Disentangling the effects of genetic and environmental factors on movement behaviour

(Article begins on next page)

12 February 2025

UNIVERSITÀ DEGLI STUDI DI TORINO

1

2

3

4

5

6

7

8

9

10

11

12

Disentangling the effects of genetic and environmental factors on movement behaviour

Giulia Bombieri[1§], Antonio Fasciolo[2,3§], Vincenzo Penteriani[1,2], Juan Carlos Illera[1], Dan Chamberlain[4] and María del Mar Delgado[1]

[1]Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain

[2]Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., c/Américo Vespucio s/n, 41092 Seville, Spain

[3]Department of Ecological and Biological Sciences, Tuscia University, Loc. Riello 01100, Viterbo, Italy.

[4]Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123, Torino, Italy.

*Corresponding author:

GB (giulipan91@gmail.com)

§These authors contributed equally to this work

1 **ABSTRACT**

2 Individual variability in animal movement behaviour is well documented for many species.
3 However, it remains unclear whether this variability reflects genetic variation, environmental
4 variation, or a combination of the two. Here, we conduct a cross-fostering experiment with the
5 aim of investigating the role of these two components in movement patterns during the post-
6 fledging dependence period and early natal dispersal of 21 eagle owls *Bubo bubo*. Our
7 experiment showed that cross-fostering did not influence any of the movement parameters
8 considered. Movement parameters were, however, affected by the age and sex of the owlets. We
9 therefore suggest that individual variability and family resemblance in movement behaviour
10 during the post-fledging dependence period and early natal dispersal might not be due to the
11 common genetic origin of siblings, but rather that it originates from factors related to the rearing
12 environment.

13 *Key-words: Bubo bubo,* cross-fostering, eagle owl, natal dispersal, post-fledging dependence
14 period

INTRODUCTION

Individual variability is well documented for many behaviours and life-history traits (Vindenes & Langangen, 2015), yet the causes and mechanisms behind it are still poorly understood. Differences **between and within** individuals, as well as similarities among relatives, may be due to genetic variation (G), environmental variation (E) or a combination of these two effects (G x E) (**Boake et al., 2002**; Clark & Ehlinger, 1987; Kruuk & Hadfield, 2007). The role of these factors has been investigated for several traits (reviewed in: **Dingemanse, Kazem, Réale, & Wright, 2010;** van Oers *et al.*, 2005). Some heritability studies have focused on individual variation in movement behaviour (Hansson, Bensch, & Hasselquist, 2003; Massot & Clobert, 2000; Massot, Huey, Tsuji, & Van Berkum, 2003; Matthysen, Van De Casteele, & Adriaensen, 2005; Noordwijk, 1984; Pasinelli, Schiegg, & Walters, 2004; Pasinelli & Walters, 2002). These studies showed that, even if many movement behaviours have a significant heritable component, it is the combination of genetic and environmental components (G x E) which mainly determines individual behavioural variation. Understanding the factors and mechanisms driving movement behaviour is indeed a key question because movement behaviour affects individuals' survival probability and reproductive success and, at a broader level, population dynamics (Morales et al., 2010).

In birds, the post-fledging dependence period (hereafter PFDP) is defined as the period between fledging and independence from the parents (Delgado, Penteriani, & Nams, 2009), whereas natal dispersal (hereafter dispersal) represents the movement of an individual from their birthplace to their first breeding location and involves three successive phases: departure, transfer and settlement (Bowler & Benton, 2005; Ronce, 2007). Together, the PFDP and dispersal represent an intensive period of experience and learning (Delgado, Penteriani, Nams, & Campioni, 2009) during which a juvenile attains the necessary physical condition and abilities to survive and eventually find a suitable breeding area. During these phases, different interacting factors, such as the internal state of the individual (e.g. sex, age, body condition) and environmental features (e.g. landscape characteristics, interaction with conspecifics), influence individual movement behaviours (Bowler & Benton, 2005; Delgado, Penteriani, Revilla, & Nams, 2010; Muriel, Ferrer, Balbontín, Cabrera, & Calabuig, 2015; Van Overveld, Adriaensen, & Matthysen, 2011). In addition, a recent study found that movements of eagle owl (*Bubo bubo*)

siblings during natal dispersal were not independent of each other, suggesting a potential 'family effect' on dispersal behaviour (Penteriani & Delgado, 2011). However, it remains difficult to unravel the role of genetic and common environment effects in non-experimental studies (Matthysen et al., 2005).

Few studies have performed brood manipulation, such as cross-fostering, to experimentally separate genetic from common environment effects in movement behaviour (Boonstra & Hochachka, 1997; Massot et al., 2003; Roche, Brown, & Brown, 2011). The technique of cross-fostering, which consists of pairing nests and switching an equal number of chicks of the same age and sex between the two families, represents a widely used tool to experimentally separate the effect of the two potential sources of similarity between relatives, i.e. genetics and a shared environment (Matthysen et al., 2005). The main assumption is that if cross-fostered offspring behave more similarly to their biological parents and/or full siblings, this behaviour probably has an important genetic component. On the contrary, if cross-fostered offspring do not behave like their biological siblings, and their behaviour is more similar to their foster siblings, environmental factors might be the dominant component determining individual variation (Clayton, 1990; Soler, Moreno, & Potti, 2003).

Here, we performed a cross-fostering experiment on eagle owls to disentangle the effect of a common rearing environment (E) from the genetic component (G) on individual movement behaviour during the PFDP and early dispersal. We hypothesized that, if environmental factors primarily shape movement behaviour and determine similar behaviour within the same brood during the PFDP and dispersal periods, we should not observe significant differences in movement between cross-fostered and control individuals of the same nest (environmental hypothesis). Alternatively, if owlets reared in the same nest show different movement patterns, with individuals behaving more similarly to their biological siblings reared in a different nest, we could then hypothesize that a genetic component is the main force driving movement behaviours (genetic hypothesis).

METHODS

Field methods

This study was conducted over two years (2015 and 2016), from March to December, in the Sierra Norte of Seville (Sierra Morena, SW Spain 37°30'N, 06°03' W). During these periods, the field work included the following temporal sequence: (a) nest checking, (b) nestling age and sex determination, (c) set up and running of the cross-fostering experiment, i.e. exchanging chicks between nests, and (d) radiotracking owls during PFDP and dispersal. We determined the age of the owlets based on plumage characters (Penteriani, Delgado, Maggio, Aradis, & Sergio, 2005) and their sex using DNA extracted from blood (Griffiths, R., Double, M.C., Orr, K. & Dawson, 1998)

The cross-fostering experiment

For the experiment, we performed partial cross-fostering, which involves pairing nests and swapping one or two chicks (depending on brood size) between the two families, while leaving at least one chick in the original nest as a control (Hadfield, Nutall, Osorio, & Owens, 2007; Mateo & Holmes, 2004; Morrison, Ardia, & Clotfelter, 2009).

To avoid initial variations in **brood structure** which may affect the outcome of the experiment, hatch date, brood size and sex ratio were maintained constant in each nest during the experiment. We switched an equal number of males and females to obtain a homogenous sample (Matthysen et al., 2005; Nicolaus et al., 2012; Winney, Nakagawa, Hsu, Burke, & Schroeder, 2015). Following these criteria, we performed the cross-fostering experiment between 7 nests (one nest was used in both years) for a total of 4 experimental blocks, each block consisting of a pair of nests ($n_{2015} = 3$; $n_{2016} = 1$). **A total number of 24 owlets were included in the study. With such a design, we obtained two treatment groups: non-fostered owls (namely treatment group 0; n = 14 owlets; 9 males and 5 females; $n_{2015} = 10$; $n_{2016} = 4$), which comprised those individuals that remained in their original nest as controls, and fostered owls (namely treatment group 1; n = 10 owlets; 4 males and 6 females; $n_{2015} = 8$; $n_{2016} = 2$), composed of those individuals that were switched between paired nests of each experimental block.** Previous experience of natural and artificial adoptions performed in the studied population have shown that the survival of juveniles is not affected by brood switching (Penteriani & Delgado, 2008).

Radiotracking procedure

1   We radio tagged the birds and performed the cross-fostering experiment when owlets were 30-35

2   days old. Individuals were fitted with a Teflon ribbon backpack harness that carried a 30 g radio

3   transmitter (henceforth 'tag'; see Delgado & Penteriani, 2008). The weight of the tag was < 3%

4   of the weight of the smallest adult male (1550 g, mean ± SD = 1667 ± 104.8) and 3.5% of the

5   smallest fledgling weight (850 g, mean ± SD = 1267 ± 226.4 g). Because the chicks were still

6   growing when they were radio tagged, backpacks were adjusted so that the Teflon ribbon could

7   expand and allow for the increase in body size. We manipulated and marked owls under: (1) the

8   Junta de Andalucía – Consejería de Medio Ambiente permits No. SCFFSAFR⁄GGG RS 260⁄02

9   and SCFFS AFR ⁄CMM RS 1904 ⁄ 02; and (2) the approval of the Comité de Ética de

10   Experimentación Animal of the Estación Biológica de Doñana-CSIC (CEEA-EBD_12_41).

11   Locations of radio tagged owls were determined using a 3-element hand held Yagi

12   antenna connected to a BIOTRACK portable receiver via bi-angulation. The **accuracy of**

13   **localizations was 83.5 ± 49.5 m, estimated when, after a radiolocation, we needed to locate**

14   **where exactly one individual was (e.g. if it died)**. During the PFDP, owlets were followed by

15   radio tracking during night sessions, which took place with an interval of 10 days. During these

16   sessions, all the owlets were radio-located throughout the entire night, from one hour before

17   sunset to one hour after sunrise. The time interval between successive individual locations was

18   ca. 1 hour and 30 minutes. During dispersal, owls were located on a weekly basis at their

19   daytime roosting sites (mean time between consecutive locations ± SE = 6.9 ± 0.1 days). During

20   the experiment, six owls were predated ($n_{2015} = 5$; $n_{2016} = 1$) and we lost the signal of three other

21   individuals. Thus, our final sample size was 21 owls for the PFDP sample and 15 owls for the

22   dispersal sample.

23

24

25   *Determination of PFDP and dispersal phases*

26   PFDP started when the juveniles left the nest (mean age = 40-45 days), and lasted until the

27   juveniles started to disperse (Delgado, Penteriani, & Nams, 2009). To identify the start of

28   dispersal, we plotted both the beeline distance from the natal nest for each location and the

29   average of the beeline distance between the whole set of locations and the nest, with the latter

30   value representing the global mean distance covered by each individual during dispersal

1 (Delgado & Penteriani, 2008). Dispersal started when the distance between successive moves

2 became larger than the average distance travelled by each bird. This happens when the distance

3 of each location from the nest starts to increase rather than fluctuate around a low value (Delgado

4 & Penteriani, 2008).

5

6 *Movement parameters*

7 To compare the two treatment groups, we quantitatively described the movement behaviour of

8 individuals during PFDP and dispersal. For each juvenile ($n_{PFDP} = 21$; $n_{dispersal} = 15$) and for the

9 two phases, we estimated seven movement parameters. (1) Step distance: distance between

10 consecutive locations. (2) Total distance: total distance covered by the owl. (3) Net distance: the

11 distance between the first and the last location collected. (4) Distance between the nest and each

12 of the location points. (5) Distance between different owls, via individual locations recorded at

13 the same time. (6) Movement speed: obtained by dividing the step distance by the time interval

14 between consecutive locations. (7) Movement direction (i.e. turning angles) between successive

15 locations. In addition, we estimated the size of the area explored by each owl during the whole

16 PFDP using the 100% minimum convex polygon in QGIS 2.14.3 Geographic Information

17 System (QGIS Development Team, 2016).

18

19 *Statistical analyses*

20 **For the statistical analyses, we considered all parameters except the step distance, as this**

21 **variable was highly correlated with speed ($r = XX$, $P = YY$).** Correlations between the other

22 variables were low ($r < ZZ$ in each case). For each of the six movement parameters considered,

23 we built a set of competing models which included all possible combinations of explanatory

24 variables, starting from the simplest null model (intercept-only model) to a full model that

25 included all the explanatory variables (Tables S2 and S4). To check model assumptions

26 (normality, independence, the presence of outliers), we first conducted a graphical data

27 exploration. Response variables following a normal distribution were modelled using linear

28 mixed models. When residuals did not follow a normal distribution, data were log transformed

1 and then checked again for the assumptions. When log transformation was not sufficient, we

2 applied a generalized linear mixed model with gamma distributions.

3   In each set of competing models, we included treatment group, age (except for net and

4 total distance in the dispersal phase) and sex of individuals, as well as their interactions, as fixed

5 factors. Random effects were held constant. For modelling movement parameters during the

6 PFDP, we included 5 random hierarchical factors, organized as follows: (1) year, (2)

7 experimental block, (3) nest, (4) night of radio tracking, and (5) individual. The night of radio

8 tracking was not included in the models built for net and total distance, as we only had one

9 observation per night for these variables. For dispersal, we included the same random factors,

10 except the night of radio tracking, as we had weekly observations for this period. In the models

11 built for net and total distance of dispersal, we also excluded the individual as a random factor,

12 given that for these two parameters we only had one observation per owl.

13   We selected the best competing model based on the Akaike's Information Criterion

14 corrected for small sample sizes (AICc; Burnham & Anderson, 2002), and calculated two

15 additional statistics for each model: ΔAICc and Weighted AICc, indicating the probability that

16 the model selected was the best among the competing candidates (Gelman & Hill, 2006). We

17 considered models with ΔAICc values lower than 2 as competitive. For each set of models, we

18 then employed model averaging on the 95% confidence set to derive parameter coefficients and

19 the relative importance values (RIV) of each explanatory variable using the full-model averaging

20 approach (Burnham & Anderson, 2002). **When high model selection uncertainty exists, model**

21 **averaging allows formal inference based on the entire set of models (or, in our case, the**

22 **95% confidence set) (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, &**

23 **Jamieson, 2011; Symonds & Moussalli, 2011). Parameter estimates produced by model**

24 **averaging derive from weighted averages of these values across all models in the set**

25 **considered (Symonds & Moussalli, 2011). In particular, the relative importance value**

26 **(RIV) of each explanatory variable is calculated by summing Akaike weights across all**

27 **models which contain the variable (Burnham & Anderson, 2002)**.

28   Significance was assessed using P-values derived from the model averaged parameter

29 estimates and was set at $P \leq 0.05$.

To assess the variability between/within nests and between/within individuals, we calculated the intraclass correlation coefficient (ICC) (Stoffel, Nakagawa, & Schielzeth, 2017; Zuur et al., 2009) for two of the random factors included in our models: "nest" and "owl". This coefficient represents the fraction of the total variance attributable to variation among groups of the same class (Stoffel et al., 2017) and, in our case, describes the correlation between owls reared in the same nest (random factor "nest") and the correlation between observations of the same individual (random factor "owl").

For all selected models, we calculated the conditional deviance following Nakagawa & Schielzeth, (2013). All analyses were performed using R 3.2.5 statistical software (R Development Core 2016). GLMMs were run using the "lme4" (Bates & Sarkar, 2007), and "nlme" (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) packages. Multi-model inference and model averaging were run using the "MuMIn" (Bartón, 2013) package.

RESULTS

GENERAL PATTERNS OF OWL MOVEMENTS

Post-fledging dependence period

During a total of 21 nights of radio tracking ($n_{2015} = 12$; $n_{2016} = 9$) we registered 1213 locations ($n_{2015} = 887$ with $n_0 = 488$ and $n_1 = 399$; $n_{2016} = 326$ with $n_0 = 254$ and $n_1 = 72$). A summary of post-fledging movement parameters is given in Table S1.

During this phase, the average of all parameters considered (except total distance) increased with time, with females generally showing higher values than males (Figure 1a).

Dispersal

During a total of 62 days of radio tracking ($n_{2015} = 38$; $n_{2016} = 24$), we registered 258 locations ($n_{2015} = 183$ with $n_0 = 93$ and $n_1 = 90$; $n_{2016} = 75$ with $n_0 = 54$ and $n_1 = 21$).

In 2015, dispersal started when owlets were 172 ± 5.9 days old (mean ± SE) (n = 11; range = 148-220 days), and in 2016 when owlets were 158 ± 19.2 days old (n = 4; range = 123-192 days). For both years combined, dispersal started at the age of 168 ± 6.5 days (n = 15; range = 123-220 days). A summary of dispersal movement parameters is given in Table S3.

As for the PFDP, female average values were generally higher than male values. Average distances from the nest and between-owl distances increased with time, while average speed decreased (Figure 2a).

To give an idea of how the owls were moving during the two phases considered, we plotted the path followed by one selected owl at different ages (Figures 1b and 2b).

THE CROSS-FOSTERING EXPERIMENT

Post-fledging dependence period

For all movement parameters, selected models always included age. Treatment group appeared in selected models of all parameters except speed, while sex appeared in selected models of all parameters (Table S2). However, P and RIV values only supported the effect of age (Table 1), which was significant (P ≤ 0.05) and had a relatively high importance (RIV > 0.90) in 5 parameters (net distance, total distance, speed, distance between each recorded location and the nest, distance between owls). The effect of treatment group was never significant, nor did it have an especially high RIV (always < 0.80; Table 1). Values of ICC (Table 2) for the random factor "owl" (i.e. individual) were always 0.00, which means there was no correlation between observations of the same individual. ICCs for the random factor "nest" ranged between 0.35 and 0.99, which means there was a correlation between individuals raised in the same nest, indicating that within-nest variation was greater than between nest variation.

Dispersal

Out of 6 parameters considered, for two of them (net and total distance) the best model was the null model (intercept-only model; Table S4). For all remaining parameters, the selected models always included age and sex, while the treatment group appeared in 2 models. P and RIV values suggested that age had the main effect, showing P ≤ 0.05 and RIV > 0.90 in 3 parameters (speed,

distance between each recorded location and the nest, distance between owls; Table 3). **Sex had a significant effect** and had a high RIV value in 2 parameters (distance between each location and the nest, distance between owls). **The effect of treatment group was never significant**. In the majority of cases, the RIV was low (< 0.50; Table 3), with the exception of distance between owls, where RIV = 0.86. **Values of ICC (Table 2) for the random factor "owl" were 0.00 for the speed and 0.36 for the distance between owls and the nest. ICCs for "nest" were higher (always ICC>0.40; except for the speed). This suggests that there was a relatively high correlation between owls raised in the same nest.**

DISCUSSION

Our results showed that the treatment group of the cross-fostering experiment did not affect movement parameters during the two successive phases of eagle owl development. **Moreover, we found variability in movement characteristics of owls reared in different nests. This outcome reveals a scenario where all owls reared in the same nest, regardless of whether they were cross-fostered or not, behaved similarly between each other and differently from the owls reared in the other nests.** Thus, our experiment does not support the hypothesis of a genetic basis for movement behaviour during PFDP and early dispersal. Our findings are in line with previous studies on other species (Greenwood, Harvey, & Perrins, 1979; Massot & Clobert, 2000; Matthysen et al., 2005; Pasinelli & Walters, 2002; Waser & Thomas Jones, 1989), which found no evidence for the heritability of movement behaviour during the dispersal phase. These authors suggested that individual variability and family resemblance in movement behaviour may instead be explained by environmental and social factors, such as nest location, the landscape surrounding the nest site, family bonds and other factors acting on the whole brood during rearing. In contrast, few other studies on birds (Hansson et al., 2003; Pasinelli et al., 2004) have found evidence of a genetic basis for movement behaviour. However, although these studies support a heritable component, they acknowledge that this behaviour may also be partly modulated by environmental and social factors.

The moderate sample size utilized in the current study might have decreased the statistical power of our findings and, thus, the probability of detecting a small genetic effect. However, our results clearly support the hypothesis that environmental and social factors have a stronger effect than genetics on the development of individual behaviour, and hence in determining similarity in movement behaviour between siblings. In particular, during the PFDP, offspring are reared together in the same environment. This implies that young birds move in the same area during this crucial stage of their life and, thus, they are exposed to the same external conditions. Moreover, during the PFDP, young eagle owls spend most of their time together, often exploring nest surroundings, and remain in constant contact with their parents (Delgado, Penteriani, & Nams, 2009). All of the common factors that owlets share during rearing may lead them to adopt similar behavioural movement responses during the PFDP.

Environmental characteristics (e.g. landscape structure and composition) of the habitat explored by an individual during the dispersal phase have already been shown to play an important role in shaping movement behaviour in this species (Delgado et al., 2010; Penteriani & Delgado, 2011), as owls born in the same place displayed similar movement patterns and started the dispersal process at a similar age (Penteriani & Delgado, 2011). Furthermore, different individuals moving through the same area had similar movement patterns (Delgado et al., 2010). These authors suggested that individuals born in the same nest and/or moving through the same area may face similar constraints, and this may lead to similar individual movement decisions. **Another study on natural brood-switching in fledglings of eagle owls (Penteriani & Delgado, 2008), which somewhat anticipated our results, showed that switched owls not only were adopted by foster parents, but moved similarly to the resident fledglings.**

Furthermore, our results also showed that age influences the movement behaviour of individuals during both the PFDP and dispersal phases. During the PFDP, young owls are still developing their flight and cognitive abilities and, thus, the way they move around the natal area changes over time (Delgado, Penteriani, & Nams, 2009). These progressive changes have already been recorded in this and other avian species (O'Toole L. T., Kennedy P. L., Knight R. L., 1999; Wood, Collopy, & Sekerak, 1998). During dispersal, an age effect may be explained by the fact that this phase represents a multistep process during which individuals may show different behaviours depending on their physical condition, as well as on their abiotic and social environments (Bowler & Benton, 2005; Delgado & Penteriani, 2008; Delgado et al., 2010). The

sex of individuals also showed some effect on some movement parameters during early dispersal. Although sex-biased dispersal has not been detected in previous studies on this eagle owl population (Delgado et al., 2010), sex differences in dispersal behaviour are relatively well documented for several bird species (Paul J. Greenwood, 1980; Massot & Clobert, 2000; Newton, 2002). Nonetheless, it is worth mentioning here that we only analysed movement behaviour during the early phases of dispersal and that different patterns may emerge when considering the whole dispersal phase.

Overall, our experimental approach, which aimed to disentangle the contribution of environmental and genetic effects on the movement behaviour of a long-lived species, did not support the hypothesis of a genetic predetermination of individual movement behaviour during the early stages of its life. On the contrary, the experiment supported an effect of the local environment in influencing movement behaviour. However, we acknowledge that our approach represents a first step towards a better understanding of a very complex process in behavioural ecology. Further studies including other populations, larger sample sizes and detailed dispersal movements spanning the entire year are undoubtedly needed to confirm the potentially limited effect of the genetic component on animal movement behaviour.

REFERENCES

Bartón, K. (2013). Model selection and model averaging based on information criteria (AICc and alike). *The Comprehensive R Archive Network*, *1*, 13.

Bates, D., & Sarkar, D. (2007). lme4: Linear mixed-effects models using S4 classes.

Boake, C. R. B. C. R. B., Arnold, S. J. S. J., Breden, F., Meffert, L. M. L. M., Ritchie, M. G. M. G., Taylor, B. J. B. J., … Moore, a. J. A. J. (2002). Genetic tools for studying adaptation and the evolution of behavior. *The American Naturalist*, *160 Suppl*(december), S143–S159.

https://doi.org/10.1086/342902

Boonstra, R., & Hochachka, M. (1997). Maternal effects and additive genetic inheritance in the collared lemming Dicrostonyx groenlandicus. *Evolutionary Ecology*, (2), 169–182. https://doi.org/10.1023/A:1018447815825

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society*, *80*(2), 205–225. https://doi.org/10.1017/s1464793104006645

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). Ecological Modelling* (Vol. 172). https://doi.org/10.1016/j.ecolmodel.2003.11.004

Clark, A. B., & Ehlinger, T. J. (1987). Pattern and adaptation in individual behavioral differences. *Perspectives in Ethology*, *7*, 1–47. https://doi.org/10.1007/978-1-4613-1815-6

Clayton, N. S. (1990). The effects of cross-fostering on assortative mating between zebra finch subspecies. *Animal Behaviour*, *40*(6), 1102–1110. https://doi.org/10.1016/S0003-3472(05)80176-9

Delgado, M. M., & Penteriani, V. (2008). Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. *The American Naturalist*, *172*(4), 475–485. https://doi.org/10.1086/590964

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*(c), 7–15. https://doi.org/Doi 10.5253/078.097.0102

Delgado, M. M., Penteriani, V., Nams, V. O., & Campioni, L. (2009). Changes of movement patterns from early dispersal to settlement. *Behavioral Ecology and Sociobiology*, *64*(1), 35–43. https://doi.org/10.1007/s00265-009-0815-5

Delgado, M. M., Penteriani, V., Revilla, E., & Nams, V. O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology*, *79*(3), 620–632. https://doi.org/10.1111/j.1365-2656.2009.01655.x

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms:

animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Gelman, A., & Hill, J. (2006). Data Analysis Using Regression and Multilevel/Hierarchical Models. *Cambridge University Press*, *Analytical*(July), 625. Retrieved from http://www.loc.gov/catdir/enhancements/fy0668/2006040566-d.html

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*(4), 1140–1162. https://doi.org/10.1016/S0003-3472(80)80103-5

Greenwood, P. J., Harvey, P. H., & Perrins, C. M. (1979). The Role of Dispersal in the Great Tit (Parus major): The Causes , Consequences and Heritability of Natal Dispersal. *Journal of Animal Ecology*, *48*(1), 123–142.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R. J. G. (1998). A DNA test to sex most birds. *Molecular Ecology*, *7*(8), 1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, *24*(4), 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hadfield, J. D., Nutall, A., Osorio, D., & Owens, I. P. F. (2007). Testing the phenotypic gambit: Phenotypic, genetic and environmental correlations of colour. *Journal of Evolutionary Biology*, *20*(2), 549–557. https://doi.org/10.1111/j.1420-9101.2006.01262.x

Hansson, B., Bensch, S., & Hasselquist, D. (2003). Heritability of dispersal in the great reed warbler. *Ecology Letters*, *6*(4), 290–294. https://doi.org/10.1046/j.1461-0248.2003.00436.x

Ingleby, F. C., Hunt, J., & Hosken, D. J. (2010). The role of genotype-by-environment interactions in sexual selection. *Journal of Evolutionary Biology*, *23*(10), 2031–2045. https://doi.org/10.1111/j.1420-9101.2010.02080.x

Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology*, *20*(5), 1890–1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Massot, M., & Clobert, J. (2000). Processes at the origin of similarities in dispersal behaviour among siblings. *Journal of Evolutionary Biology*, *13*(4), 707–719.

1 https://doi.org/10.1046/j.1420-9101.2000.00202.x

2 Massot, M., Huey, R. B., Tsuji, J., & Van Berkum, F. H. (2003). Genetic, prenatal, and postnatal

3 correlates of dispersal in hatchling fence lizards (Sceloporus occidentalis). *Behavioral*

4 *Ecology*, *14*(5), 650–655. https://doi.org/10.1093/beheco/arg056

5 Mateo, J. M., & Holmes, W. G. (2004). Cross-fostering as a means to study kin recognition.

6 *Animal Behaviour*, *68*(6), 1451–1459. https://doi.org/10.1016/j.anbehav.2004.01.017

7 Matthysen, E., Van De Casteele, T., & Adriaensen, F. (2005). Do sibling tits (Parus major, P.

8 caeruleus) disperse over similar distances and in similar directions? *Oecologia*, *143*(2),

9 301–307. https://doi.org/10.1007/s00442-004-1760-7

10 Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. a, …

11 Haydon, D. T. (2010). Building the bridge between animal movement and population

12 dynamics. *Philosophical Transactions of the Royal Society B Biological Sciences*,

13 *365*(1550), 2289–301. https://doi.org/10.1098/rstb.2010.0082

14 Morrison, E. S., Ardia, D. R., & Clotfelter, E. D. (2009). Cross-fostering reveals sources of

15 variation in innate immunity and hematocrit in nestling tree swallows Tachycineta bicolor.

16 *Journal of Avian Biology*, *40*(6), 573–578. https://doi.org/10.1111/j.1600-

17 048X.2009.04910.x

18 Muriel, R., Ferrer, M., Balbontín, J., Cabrera, L., & Calabuig, C. P. (2015). Disentangling the

19 effect of parental care, food supply, and offspring decisions on the duration of the

20 postfledging period. *Behavioral Ecology*, *26*(6), 1587–1596.

21 https://doi.org/10.1093/beheco/arv114

22 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from

23 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142.

24 https://doi.org/10.1111/j.2041-210x.2012.00261.x

25 Newton, I. (2002). Ecology and conservation of owls. *Ecology and Conservation of Owls*.

26 https://doi.org/10.2307/3849247

27 Nicolaus, M., Michler, S. P. M., Ubels, R., van der Velde, M., Bouwman, K. M., Both, C., &

28 Tinbergen, J. M. (2012). Local sex ratio affects the cost of reproduction. *Journal of Animal*

29 *Ecology*, *81*(3), 564–572. https://doi.org/10.1111/j.1365-2656.2011.01933.x

Noordwijk, A. J. Van. (1984). Problems in the Analysis of Dispersal and a Critique on its `Heritability' in the Great Tit. *Journal of Animal Ecology*, *53*(2), 533–544. Retrieved from http://www.jstor.org/stable/4532

O'Toole L. T., Kennedy P. L., Knight R. L., M. L. C. (1999). Postfledging of Golden. *Wilson Bull.*, *111*(4), 472–477.

Pasinelli, G., Schiegg, K., & Walters, J. R. (2004). Genetic and environmental influences on natal dispersal distance in a resident bird species. *The American Naturalist*, *164*(5), 660–669. https://doi.org/10.1086/424765

Pasinelli, G., & Walters, J. R. (2002). Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. *Ecology*, *83*(8), 2229–2239. https://doi.org/10.1890/0012-9658(2002)083[2229:SAEFAN]2.0.CO;2

Penteriani, V., & Delgado, M. M. (2008). Brood-switching in Eagle Owl Bubo bubo fledglings. *Ibis*, *150*(4), 816–819. https://doi.org/10.1111/j.1474-919X.2008.00831.x

Penteriani, V., & Delgado, M. M. (2011). Birthplace-dependent dispersal: Are directions of natal dispersal determined a priori? *Ecography*, *34*(5), 729–737. https://doi.org/10.1111/j.1600-0587.2010.06773.x

Penteriani, V., Delgado, M. M., Maggio, C., Aradis, A., & Sergio, F. (2005). Development of chicks and predispersal behaviour of young in the Eagle Owl Bubo bubo. *Ibis*, *147*(1), 155–168. https://doi.org/10.1111/j.1474-919x.2004.00381

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2017). {nlme}: Linear and Nonlinear Mixed Effects Models. Retrieved from https://cran.r-project.org/package=nlme

QGIS Development Team. (2016). QGIS Geographic Information System. Open Source Geospatial Foundation. Retrieved from http://qgis.osgeo.org

Roche, E. A., Brown, C. R., & Brown, M. B. (2011). Heritable choice of colony size in cliff swallows: does experience trump genetics in older birds? *Animal Behaviour*, *82*(6), 1275–1285. https://doi.org/10.1016/j.anbehav.2011.09.005

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, *38*(2007), 231–253.

https://doi.org/10.1146/annurev.ecolsys.38.091206.095611

Soler, J. J., Moreno, J., & Potti, J. (2003). Environmental, genetic and maternal components of immunocompetence of nestling pied flycatchers from a cross-fostering study. *Evolutionary Ecology Research*, *5*(2), 259–272.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.12797

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

van Oers, K., de Jong, G., van Noordwijk, A., Kempenaers, & Drent, P. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, *142*(9), 1185–1206. https://doi.org/10.1163/156853905774539364

Van Overveld, T., Adriaensen, F., & Matthysen, E. (2011). Postfledging family space use in great tits in relation to environmental and parental characteristics. *Behavioral Ecology*, *22*(4), 899–907. https://doi.org/10.1093/beheco/arr063

Vindenes, Y., & Langangen, O. (2015). Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecology Letters*, *18*(5), 417–432. https://doi.org/10.1111/ele.12421

Waser, P. M., & Thomas Jones, W. (1989). Heritability of dispersal in banner-tailed kangaroo rats, Dipodomys spectabilis. *Animal Behaviour*, *37*, *Part 6*, 987–991. https://doi.org/https://doi.org/10.1016/0003-3472(89)90142-5

Winney, I., Nakagawa, S., Hsu, Y. H., Burke, T., & Schroeder, J. (2015). Troubleshooting the potential pitfalls of cross-fostering. *Methods in Ecology and Evolution*, *6*(5), 584–592. https://doi.org/10.1111/2041-210X.12341

Wood, P. B., Collopy, M. W., & Sekerak, C. M. (1998). Postfledging Nest Dependence Period for Bald Eagles in Florida. *The Journal of Wildlife Management*, *62*(1), 333–339. https://doi.org/10.2307/3802296

1 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., Smith, G. M., & Park, W. (2009). Mixed

2   effects modelling and extensions in ecology with R.

3

4

5

6 **Table 1.** Model-averaged coefficients and RIV values for the post-fledging dependence period.

DEPENDENT VARIABLE	EXPLANATORY VARIABLE	MODEL-AVERAGED COEFFICIENTS AND RELATIVE IMPORTANCE VALUES			
		β	SE	P	RIV
NET DISTANCE	Intercept	4.86	0.45	<2e-16	
	Age	0.01	0.00	0.0119	1.00
	SexM[2]	0.25	0.42	0.5549	0.55
	Treatment1[1]	-0.20	0.41	0.6209	0.47
	Age:SexM	-0.00	0.00	0.6389	0.27
	Age:Treatment1	0.00	0.00	0.6359	0.25
	Treatment1:SexM	0.02	0.11	0.8637	0.08
TOTAL DISTANCE	Intercept	6.56	3.32	< 2e-16	
	Age	6.31	1.99	0.00162	1.00
	SexM[2]	1.77	1.96	0.36912	0.78
	Treatment1[1]	-4.79	2.08	0.81896	0.45
	Age:SexM	-9.30	1.38	0.94661	0.19
	Age:Treatment1	7.60	2.09	0.71705	0.19
	Treatment1:SexM	-2.66	6.71	0.96864	0.09
SPEED	Intercept	9.19	1.77	2e-07	
	Age	3.13	1.14	0.00625	0.98
	SexM[2]	1.27	5.74	0.82442	0.38
	Treatment1[1]	-5.45	5.36	0.91907	0.37
	Age:SexM	-5.18	4.68	0.91194	0.10
	Age:Treatment1	7.07	4.72	0.88092	0.10
	Treatment1:SexM	7.28	1.90	0.96942	0.04
TURNING ANGLE	Intercept	0.09	0.13	0.488	
	Age	0.00	0.07	0.990	0.41
	SexM[2]	-0.12	0.16	0.432	0.61
	Treatment1[1]	0.21	0.19	0.266	0.74
	Age:SexM	-0.02	0.08	0.773	0.13
	Treatment1:SexM	-0.01	0.11	0.950	0.13
	Age:Treatment1	0.01	0.06	0.837	0.11
	Intercept	5.43	3.38	<2e-16	
	Age	3.90	2.10	0.0634	0.91
	SexM[2]	7.24	1.11	0.5152	0.64

NEST DISTANCE	Treatment1[1]	6.12	5.42	0.9103	0.42
	Age:SexM	-3.36	9.19	0.7150	0.23
	Age:Treatment1	3.02	4.54	0.9471	0.11
	Treatment1:SexM	1.86	2.58	0.9428	0.08
AREA	Intercept	4.08	0.64	<2e-16	
	SexM[2]	-0.04	0.13	0.785	0.09
	Treatment1[1]	-0.17	0.12	0.151	0.77
	Treatment1:SexM	0.00	0.03	0.930	0.01
DISTANCE BETWEEN OWLS	Intercept	7.66	1.28	<2e-16	
	Age	1.57	7.38	0.0329	0.95
	SexM[2]	1.16	2.05	0.5725	0.58
	Treatment1[1]	1.10	1.79	0.9109	0.53
	Age:SexM	-3.26	1.53	0.8311	0.17
	Age:Treatment1	4.09	1.56	0.7936	0.17
	Treatment1:SexM	-2.24	9.31	0.8102	0.12

[1] = Treatment group 1 (fostered owls)
[2] = Males

1

1 **Table 2. ICC values of the random factors "owl" and "nest" for the post-fledging**

2 **dependence period and dispersal.**

DEPENDENT VARIABLE	RANDOM FACTORS	ICC VALUES PFDP	ICC VALUES DISPERSAL
NET DISTANCE	Owl	0.00	
	Nest	0.35	0.90
TOTAL DISTANCE	Owl	0.00	
	Nest	0.73	0.58
SPEED	Owl	0.00	0.01
	Nest	0.35	0.00
NEST DISTANCE	Owl	0.00	0.36
	Nest	0.74	0.44
AREA	Nest	0.99	

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

Table 3. Model-averaged coefficients and RIV values for early dispersal.

DEPENDENT VARIABLE	EXPLANATORY VARIABLE	MODEL-AVERAGED COEFFICIENTS AND RELATIVE IMPORTANCE VALUES			
		β	SE	P	RIV
NET DISTANCE	Intercept	7.90	3.56	<2e-16	
	SexM[2]	-3.16	1.75	0.869	0.06
	Treatment1[1]	2.15	1.55	0.900	0.04
	Treatment1:SexM	-5.61	3.49	0.999	<0.01
TOTAL DISTANCE	Intercept	9.99	2.13	<2e-16	
	Treatment1[1]	1.15	8.92	0.909	0.04
	SexM[2]	4.80	6.87	0.952	0.04
	Treatment1:SexM	-6.47	8.53	1.000	<0.01
SPEED	Intercept	8.54	1.06	<2e-16	
	Age	-1.63	4.48	0.000298	1.00
	SexM[2]	-2.63	1.42	0.065174	0.90
	Age:SexM	1.11	6.04	0.66097	0.86
	Treatment1[1]	9.14	3.32	0.978140	0.37
	Treatment1:SexM	-8.29	1.21	0.945717	0.09
	Age:Treatment1	2.98	1.31	0.981901	0.09
TURNING ANGLE	Intercept	0.14	0.23	0.540	
	Age	0.05	0.25	0.834	0.84
	SexM[2]	0.21	0.26	0.934	0.59
	Age:SexM	0.26	0.36	0.462	0.43
	Treatment1[1]	0.04	0.24	0.854	0.41
	Treatment1:SexM	0.05	0.25	0.826	0.09
	Age:Treatment1	0.00	0.08	0.965	0.09
NEST DISTANCE	Intercept	6.92	0.36	<2e-16	
	Age	0.01	0.00	<2e-16	1.00
	SexM[2]	1.27	0.41	0.00193	1.00
	Age:SexM	-0.01	0.00	6e-06	1.00
	Treatment1[1]	0.05	0.27	0.83999	0.45
	Treatment1:SexM	-0.13	0.33	0.70568	0.19
	Age:Treatment1	0.00	0.00	0.90387	0.12
DISTANCE BETWEEN OWLS	Intercept	6.81	0.51	<2e-16	
	Age	0.01	0.00	5.4e-06	1.00
	Treatment1[1]	0.85	0.57	0.140769	0.86
	SexM[2]	1.35	0.46	0.003573	1.00
	Age:Treatment1	-0.01	0.00	0.172951	0.76
	Age:SexM	-0.01	0.00	0.000313	0.99
	Treatment1:SexM	-0.11	0.26	0.678530	0.31

[1] = Treatment group 1 (fostered owls)
[2] = Males

Figure legends

Figure 1. a. Movement characteristics of owls in 20-day periods during the post-fledging

dependence period. Means of males (dotted lines) and females (full lines) are presented.

(1.) Net distance. (2.) Total distance. (3.) Speed. (4.) Distance between each location and the

nest. (5.) Distance between owls.

b. Example of real paths followed by one individual at different ages during the post-

fledging dependence period. The black points represent the starting point of the path.

(1.) Path at 66 days. (2.) Path at 104 days. (3.) Path at 118 days.

Figure 2. a. Movement characteristics of owls in 20-day periods during dispersal. Means of

males (dotted lines) and females (full lines) are presented.

(1.) Speed. (2.) Distance between each location and the nest. (3.) Distance between owls.

b. Example of a real path followed by one individual during the whole dispersal phase

considered. The black point represents the starting point of the path.

Supplemental files

Table S1. Movement parameter values for the post fledging dependence period.

Table S2. Comparison of the competing models built to study variation in eagle owl movements

during the post-fledging dependence period. A summary of model-averaged coefficients and RIV

values is shown for all candidate models. Competitive models are ranked from the lowest (best

model) to the highest AICc value.

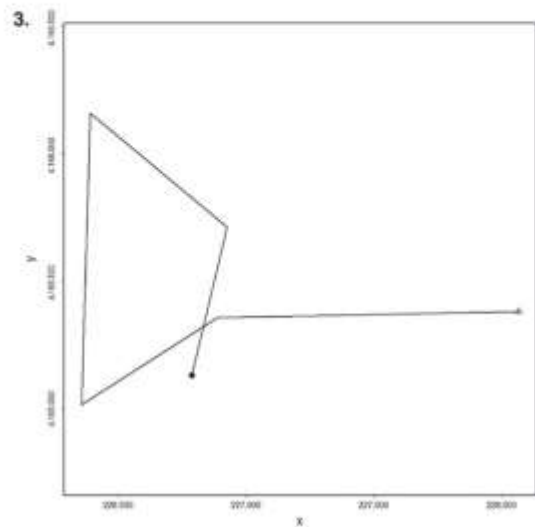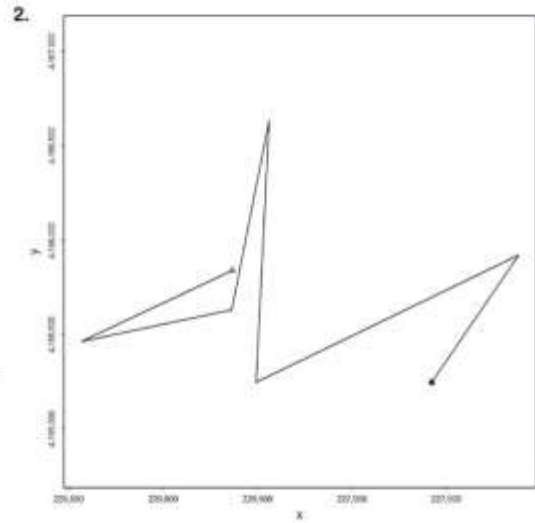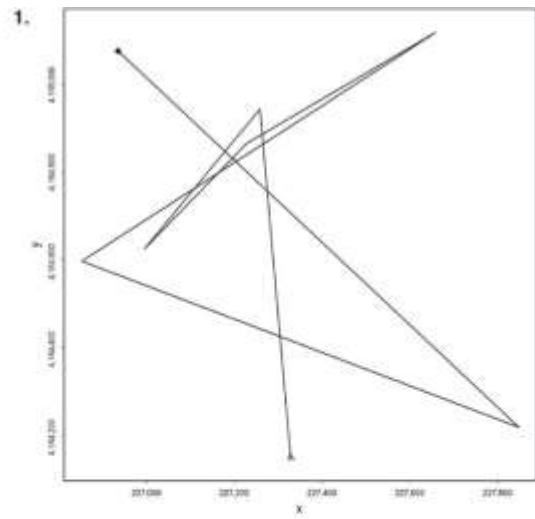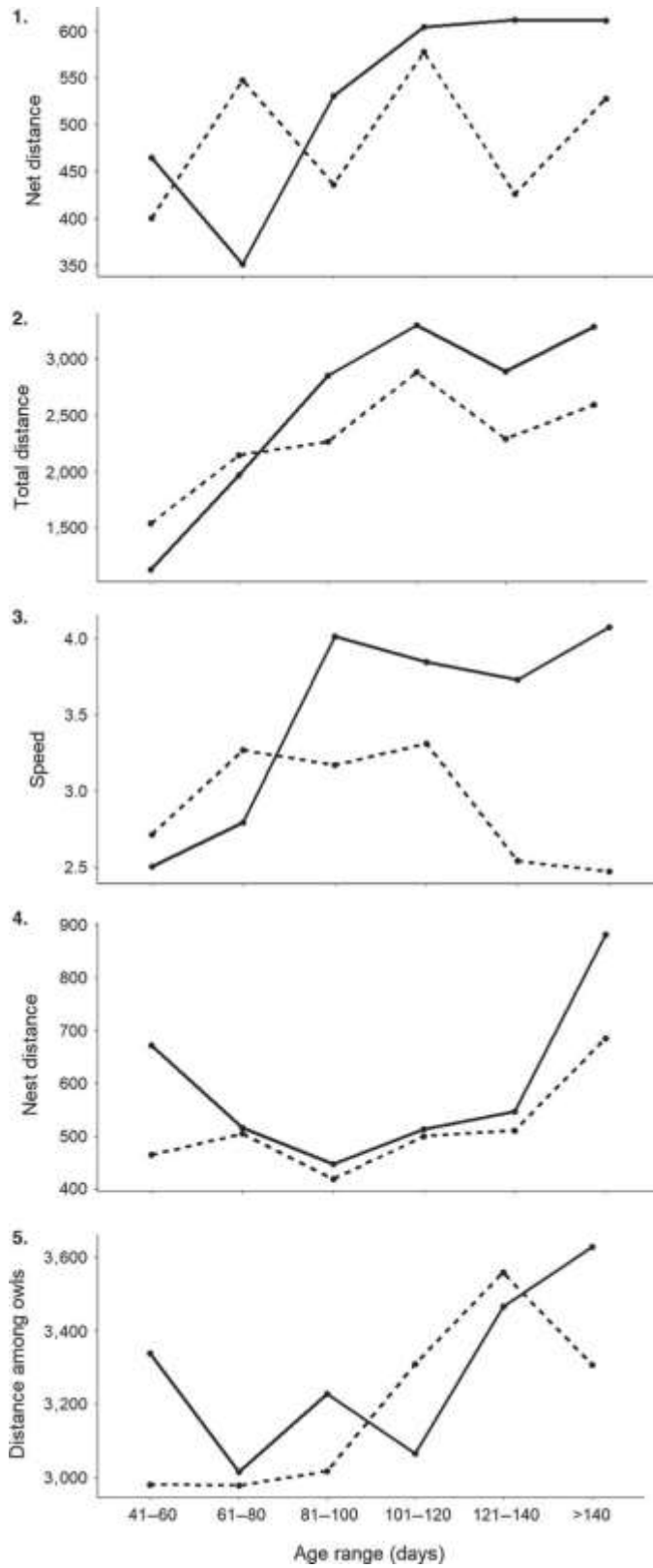**Table S3**. Movement parameter values for early dispersal.

Table S4. Comparison of the competing models built to study variation in eagle owl movements

during early dispersal. A summary of model-averaged coefficients and RIV values is shown for

all candidate models. Competitive models are ranked from the lowest (best model) to the highest
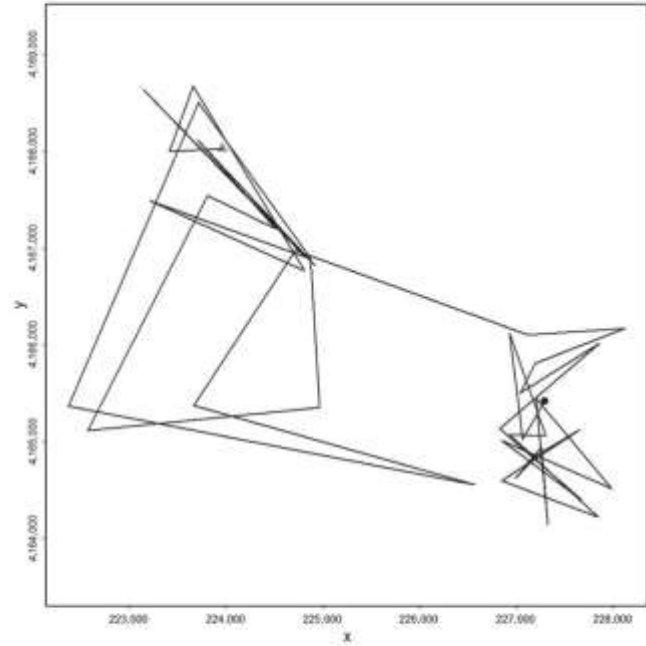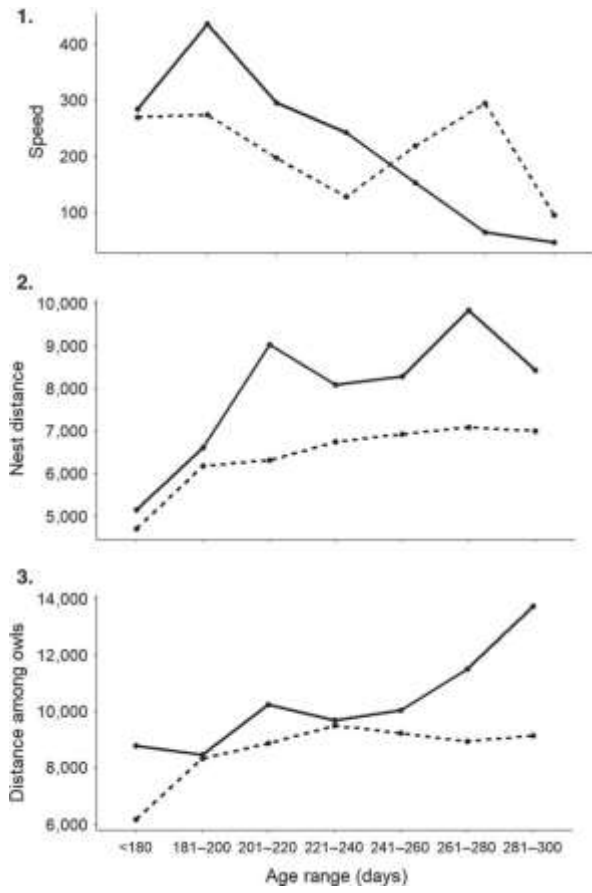
AICc value.

1   **Fig. 1.**

2

1   **Fig. 2.**

2

3