the spatial structure, demographics and genetic structure of animal populations (Turchin 1998). As a consequence, in a still higher organizational level, movements affect population dynamics, community structures, and ecosystem biodiversity. Therefore, movements have important consequences at different ecological levels and scales for a variety of ecological processes and patterns (Crist *et al.* 1992, Wiens *et al.* 1995, Goodwing & Farhig 2002).

Until now, most movement studies have focused on: (a) movements within the home range (Worton 1987, Sunde & Redpath 2006), (b) search strategies directed toward favourable habitat patches (Zollner & Lima 1999), (c) the response to fragmented habitat (Crist *et al.* 1992, With & Crist 1995, Wiens *et al.* 1997), and (d) foraging movements in heterogeneous landscapes (Chris *et al.* 2002, Bailey & Thompson 2006). Due to the impact of floaters on breeding (meta)population dynamics (Heino *et al.* 1997, Hanski 1999, Penteriani *et al.* 2005a,b, 2006), dispersal has also become the focus of much current research on animal movements (Bowler & Benton 2005). However, few studies have analysed the temporal and spatial movement patterns before dispersal.

In birds, the period from fledging to independence is known as the post-fledging dependence period (hereafter, PFDP). During this stage, juveniles gradually have to: (1) enhance muscular development, (2) experiment with the external world and conspecifics without the protection of the nest, and (3) learn essential skills to survive as an adult. The different behavioural options of search strategy in this critical period might affect the fate of individuals. This period is a crucial phase in life history because it represents the time during which individuals reach the necessary body condition for dispersal. Reproductive efforts invested by parents during the previous stages may be lost if the PFDP occurs in hostile and uncertain environments or conditions. The PFDP is also a dynamic phase, in which juveniles increase their mobility and parental protection decreases (Bogner & Baldassarre 2002, Kershner *et al.* 2004, Myers & Vaughan 2004, Penteriani *et al.* 2005c, Wiens *et al.* 2006). If the increased travel occurs in hostile or unknown habitats, mortality could increase due to, for example, predation (Sunde 2005), electrocution (Sergio *et al.* 2004), as well as starvation and diseases (Aebischer *et al.* 2005). This increase in juvenile mortality may affect breeding populations because of the reduction of the floater segment of a population (Delibes *et al.* 2001, Penteriani *et al.* 2005a,b, 2006).

Despite the importance of the PFDP, information on this phase is scarce and is considered one of the missing links in our understanding of avian life histories (Sullivan 1989, Weatherhead & McRae 1990, Rappole 1995). The few studies analysing the PFDP have mainly focused on survival (e.g. Monrós *et al.* 2002, Sunde 2005, Hylton *et al.* 2006, Adams *et al.* 2006) and the length of the dependence period (Ferrer 1992, Amar *et al.* 2000, Mínguez *et al.* 2001). Little is known about the spatial and temporal movement patterns of juveniles and, although some studies have measured movements, they mainly focused on displacements from the nest or on the area used by juveniles (Kershner *et al.* 2004, Myers & Vaughan 2004, McClaren *et al.* 2005, Penteriani *et al.* 2005c, Wiens *et al.* 2006). However, knowledge of movement patterns during PFDP could be one of the most useful tools to allow one to better understand this final phase of the breeding cycle, as well as to be aware of the possible risks that the fledglings are confronted with. This is particularly important in the case of endangered species (as many raptor species), who during their exploratory PFDP moves may be faced with various stochastic events.

The main objective of our study was to describe and analyse the patterns of PFDP movements of fledgling Eagle Owls *Bubo bubo*, mainly focusing on: (1) the essential characteristics of individual movements, family unit interactions and territory use throughout the PFDP; (2) how movement patterns change during this stage of the breeding cycle; and (3) potential interactions between fledglings' physical conditions and features of movement patterns. In particular, we tested if individuals in better physical condition changed movement patterns sooner than other individuals.

METHODS

Study area and study species

We conducted field research from late March to early August 2004 and 2005 on 41 Eagle Owl fledglings (24 males; 17 females) from 13 different nests located in the Sierra Norte of Seville (37°30'N, 06°03'W, SW Spain; more details in Penteriani *et al.* 2005c).

The Eagle Owl, the largest owl in Europe, is a sexually plumage-monomorphic and socially monogamous long-lived species. It is a sedentary and territorial owl, with a high reproductive rate (Penteriani 1996). It is a generalist both in diet (Mikkola 1994, Lourenço 2006) and nest choice (Mikkola 1994, Penteriani *et al.* 2001, 2002, Marchesi *et al.* 2002, Martinez *et al.* 2003), having an important impact on bird communities (Sergio *et al.* 2003). However, in Mediterranean regions where rabbits may be widespread and abundant, Eagle Owl can turn into a predator specializing on rabbits. This top predator, with a vulnerable conservation status (Sergio *et al.* 2004), is widely distributed throughout Palaearctic Regions (Mikkola 1994, Penteriani 1996). It occurs in a variety of habitats, ranging from boreal forests to Mediterranean scrubland and steppes, including rocky and sandy deserts (Mikkola 1994, Penteriani 1996).

Field methods

At the age of 30–35 days, nestlings were fitted with a teflon ribbon backpack harness that carried a 30 g radio-transmitter (Biotrack Ltd, Wareham BH20 5AJ, Dorset, UK). The weight of the tags corresponded to less than 3% of the weight of the smallest adult male (1550 g) and 3.5% of the smallest fledgling weight (850 g) of our Eagle Owl population. Because at this time the young are still growing (Penteriani *et al.* 2005c), backpacks were adjusted so that the teflon ribbon could expand with increasing body size. We manipulated and marked owls under the Junta de Andalucía – Consejería de Medio Ambiente permits No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02. After 4 years of continuous radiotracking of 23 breeders and 74 floaters, we never recorded a possible adverse effect that could be directly attributed to backpacks on birds (Delgado & Penteriani, unpubl. data; see also Petty *et al.* 2004, Sunde 2006).

Based on earlier visits to the nests we estimated the age of the chicks (Penteriani *et al.* 2005c) and sexed them by molecular procedures using DNA extracted from blood (Griffiths *et al.* 1998). To determine individual physical condition we measured morphological, biometrical and biochemical parameters. Morphological and biometrical measurements were summarized into a body condition index estimated by a reduced major axis (RMA) regression (Green 2001), using log of both body mass (to the nearest 10 g, with 1 kg Pesola scales) and wing length (using a digital calliper, ±0.1 mm). Higher values of the BCI represent higher-quality individuals (Green 2001). To obtain biochemical measurements, blood samples were collected and stored in tubes with heparin at 4°C until arrival at the laboratory, where they were centrifuged for 10 min at 4000 rpm and the plasma was separated and stored at –78ºC. From plasma samples, cholesterol urea and total protein concentrations were determined using a spectrophotometer (Screenpoint 2, COR SRL; Ginestra Florentina, Italy), using commercial kits (BIOLABO). These biochemical parameters have been shown to be good indices of body condition in birds (e.g. Alonso-Alvarez *et al.* 2002).

We defined the different life history phases as follows. The PFDP started when the first juveniles left the nest. Because the majority of nests in our study area were on the ground or on small cliffs, this happened approximately at an age of 40–45 days (late March in our study area; see Penteriani *et al.* 2005c). This period lasted until the beginning of natal dispersal. Natal dispersal started when the distance between successive moves became larger than the average distance travelled by each animal (Palomares *et al.* 2000, Delgado & Penteriani 2008). This happened at the end of August in our study area, when birds were 170 ± 20.5 days old (range 131–232 days).

During the PFDP we performed periods of intensive radiotracking two times per week during the whole night, from one hour before sunset to one hour after sunrise. In these radiotracking sessions we visited all the nests and radiolocated owlets from all family units simultaneously, with 1-hour time interval between successive individual locations. As fledglings are not very mobile and alternate movements with long resting stages (Delgado & Penteriani, unpubl. data), we suspect to have obtained similar results when taking more fixes per time unit. Night locations of radio-marked animals were carried out via biangulation with a 3-element hand-held Yagi-antenna connected to ICOM (IC-R20) portable receivers (www.icom.co.jp). Biangulations were analysed by ArcView 3.2 geographic information system (GIS) software.

Post-fledging paths analysis

CHARACTERISTICS OF MOVEMENTS, TERRITORY USE AND FAMILY UNIT INTERACTIONS

We divided the PFDP into 6 periods of 20 days, following Penteriani *et al.* (2005c) and Delgado & Penteriani (2007). To study the essential characteristics of movements, for each of the 20-day period we calculated the mean distance between successive owlet locations (i.e. mean step length), and the mean distance between the nest and each location point collected with an hour time fixed interval during the nights of radiotracking. To evaluate the interactions between siblings (i.e. family unit interactions) we estimated the between-sibling distances, that is the mean distance between owlets from the same family unit (by using individual locations recorded simultaneously). Finally, to understand how the fledglings explored surroundings of the nest, we estimated the post-fledging areas (hereafter PFAs) using 95% minimum convex polygons (Hayne 1949). These areas were calculated for each individual for each night; then, we computed the mean of these areas in each 20-day period.

SPATIAL AND TEMPORAL MOVEMENT PATTERNS

We estimated movement path tortuousity using fractal dimension, D. Fractal D is the continuous analogue of geometric dimensions, and ranges from a minimum of 1 for a straight line to a maximum of 2 when the path completely covers the plane. Fractal D was computed using the Fractal Mean estimator with the program Fractal 3.16 (Nams 2006a). We calculated an overall estimate of fractal D for each path, using the same range of scales for all movement paths (from 10 to 100 m). The upper limit was less than half the lengths of the longest paths (Halley *et al.* 2004). Using the same range of scales allowed us to compare fractal D among paths even though D varied with scale, thus avoiding the problems pointed out by Turchin (1996). Like most movement parameters, there is some correlation among fractal *D*, step length and home range size. However using the same range of scales for all animals ensured that fractal D is not totally dependent on either step length or range size. We calculated the average fractal *D* in each 20-day period, estimating values of confidence intervals from the variation among the paths. Error values are given as 95% confidence intervals.

We also analysed the movement mechanisms during the PFDP. This was done using the $\mathrm{CRW}_{\mathrm{Diff}}$ statistic, which measures the deviation in squared net distance traversed between the observed and correlated random walk (CRW) expected paths (Scaling test, Nams 2006b). That is, the index measures how similar the path is to a CRW. The Scaling test is based on the biological distinction that the mechanisms for unoriented movements act locally (i.e. at small spatial scale), while all oriented movements imply long-distant behavioural mechanisms. Although $\mathrm{CRW}_{\mathrm{Diff}}$ was initially designed in order to test for oriented movement by dispersing animals, we are using it simply as a general index to compare different paths. We treated each path as an individual sample, estimating the average $\mathrm{CRW}_{\mathrm{Diff}}$ values for each 20-day period, and estimating values of confidence intervals from variation among paths.

Statistical analyses

Repeated measurement mixed models were applied (PROC MIXED in SAS software; SAS Institute 2001) to analyse the variability in movement characteristics, space use and family unit interactions as a function of the 20-day period, sex and year. Because repeated measures were made for each owlet we considered individuals as subjects (SUBJECT statement in PROC MIXED), with nests as an additional random effect because they represent only a subsample of all potential territories (Littell *et al.* 1996, Revilla *et al.* 2002). We used the restricted maximum likelihood method (REML) to estimate all the unknown variance-covariance parameters (Jennrich & Schluchter 1986) and selected compound symmetry as the covariance structure that was the best fit, using the Akaike Information Criterion to measure model fit. Finally, statistical significance was considered to be $P < 0.05$.

The original fractal *D* was non-normal, but the logarithm of *D*–1 fitted a Gaussian distribution (Katz & George 1985). Then, we used Pearson's bivariate correlation to analyse the degree of tortuousity of the search paths among 20 days-periods.

RELATING MOVEMENT PATTERNS TO INDIVIDUAL QUALITY

To explore if changes in movement patterns were related to fledgling physical condition (that is, if individuals in better physical condition changed movement patterns sooner), we estimated the slope of the curves of both fractal *D* and CRWDiff against time. This was done for the 20-day periods of the 10 individuals who were continuously followed during the whole PFDP. Individuals that changed their movement patterns sooner should have curves with steeper slopes. Then, we used Generalized Linear Models (GLM, McCullagh & Nelder 1989) to explore if these slope values were relate to fledgling physical condition. Each explanatory variable (physical condition parameters) and their interactions were fitted to the observed data using the GENMOD procedure of the SAS package (SAS Institute 2001).

RESULTS

Movement characteristics, territory use and family unit interactions

We obtained 1962 locations of the 41 tagged owlets (Table 1).

Average step length, distance from the nest, between-sibling distances and PFAs size increased with time throughout the post-fledging dependence period (Fig. 1). Step lengths were short (mean ± 95% CI: 343.6 ± 32.0 m) when juveniles left the nest and until

Table 1. Number of owl fledglings, total number of owlet locations, the average number of locations per individual, with SD and range, in each 20-day period used to analyse owlet movement patterns during the post-fledging dependence period. The total number of owlets was 41, but not all were recorded in each 20-day period.

	Time since fledging (days)					
	0	20	40	60	80	100
Number of owlets	27	35	29	25	29	30
Number of locations	335	313	320	315	379	300
Mean per owlet ± SD	12.4 ± 4.3	8.9 ± 3.9	10 ± 4.1	12.6 ± 7.0	13.1 ± 8.6	10 ± 4.0
Range	(4–20)	(4–16)	(4–18)	(5–23)	(4–28)	(4–17)

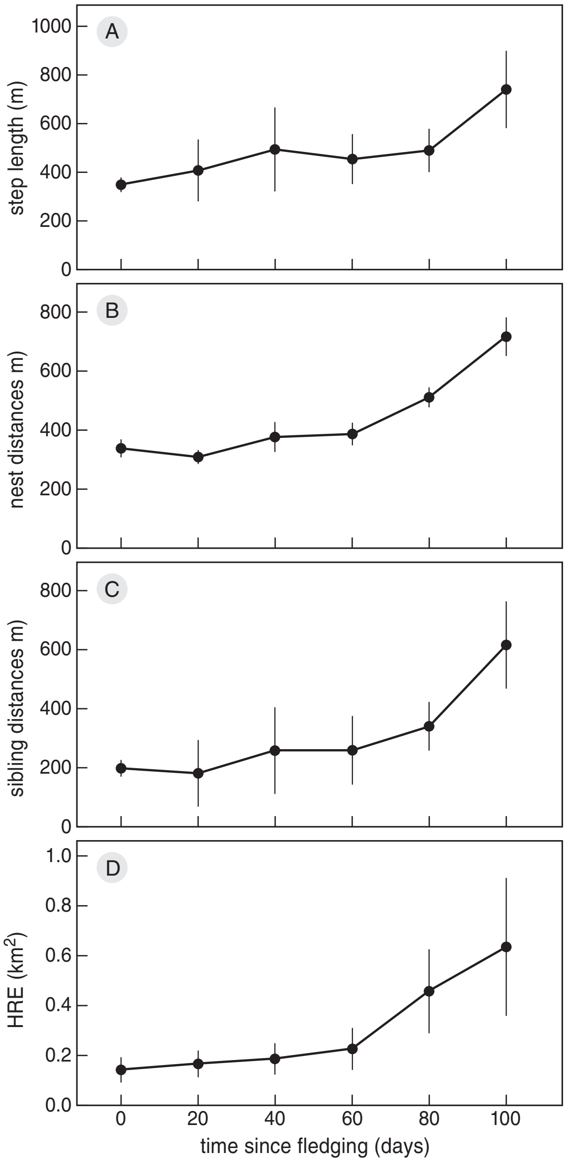

Figure 1. Movement characteristics of fledged Eagle Owls (n = 41) by 20-day periods during the post-fledging dependence period. Given are means and 95% confidence intervals. (A) Mean distance between successive nightly locations, (B) distance from the nest, (C) distances among siblings, and (D) size of post-fledging areas.

20 days after fledging. In the next 60 days, the distance travelled between successive moves significantly increased (GLIMMIX, $F_5 = 6.66$, $P < 0.0001$; Fig. 1A), reaching the highest values close to dispersal (mean 734.2 ± 160.8 m). Also, juveniles were closer to the nest during the first 20-day period (334.8 ± 25.5 m), travelling further from the nest during the rest of the PFDP (GLIMMIX, $F_5 = 61.66$, $P < 0.0001$), reaching a maximum distance just before dispersal (Fig. 1B). There were no significant effects on any of the movement characteristics of owlet sex, year, or their interactions (all $P > 0.40$).

Between-sibling distances showed a significant interaction between the effects of sex and time (GLIMMIX, $F_{1,5} = 28.73$, $P < 0.0001$). Until 20 days after owlets left the nest, family units were closer together, independently of the sex of juveniles (mean 197.3 ± 30.3 m). Between-sibling distances increased with time as individuals became increasingly mobile (Fig. 1C). The closest proximity was between siblings of different sex (mean 237.8 ± 30.6 m), the next closest was between males (mean 289.9 ± 18.9 m), and the furthest was between females (mean 309.5 ± 24.9 m). Just before dispersal, family units seemed to dissolve, with a mean spacing between individuals of 613.4 ± 148.9 m. PFAs showed two main significant effects. PFAs varied between years with owlets having larger PFAs in 2004 (mean 0.4 ± 0.10 km^2) than 2005 (mean 0.1 ± 0.04 km^2) and with time since fledging: owlets increased the areas prospected from 0.16 ± 0.05 km^2 when they left the nest to a maximum of 0.94 ± 0.28 km^2 just before dispersal (GLIMMIX, $F_{1,5} = 308.74$, $P < 0.0001$; Fig. 1D). We did not detect any effects of sex on PFAs.

Scaling test for directed movement and fractal analysis

Path tortuousity significantly decreased with time since fledgling ($r = -0.89$, $P < 0.05$; Fig. 2A). Paths were more tortuous when owlets left the nest (mean 1.19; 95% CI: 1.12–1.27) than at the end of the dependence period (mean 1.09; 95% CI: 1.06–1.11). At the time that owlets travelled significantly farther distances, their movements described straighter paths.

The statistic CRWDiff was negative during the entire PFDP (Fig. 2B), indicating that the movement paths covered a shorter distance than a CRW would. The confidence intervals do not include zero, so juvenile paths during the dependence period were significantly unoriented.

Movement patterns and individual condition

We did not detect any significant effects of the condition parameters (body condition index, blood cholesterol urea and total blood protein concentrations: all $P > 0.5$) on slope of the curves of either fractal D or CRW$_{\text{Diff}}$. That is, fledglings seemed to change their movement behaviour during the PFDP independently of their physical condition: individuals in better condition did not change their movement behaviour sooner during the PDFP.

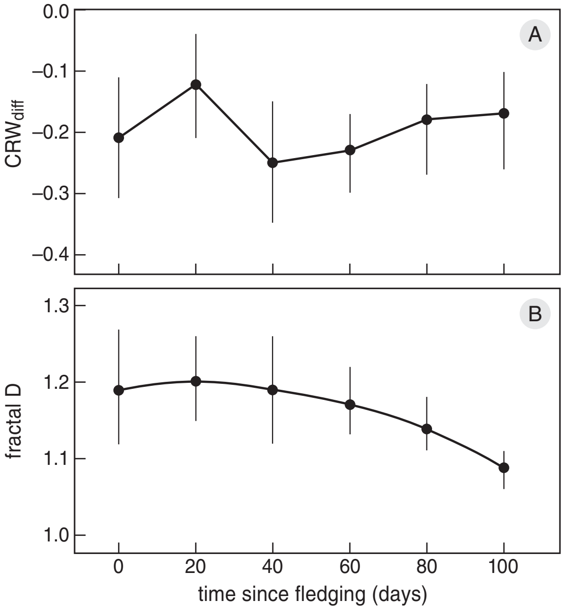

Figure 2. Change in movement paths of fledgling Eagle Owls ($n = 41$) during the post-fledging dependence period. (A) Scaling test applied to movement paths of young Eagle Owls during the PFDP. CRWDiff measures the distance travelled by the movement path as compared to a correlated random walk (CRW). (B) Path tortuousity (Fractal *D*; means and 95% confidence intervals) decreased with time throughout the post-fledging period. Given are means and 95% confidence intervals.

DISCUSSION

The analysis of fledgling movements allowed us to detect several notable behaviours during the PFDP. After leaving the nest, owlets moved with short steps, focusing their activities at, or very close to, the nest. Consequently, at this time, the PFAs prospected by young were limited to areas around the nest. After a few weeks, the movements of fledglings showed a marked change, with their movement trajectories longer than initially observed. Moreover, they were frequently located farther from their nests. This change in post-fledging behaviour may be probably due to the increased flying ability of owlets, as reported for other species (Belthoff & Ritchison 1989, Ferrer 1992, King & Belthoff 2001, Mínguez *et al.* 2001). In fact, when the young leave the nest (approximately 40–45 days): (a) remiges and rectrices are only 80% and 40% of their final length, respectively; (b) secondaries are still encased in 7–8 cm sheathings; and (c) wing coverts are only starting to emerge (Penteriani *et al.* 2005c). Because at this stage owlets cannot fly but rather walk and jump among rocks and brushes, the movement patterns we observed mainly reflect this form of displacement, i.e. that of a 'terrestrial bird' that cannot use its wings.

Although fledglings continued to expand their PFA size indefinitely until departing from the parent territories, most of PFAs included the nest within their activity area throughout the entire PFDP. Similar patterns reported by McClaren *et al.* (2005: Goshawks *Accipiter gentilis*), Wood *et al.* (1998: Bald Eagles *Haliaeetus leucocephalus*), and Belthoff & Ritchison (1989: Eastern Screech-Owls *Megascops asio*) suggest that nests still represent a focal point throughout the post-fledging period.

In the early PFDP, siblings tended to move together, with a constant distance between them during the first weeks. But, as independence neared, the distance increased progressively and family units seemed to partially dissolve. This is in accordance with Newton's (1979) idea that fledglings of raptors tend to perch apart, as also observed by Bustamante & Hiraldo (1990), Ceballos & Donázar (1990) and Bustamante (1994; but see O'Toole *et al.* 1999), but at later stages of PFDP only. Increased sibling distance can be due, in a non-mutually exclusive way, to conflict behaviours between juveniles or increased flight abilities.

Although inter-sibling distances increased during the entire dependence period, juveniles of different sexes tended to stay close together during the whole PFDP. Such a link among siblings during the whole PFDP does not necessarily break up after the start of dispersal: in contrast to other raptor species (e.g. Black Kites *Milvus migrans*, Bustamante & Hiraldo 1990 and Lesser Kestrels *Falco naumanni*, Bustamante & Negro 1994), some Eagle Owls move together during the first steps of dispersal (Delgado & Penteriani, unpubl. data).

Spatial and temporal movement patterns

The spatial and temporal movement patterns were not related with individual physical condition, showing all fledglings have a similar pattern in movement behaviour during the PDFP. This suggests that post-fledging movement behaviour may be a general ability acquired during this phase as the result of the combination of several traits, as follows. Our fledgling Eagle Owls showed unoriented movement ($CRW_{Diff} \le 0$; Nams 2006b). This is not surprising for the following three reasons. (A) They are fed and protected by their parents. Consequently, they do not need to direct their movements towards specific shelters or foraging areas. (B) After leaving the nest, young are embedded in new surroundings that they have to learn, i.e. they move randomly during territory explorations. (C) Their flight abilities and perceptual range are not yet completely developed, so unoriented walks represent the best strategy to cover larger areas at small scales (Garcia *et al.* 2005). Moreover, during early PFDP, movement paths were more tortuous and became progressively straighter as independence approached. Since the paths were unoriented, we suggest that this increase in straightness may indicate an increase in their perceptual range (i.e. the maximum distances from which an animal can perceive the presence of a particular landscape element as such; Zollner 2000). That is, when animals are moving with an unoriented search strategy, the behavioural mechanisms governing movement are working at small spatial scales (Nams 2006b), and those small scales are determined by the perceptual range. Increasing the perceptual range would increase the natural step length of their movement path, resulting in straighter paths.

From early PFDP individuals are developing, day to day, their perceptual range (i.e. the ability to perceive habitat at a distance). Perceptual range has important ecological implications since it may determine the appropriate search strategy (Zollner & Lima 1999) and, consequently, influences both fledgling survival (i.e. their availability as future floaters of a population) and distribution patterns and dynamics of (meta)populations (Pulliam *et al.* 1992, Lima & Zollner 1996, Zollner 2000).

Finally, tortuous paths may have resulted from both incomplete growth and cognitive abilities (as perception and imperfect knowledge of the parental territory). With age, individuals increase in both flight and cognitive abilities, and perceptual range increases as fledglings become more familiar with their surroundings. This combination of traits enables them to search more rapidly and over larger areas, resulting in straighter movement paths. In fact, when their wings are fully developed, their displacements are over brushes, rocks and trees and not by walking and jumping among them. The existence of a trade-off between the relative path sinuosity and the size of the area searched has been also demonstrated by Doerr & Doerr (2004), which found that individuals who explored larger areas did so with less tortuousity.

Because the PFDP represents an intensive phase of experience and learning, and its influence may well shape fledglings' behavioural strategies during their successive, crucial phase, the natal dispersal, more information on the PFDP is needed to better understand avian breeding cycles and its consequences on individual survival.

ACKNOWLEDGEMENTS

For their help with logistics we are grateful to P. Bartolommei, L. Campioni, R. Lourenço and G. Penteriani. The first draft was improved by the criticisms of A. Banks. Funding for this study was provided by a research project No. CGL2004-02780/BOS of Spanish Ministry of Education and Science and LICOR43 (Diego Zamora S.A.; www.buho-ebd.com). During this work M.M. Delgado was supported by a doctoral grant of the Junta de Andalucía (Consejería de Educación y Ciencia). We manipulated and marked owls under the Junta de Andalucía – Consejería de Medio Ambiente permits No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02.

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SAMENVATTING

Er is veel onderzoek verricht naar de wijze waarop dieren zich in de ruimte verplaatsen. Er is echter weinig bekend over de bewegingen direct na het uitvliegen van jonge vogels, een periode waarin ze nog afhankelijk van de ouders zijn. Deze periode is belangrijk als voorbereiding op de zelfstandigheid van de jongen. Naarmate de vogels handiger worden en hun omgeving beter leren kennen, gaan zij zich anders gedragen. Het onderhavige onderzoek in de Sierra Norte bij Sevilla, Spanje, gaat in op de verplaatsingen van 41 pas uitgevlogen Oehoes *Bubo bubo* die met een radiozendertje waren uitgerust. Direct na het uitvliegen bleven de vogels in de buurt van het nest, waarbij ze zich vooral huppend en klauterend verplaatsten. Binnen een paar weken leerden ze echter vliegen en begonnen ze steeds sneller en verder weg te bewegen. Na ruim drie maanden werden de jongen zelfstandig en verlieten het ouderlijk territorium definitief. Naarmate de vogels zich sneller bewogen, verplaatsten ze zich meer in een rechte lijn. De manier waarop de jonge uilen zich verplaatsten, was niet afhankelijk van hun lichaamsgrootte of van conditie. De eerste 20 dagen na het uitvliegen bleven de jonge uilen dicht bij elkaar, maar snel daarna namen de onderlinge afstanden toe tot enkele honderden meters. (DH)

Corresponding editor: Dik Heg
Received 14 June 2008; accepted 12 December 2008

ARDEA

TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE (NOU)

Ardea is the scientific journal of the Netherlands Ornithologists' Union (NOU), published bi-annually in spring and autumn. Next to the regular issues, special issues are produced frequently. The NOU was founded in 1901 as a non-profit ornithological society, composed of persons interested in field ornithology, ecology and biology of birds. All members of the NOU receive *Ardea* and *Limosa* and are invited to attend scientific meetings held two or three times per year.

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Research grants – The NOU supports ornithological research and scientific publications through its Huib Kluijver Fund and the 'Stichting Vogeltrekstation'. Applications for grants can be addressed to the NOU Secretary. Donations to either fund are welcomed by the NOU treasurer.

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ARDEA

Editorial address – Jouke Prop, Allersmaweg 56, 9891 TD Ezinge, The Netherlands (ardea.nou@planet.nl)

Graphics – Dick Visser, Haren

Artwork – Jos Zwarts, Bunnik

Internet – www.ARDEAjournal.nl

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Layout by Dick Visser, Haren, The Netherlands
Printed by Van Denderen, Groningen, The Netherlands, April 2009