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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] | María del Mar Delgado[1]

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

[2]Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., Seville, Spain

[3]Department of Ecological and Biological Sciences, Tuscia University, Viterbo, Italy

[4]Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Torino, Italy

Correspondence
Giulia Bombieri, Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, Mieres, Spain.
Email: giulipan91@gmail.com

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Abstract

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

KEYWORDS

Bubo bubo, cross-fostering, eagle owl, natal dispersal, post-fledging dependence period

1 | 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 × 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, de Jong, van Noordwijk, Kempenaers, & Drent, 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; Pasinelli, Schiegg, & Walters, 2004; Pasinelli & Walters, 2002; Van Noordwijk, 1984). These studies showed that, even if many movement behaviours have a significant heritable component, it is the combination of genetic and environmental components (G × 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

*These authors contributed equally to this work

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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, that is 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 hypothesised 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 hypothesise that a genetic component is the main force driving movement behaviours (genetic hypothesis).

2 | METHODS

2.1 | Field methods

This study was conducted over 2 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: (i) nest checking, (ii) nestling age and sex determination, (iii) set up and running of the cross-fostering experiment, that is exchanging chicks between nests and (iv) radio tracking owls during PFDP and dispersal. We determined the age of the owlets based on plumage characters (Penteriani, Delgado, Maggio, Aradis, & Sergio, 2004) and their sex using DNA extracted from blood Griffiths, Double, Orr, and Dawson (1998).

2.2 | 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 seven nests (one nest was used in both years) for a total of four 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; nine males and five 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; four males and six females; n_{2015} = 8; $_{n2016}$ = 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).

2.3 | Radio tracking procedure

We radio-tagged the birds and performed the cross-fostering experiment when owlets were 30-35 days old. Individuals were fitted with a Teflon ribbon backpack harness that carried a 30 g radio transmitter (henceforth "tag;" see Delgado & Penteriani, 2008). The weight of the tag was < 3% of the weight of the smallest adult male (1550 g, mean ± *SD* = 1667 ± 104.8) and 3.5% of the smallest fledgling weight (850 g, mean ± *SD* = 1267 ± 226.4 g). Because the chicks were still growing when they were radio-tagged, backpacks were adjusted so that the Teflon ribbon could expand and allow for the increase in body size. We manipulated and marked owls under (i) the Junta de Andalucía—Consejería de Medio Ambiente permits No. SCFFSAFR/GGG RS 260 / 02 and SCFFS AFR /CMM RS 1904 / 02; and (ii) the approval of the Comité de Ética de Experimentación Animal of the Estación Biológica de Doñana-CSIC (CEEA-EBD_12_41).

Locations of radio-tagged owls were determined using a three-element hand-held Yagi antenna connected to a BIOTRACK portable receiver via bi-angulation. The mean (± *SD*) accuracy of localisations was 83.5 ± 49.5 m, estimated as the difference between the radio location and the locations of tagged individuals when, after a radiolocation, we needed to locate where exactly one individual was (e.g., if it died). During

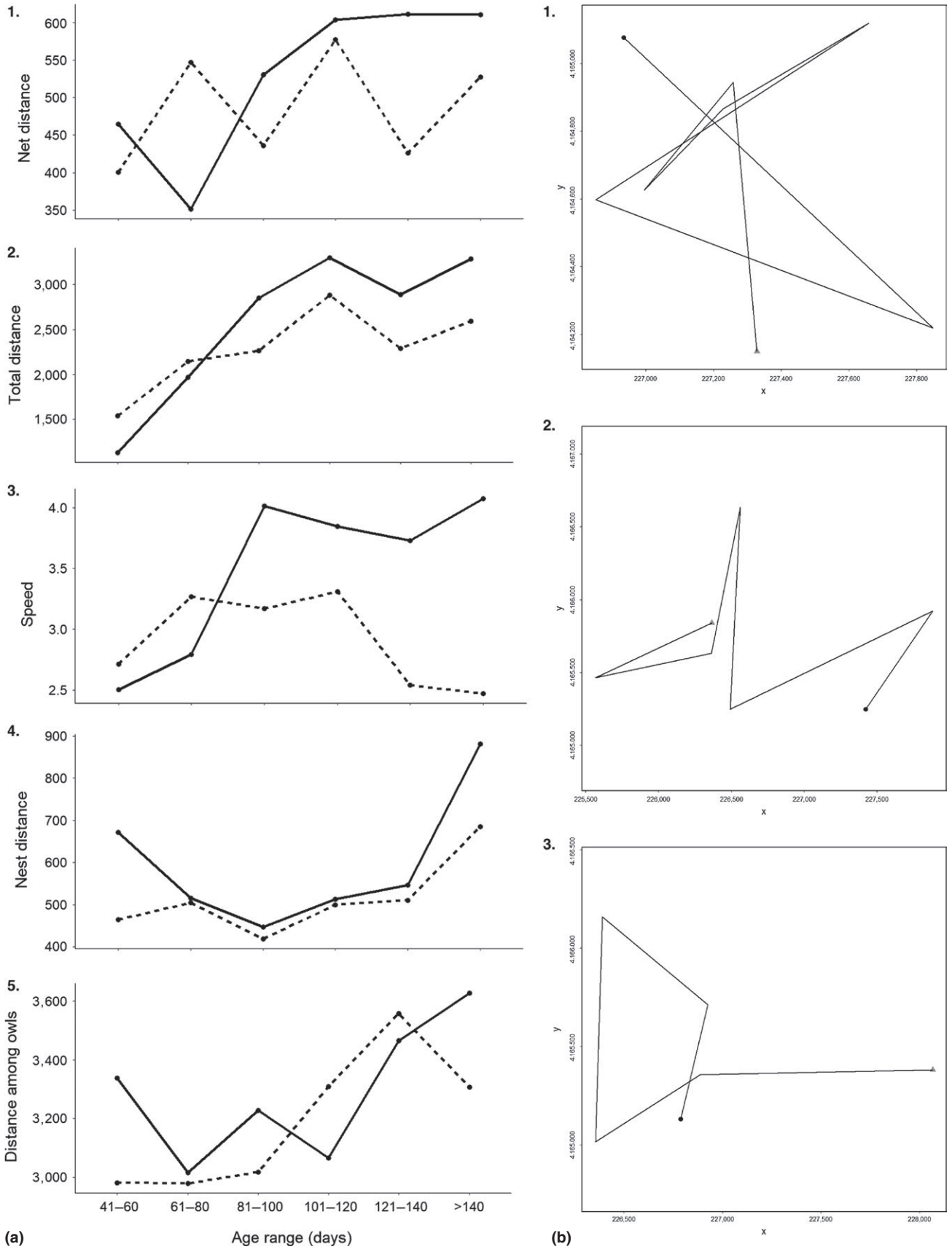

FIGURE 1 (a) Movement characteristics of owls in 20-day periods during the post-fledging dependence period. Means of males (dotted lines) and females (full lines) are presented. (1) Net distance. (2) Total distance. (3) Speed. (4) Distance between each location and the nest. (5) Distance between owls. (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

the PFDP, owlets were followed by radio tracking during night sessions, which took place with an interval of 10 days. During these sessions, all the owlets were radio-located throughout the entire night, from 1 hr before sunset to 1 hr after sunrise. The time interval between successive individual locations was ca. 1 hr and 30 min. During dispersal, owls were located on a weekly basis at their daytime roosting sites (mean time between consecutive locations ± SE = 6.9 ± 0.1 days). During the experiment, six owls were predated (n_{2015} = 5; n_{2016} = 1) and we lost the signal of three other individuals. Thus, our final sample size was 21 owls for the PFDP sample and 15 owls for the dispersal sample.

2.4 | Determination of PFDP and dispersal phases

PFDP started when the juveniles left the nest (mean age = 40-45 days) and lasted until the juveniles started to disperse (Delgado, Penteriani, & Nams, 2009). To identify the start of dispersal, we plotted both the beeline distance from the natal nest for each location and the average of the beeline distance between the whole set of locations and the nest, with the latter value representing the global mean distance covered by each individual during dispersal (Delgado & Penteriani, 2008). Dispersal started when the distance between successive moves became larger than the average distance travelled by each bird. This happens when the distance of each location from the nest starts to increase rather than fluctuate around a low value (Delgado & Penteriani, 2008).

2.5 | Movement parameters

To compare the two treatment groups, we quantitatively described the movement behaviour of individuals during PFDP and dispersal. For each juvenile (n_{PFDP} = 21; $n_{dispersal}$ = 15) and for the two phases, we estimated seven movement parameters. (i) Step distance: distance between consecutive locations. (ii) Total distance: total distance covered by the owl. (iii) Net distance: the distance between the first and the last location collected. (iv) Distance between the nest and each of the location points. (v) Distance between different owls, via individual locations recorded at the same time. (vi) Movement speed: obtained by dividing the step distance by the time interval between consecutive locations. (vii) Movement direction (i.e., turning angles) between successive locations. In addition, we estimated the size of the area explored by each owl during the whole PFDP using the 100% minimum convex polygon in QGIS 2.14.3 Geographic Information System (QGIS Development Team, 2016).

2.6 | Statistical analyses

For the statistical analyses, we considered all parameters except the step distance, as this variable was highly correlated with speed (r = .97, p = .001). Correlations between the other variables were low (r < .2 in each case). For each of the six movement parameters considered, we built a set of competing models which included all possible combinations of explanatory variables, starting from the simplest null model (intercept-only model) to a full model that included all the explanatory variables (Tables S2 and S4). To check model assumptions (normality, independence, the presence of outliers), we first conducted a graphical data exploration. Response variables following a normal distribution were modelled using linear mixed models. When residuals did not follow a normal distribution, data were log transformed and then checked again for the assumptions. When log transformation was not sufficient, we applied a generalised linear mixed model with gamma distributions.

In each set of competing models, we included treatment group, age (except for net and total distance in the dispersal phase) and sex of individuals, as well as their interactions, as fixed factors. Random effects were held constant. For modelling movement parameters during the PFDP, we included five random hierarchical factors, organised as follows: (1) year, (2) experimental block, (3) nest, (4) night of radio tracking and (5) individual. The night of radio tracking was not included in the models built for net and total distance, as we only had one observation per night for these variables. For dispersal, we included the same random factors, except the night of radio tracking, as we had weekly observations for this period. In the models built for net and total distance of dispersal, we also excluded the individual as a random factor, given that for these two parameters, we only had one observation per owl.

We selected the best competing model based on the Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002) and calculated two additional statistics for each model: ΔAICc and weighted AICc, indicating the probability that the model selected was the best among the competing candidates (Gelman & Hill, 2006). We considered models with ΔAICc values lower than 2 as competitive. For each set of models, we then employed model averaging on the 95% confidence set to derive parameter coefficients and the relative importance values (RIV) of each explanatory variable using the full-model averaging approach (Burnham & Anderson, 2002). When high model selection uncertainty exists, model averaging allows formal inference based on the entire set of models (or, in our case, the 95% confidence set) (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011; Symonds & Moussalli, 2011). Parameter estimates produced by model averaging derive from weighted averages of these values across all models in the set considered (Symonds & Moussalli, 2011). In particular, the relative importance value (RIV) of each explanatory variable is calculated by summing Akaike weights across all models which contain the variable (Burnham & Anderson, 2002).

Significance was assessed using p-values derived from the model-averaged parameter estimates and was set at $p \leq .05$.

To assess the variability between/within nests and between/within individuals, we calculated, for each movement statistics, the within-nest and the within-individual repeatability (R; Stoffel, Nakagawa, & Schielzeth, 2017; Zuur et al., 2009) as:

$$R = \frac{\sigma_\alpha^2}{(\sigma_\alpha^2 + \sigma_\beta^2)},$$

where σ_α^2 is the group (in our case, nest or individual identity, respectively) variance and σ_β^2 is the residual (error) variance (Sokal & Rohlf, 1995). R thus informs us about the strength of the differentiation between nests or individuals (σ_α^2) relative to the total variation. The total variation includes within-nest or within-individual variance, respectively

(i.e., variance between observations of each nest or of each individual; σ^2_β), and the variance between nests or individuals (σ^2_α). These variances were taken from our linear mixed models that included nest and individual identity, together with treatment and year, as random factors according to our experimental design. Specifically, R < 0.40 means low variability between groups and high variability within groups, whereas R > 0.60 corresponds to high variability between groups and low variability within groups (Stoffel, Nakagawa, & Schielzeth, 2017).

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

3 | RESULTS

3.1 | General patterns of owl movements

3.1.1 | 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).

3.1.2 | 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).

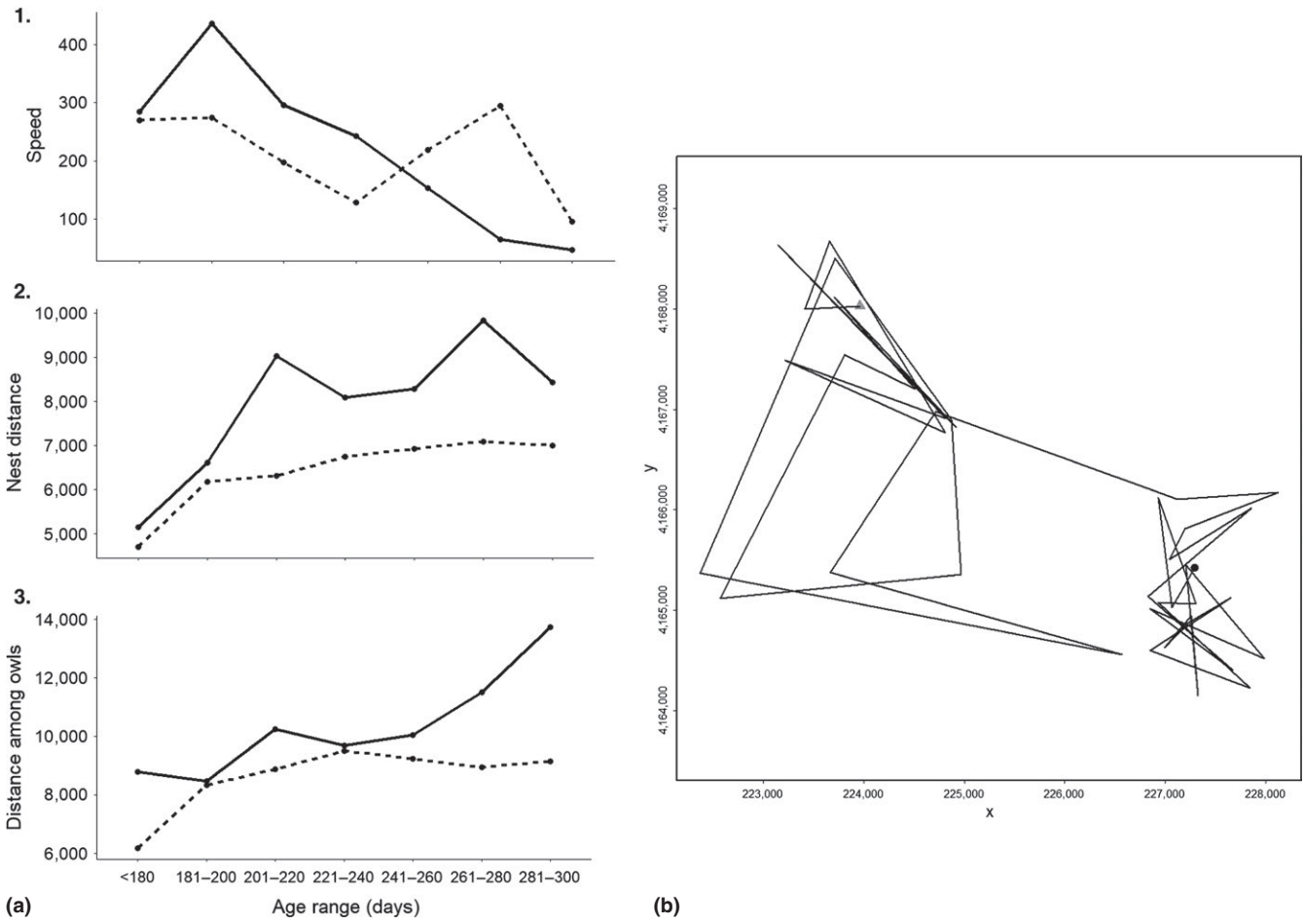

FIGURE 2 (a) Movement characteristics of owls in 20-day periods during dispersal. Means of males (dotted lines) and females (full lines) are presented. (1) Speed. (2) Distance between each location and the nest. (3) Distance between owls. (b) Example of a real path followed by one individual during the whole dispersal phase considered. The black point represents the starting point of the path

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	.0119	1.00
	SexM[b]	0.25	0.42	.5549	0.55
	Treatment1[a]	−0.20	0.41	.6209	0.47
	Age:SexM	−0.00	0.00	.6389	0.27
	Age:Treatment1	0.00	0.00	.6359	0.25
	Treatment1:SexM	0.02	0.11	.8637	0.08
Total Distance	Intercept	6.56	3.32	< 2e-16	
	Age	6.31	1.99	.00162	1.00
	SexM[b]	1.77	1.96	.36912	0.78
	Treatment1[a]	−4.79	2.08	.81896	0.45
	Age:SexM	−9.30	1.38	.94661	0.19
	Age:Treatment1	7.60	2.09	.71705	0.19
	Treatment1:SexM	−2.66	6.71	.96864	0.09
Speed	Intercept	9.19	1.77	2e-07	
	Age	3.13	1.14	.00625	0.98
	SexM[b]	1.27	5.74	.82442	0.38
	Treatment1[a]	−5.45	5.36	.91907	0.37
	Age:SexM	−5.18	4.68	.91194	0.10
	Age:Treatment1	7.07	4.72	.88092	0.10
	Treatment1:SexM	7.28	1.90	.96942	0.04
Turning Angle	Intercept	0.09	0.13	.488	
	Age	0.00	0.07	.990	0.41
	SexM[b]	−0.12	0.16	.432	0.61
	Treatment1[a]	0.21	0.19	.266	0.74
	Age:SexM	−0.02	0.08	.773	0.13
	Treatment1:SexM	−0.01	0.11	.950	0.13
	Age:Treatment1	0.01	0.06	.837	0.11
Nest Distance	Intercept	5.43	3.38	<2e-16	
	Age	3.90	2.10	.0634	0.91
	SexM[b]	7.24	1.11	.5152	0.64
	Treatment1[a]	6.12	5.42	.9103	0.42
	Age:SexM	−3.36	9.19	.7150	0.23
	Age:Treatment1	3.02	4.54	.9471	0.11
	Treatment1:SexM	1.86	2.58	.9428	0.08
Area	Intercept	4.08	0.64	<2e-16	
	SexM[b]	−0.04	0.13	.785	0.09
	Treatment1[a]	−0.17	0.12	.151	0.77
	Treatment1:SexM	0.00	0.03	.930	0.01
Distance Between Owls	Intercept	7.66	1.28	<2e-16	
	Age	1.57	7.38	.0329	0.95
	SexM[b]	1.16	2.05	.5725	0.58
	Treatment1[a]	1.10	1.79	.9109	0.53
	Age:SexM	−3.26	1.53	.8311	0.17
	Age:Treatment1	4.09	1.56	.7936	0.17
	Treatment1:SexM	−2.24	9.31	.8102	0.12

[a]Treatment group 1 (fostered owls).
[b]Males.

3.2 | The cross-fostering experiment

3.2.1 | 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 ($p \leq .05$) and had a relatively high importance (RIV > 0.90) in five 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). We found that R values (Table 2) for the individual identity were always < 0.4, whereas R values for nest identity ranged between 0.35 and 0.99. These results suggest that, when comparing different eagle owls that have been raised in the same nest, such groups of individuals showed high and significant levels of repeatability (i.e., high within-nest repeatability) in their movement parameters. That is, the low consistent behavioural differences we found within the same individuals are still maintained when eagle owls confront the same environment. This result seems to support the hypothesis that movement behaviour in our experiment is firstly related to the external environment, namely the spatial characteristics of the nest, and then to the individual component.

3.2.2 | Dispersal

Out of six 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 two models. *p* and RIV values suggested that age had the main effect, showing $p \leq .05$ and RIV > 0.90 in three 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 two 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. As in the post-fledging dependence period, values of R (Table 2) for the individual identity were < 0.4, whereas for nest identity, R values were higher (always R > 0.40, except for the speed; Table 2).

TABLE 2 ICC values of the random factors "owl" and "nest" for the post-fledging dependence period and dispersal

Dependent variable	Random factors	Icc values pfdp	Icc values dispersal
Net Distance	Owl	0.00	0.90
	Nest	0.35	
Total Distance	Owl	0.00	0.58
	Nest	0.73	
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	

4 | 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 (see also Delgado et al., 2010; Penteriani & Delgado, 2011). 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 utilised 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

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[b]	−3.16	1.75	.869	0.06
	Treatment1[a]	2.15	1.55	.900	0.04
	Treatment1:SexM	−5.61	3.49	.999	<0.01
Total Distance	Intercept	9.99	2.13	<2e-16	
	Treatment1[a]	1.15	8.92	.909	0.04
	SexM[b]	4.80	6.87	.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	.000298	1.00
	SexM[b]	−2.63	1.42	.065174	0.90
	Age:SexM	1.11	6.04	.66097	0.86
	Treatment1[a]	9.14	3.32	.978140	0.37
	Treatment1:SexM	−8.29	1.21	.945717	0.09
	Age:Treatment1	2.98	1.31	.981901	0.09
Turning Angle	Intercept	0.14	0.23	.540	
	Age	0.05	0.25	.834	0.84
	SexM[b]	0.21	0.26	.934	0.59
	Age:SexM	0.26	0.36	.462	0.43
	Treatment1[a]	0.04	0.24	.854	0.41
	Treatment1:SexM	0.05	0.25	.826	0.09
	Age:Treatment1	0.00	0.08	.965	0.09
Nest Distance	Intercept	6.92	0.36	<2e-16	
	Age	0.01	0.00	<2e-16	1.00
	SexM[b]	1.27	0.41	.00193	1.00
	Age:SexM	−0.01	0.00	6e-06	1.00
	Treatment1[a]	0.05	0.27	.83999	0.45
	Treatment1:SexM	−0.13	0.33	.70568	0.19
	Age:Treatment1	0.00	0.00	.90387	0.12
Distance Between Owls	Intercept	6.81	0.51	<2e-16	
	Age	0.01	0.00	5.4e-06	1.00
	Treatment1[a]	0.85	0.57	.140769	0.86
	SexM[b]	1.35	0.46	.003573	1.00
	Age:Treatment1	−0.01	0.00	.172951	0.76
	Age:SexM	−0.01	0.00	.000313	0.99
	Treatment1:SexM	−0.11	0.26	.678530	0.31

[a]Treatment group 1 (fostered owls).
[b]Males.

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, Kennedy, Knight, & McEwen, 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.

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ORCID

Giulia Bombieri http://orcid.org/0000-0002-0374-1985

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