

# The effect of phenotypic traits and external cues on natal dispersal movements

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## Summary

**1.** Natal dispersal has the potential to affect most ecological and evolutionary processes. However, despite its importance, this complex ecological process still represents a significant gap in our understanding of animal ecology due to both the lack of empirical data and the intrinsic complexity of dispersal dynamics.

**2.** By studying natal dispersal of 74 radiotagged juvenile eagle owls *Bubo bubo* (Linnaeus), in both the wandering and the settlement phases, we empirically addressed the complex interactions by which individual phenotypic traits and external cues jointly shape individual heterogeneity through the different phases of dispersal, both at nightly and weekly temporal scales.

**3.** Owls in poorer physical conditions travelled shorter total distances during the wandering phase, describing straighter paths and moving slower, especially when crossing heterogeneous habitats. In general, the owls in worse condition started dispersal later and took longer times to find further settlement areas. Net distances were also sex biased, with females settling at further distances. Dispersing individuals did not seem to explore wandering and settlement areas by using a search image of their natal surroundings. Eagle owls showed a heterogeneous pattern of patch occupancy, where few patches were highly visited by different owls whereas the majority were visited by just one individual. During dispersal, the routes followed by owls were an intermediate solution between optimized and randomized ones. Finally, dispersal direction had a marked directionality, largely influenced by dominant winds. These results suggest an asymmetric and anisotropic dispersal pattern, where not only the number of patches but also their functions can affect population viability.

**4.** The combination of the information coming from the relationships among a large set of factors acting and integrating at different spatial and temporal scales, under the perspective of heterogeneous life histories, are a fruitful ground for future understanding of natal dispersal.

**Key-words:** animal movements, dispersal behaviour, dispersal condition dependent, eagle owl, spatial networks

## Introduction

Natal dispersal (i.e. the movements of an individual from its natal area to the area where breeding first take place (hereafter termed dispersal)) is a life-history trait that has been extensively studied for more than a half a century. It is known that dispersal is influenced by several developmental and behavioural pathways (Dufty, Clobert & Möller 2002) and that it has the potential to affect many ecological and evolutionary processes. However, despite its importance, dispersal still represents a significant gap in our understanding of

animal ecology (Ronce 2007). Why do we still have such an incomplete understanding of dispersal? The combination of the lack of empirical data (mainly on vertebrate species; Bowler & Benton 2005) and the complexity of dispersal dynamics (Clobert, Ims & Rousset 2004) is undoubtedly one of the principal causes.

Recently, Clobert *et al.* (2009) reviewed the current knowledge of dispersal by presenting a conceptual framework to stimulate and redirect further research on individual heterogeneity (i.e. between-individual variation) in dispersal strategies. The most crucial point that emerged was the strong relationship between the stages of dispersal (i.e. *departure*, *transience* or *wandering*, and *settlement* or *stop*; Clobert *et al.* 2004; Bowler & Benton 2005) and the effects of both the

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internal state of dispersers (*phenotype-dependent dispersal*) and external factors (*condition-dependent dispersal*). It is crucial to take into account that: (i) the mechanisms linking external factors and the individual internal state could vary over these phases; and (ii) the sequential nature of the dispersal stages may determine a cascading effect, i.e. behavioural decisions taken at one stage may influence behavioural choices of the next stage and, ultimately, the fitness and fate of dispersers. However, it is still unknown (i) what are the effects of, and interactions among, external factors and internal states; and (ii) how movement strategies depend on features of the individuals and the environment, as well as their effects on settlement decisions.

Until now, a lot of researchers have mainly focused on the emigration phase (i.e. when individuals take the decision to leave their natal site) and the evolutionary causes of dispersal (e.g. inbreeding avoidance, resource and kin competition, and environmental stochasticity; reviewed in Bowler & Benton 2005), as well as the overall dispersal success, rather than the dispersal process itself. However, although dispersal distances are not a behavioural choice *per se*, there is a lack of knowledge about the process by which individuals move between patches and how this process evolves (Bartón *et al.* 2009). Here, we will focus on movements in the later dispersal stages once an organism has left its natal place, i.e. on the wandering and settlement phases (determined as in Delgado & Penteriani 2008). Using a 4-year study on the dispersal of radiotagged juveniles of an avian predator, the eagle owl *Bubo bubo* (Linnaeus), we empirically address how both the individual internal state (e.g. physiology, morphology, life-history traits) and external factors (e.g. habitat features and structure, habitat connectivity, local climatic conditions) act together through the different phases of dispersal.

The outline of our research is as follows. First, we analyse individual heterogeneity among dispersers across the whole dispersal process, to test whether (i) behaviour of dispersers changes during the dispersal process; and (ii) individuals behave in a consistent manner throughout the dispersal process. Such individual heterogeneity could represent an important source favouring the evolution of dispersal strategies (Clobert *et al.* 2009). Then, we study how individual heterogeneity in dispersal behaviours during the wandering phase can be influenced by a wide range of environmental and physiological factors. We tested here two main hypotheses: (i) if a heterogeneous environment is the main factor determining differences in dispersal movements of individuals (Wiens 2001), then we should expect that dispersing individuals under different environmental conditions should move at different rates and over different distances; and (ii) if variation in dispersal is not only based on external but also on internal factors (Ims & Hjerermann 2001; Clobert *et al.* 2009), then we should expect individuals to disperse non-randomly but matching their own internal state with respect to environmental conditions. Finally, we focus on the settlement phase of dispersal. In particular, we analyse how individual behaviours and the different factors shaping dispersal decisions while searching for settlement areas (i.e. the regions occupied

for a fairly long period of time relative to the entire dispersal process, or until the bird becomes an owner of a breeding territory) are integrated between dispersal phases, ultimately determining settlement behaviours (i.e. the decision of individuals to stop their wandering life to settle). As the decision to stop may involve various elements of habitat selection or physiological factors, our main objective here was to explore when, where and how individuals decide to stop wandering and settle in a new environment.

## Materials and methods

### DATA COLLECTION

From 2003 to 2006, we studied dispersal of eagle owls, a long-lived species with deferred sexual maturity. We radiotagged 74 owlets (2003:  $n = 8$ ; 2004:  $n = 17$ ; 2005:  $n = 27$ ; 2006:  $n = 22$ ) from 12 different nest sites when they were *c.* 35 days old in Sierra Morena (south-western Spain; more details in Penteriani *et al.* 2007). For each analysis, we used different subsamples, represented by those dispersers for which it was possible to collect the specific information we needed. Individuals were fitted with a Teflon ribbon backpack harness that carried 30 g radiotransmitters (see Delgado & Penteriani 2008). The weight of the tags was  $< 3\%$  of the weight of the smallest adult male (1550 g, mean  $\pm$  SD =  $1667 \pm 104.8$ ) and  $3.5\%$  of the smallest fledgling weight (850 g, mean  $\pm$  SD =  $1267 \pm 226.4$  g). Because at this time the young are still growing, backpacks were adjusted so that the Teflon ribbon could expand and allow for the increased body size. Owls were aged following Penteriani *et al.* (2005a) and sexed by molecular procedures using DNA extracted from blood.

Owls were followed within an area of *c.* 70 000 Ha at two different temporal scales: (i) *nightly scale* tracking (i.e. during whole nights, from 1 h before sunset to 1 h after sunrise; mean time duration of a radiotracking session  $\pm$  SD =  $11.3 \pm 2.1$  h), during which 40 different individuals were continuously and individually tracked ( $n = 178$  radiotracking sessions for a total of 2010 h). We recorded locations ( $n = 3196$ ) each time that we detected, by means of a posture mercury sensor, a change in individual posture or position (mean number of locations per radiotracking session  $\pm$  SD =  $18 \pm 4.6$ ); thus the number of locations recorded represents the effective amount of movement for an individual during the night; and (ii) *weekly scale* tracking, during which 49 owls were weekly located at their diurnal roosts ( $n = 1189$  locations). Locations were obtained using triangulation with a three-element hand-held Yagi-antenna connected to ICOM portable receivers. To ensure independency between points and because of the error in radiotracking localization (accuracy of mean  $\pm$  SE =  $83.5 \pm 49.5$  m), a minimum distance of 150 m between locations was set as the minimum threshold to consider two fixes as two real locations at nightly scale. For weekly scale, we did not consider those locations recorded with a time interval larger than 10 days.

### MAIN STATISTICAL ANALYSES

This is an overview of the common analyses. To analyse individual heterogeneity among dispersers and during the dispersal process, we built Generalized Linear Mixed Models (GLMM) for two key behavioural movement parameters (movement speed and turning angles) as a function of the time since dispersal phase. Then, to test how internal state and external factors affected individual dispersal

behaviour, we built GLMMs with movement parameters as the dependent variables and (i) individual physiology/morphology parameters; and (ii) habitat measurements at nightly and weekly scales as the explanatory variables. The statistical analyses were performed with SAS procedure GLIMMIX (version SAS 8.2, SAS Institute 2001). Some dependent variables (speed, total and net distance; see Table 1) showed skewed and leptokurtic distribution, and hence they were modelled using lognormal distributions and the default identity link function. For those variables that were normally distributed (e.g. fractal  $D$ , timing to settle), we used normal distributions with the identity link function. In addition, we simplified the variable representing turning angle as an index (1 and 0 for positive and negative cosine values, representing moving forward and backward), and modelled it using a logistic regression with a binomial response variable and a logit link function. Because we had repeated measures of the same owls, we considered individuals as a random effect. Finally, we used two stepwise logistic regressions to test whether the selections of settlement areas differ (i) from the area used within the natal home range (the dependent variable was an index: 0 for natal and 1 for settlement areas) or (ii) from areas used by dispersers during the wandering phase (again, the dependent variable was an index: 0 and 1 for wandering and settlement area). The explanatory variables presented to the stepwise logistic models were the indices calculated to describe landscape structure and composition in the natal, wandering and settlement areas. All models were built through a backward stepwise procedure where the least significant terms or interactions were sequentially removed until obtaining a minimal adequate model that only retained significant effects at the 5% probability level. All tests are two-tailed, statistical significance was set at  $\alpha < 0.05$ , and  $\pm$  deviations for means are SD or SE, when the important aspect part was the variability or the precision respectively.

#### MOVEMENT PATH ANALYSES

We quantitatively described dispersal movement behaviour at the two different temporal scales by the following parameters: (i) *movement speed*, dividing the step distance by the time interval between successive locations; (ii) *turning angles* between successive moves; (iii) the *total distance*, based on the gross distance travelled by each individual during both the wandering phase and during each night; (iv) *path tortuosity*, measured by the overall fractal dimension ( $D$ ), where  $D = 1$  indicates a perfectly straight line and  $D = 2$  indicate a line as tortuous as to completely cover a plane; for more details, see Nams 2006; Delgado, Penteriani & Nams 2009). We calculated an overall estimate of fractal  $D$  for each individual movement path, using the same range of scales for all movement paths (from 20 to 160 m); and (v) the *net distance* from the natal site to the settlement area.

Due to the multiple factors (and their interactions) affecting dispersal patterns, we will detail below both the specific background and methodological procedures of each of the topics that we took into consideration within the different phases of dispersal.

#### THE WANDERING PHASE

*Internal state of dispersers:* Patterns of dispersal are determined by a suite of individual phenotypic traits (reviewed in Clobert *et al.* 2009; Dawideit *et al.* 2009), which may engender poor quality or less-competitive individuals to disperse (reviewed in Martín *et al.* 2008). However, the reverse trends of several traits have been found both among and within the same species (Clobert *et al.* 2009).

We measured several condition indices for 35-day-old owls. First were morphological and biometrical measurements. The length of forearm, bill, tarsus and wing were measured to the nearest 0.1 mm, and body weight was measured to the nearest 10 g. To increase the precision of measurements, all of them were taken by the same person. Morphological and biometrical measurements were also summarized into a body condition index (BCI; for more details, see Delgado *et al.* 2009). Higher values of the BCI represent individuals of better quality (Green 2001). Second were physiological 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 1699 g to obtain haematocrit (HT) value. HT is used as indicator of nutritional status because nutritional deficiencies result in anaemia due to a shortage in essential amino acids (Costa & Macedo 2006). From the plasma samples, we determined cholesterol, triglycerides, uric acid, urea, glycerol and total protein concentrations, which have been recognized as indices of body condition in birds (see Penteriani *et al.* 2007, for more details). Blood smears (fixed with the GIEMSA method) were used to measure both immunodefence and the levels of stress and health. The proportion of the different types of white blood cells (eosinophils, lymphocytes, monocytes, basophiles and heterophiles) was estimated by counting 100 white blood cells in each smear by microscopy ( $\times 100$ ) using oil immersion (Ortego & Espada 2007). Relative increases in white blood cells are usually associated with the presence of blood parasites, and therefore with individuals in poorer condition (Figuerola *et al.* 1999).

#### External cues acting on dispersers

*Habitat measurements at nightly and weekly scale tracking:* At the nightly scale, to test for the effect of habitat heterogeneity on individual search strategies, we analysed the landscape structure and the composition of habitats crossed during dispersal. We evaluated both landscape structure and composition using ArcMap of ARCGIS version 9.0 (ESRI, Inc., Redlands, CA, USA). We reclassified the map into 10 simpler landcover elements: urban areas, water bodies, forest, dense scrublands with trees, sparse vegetation with trees, herbaceous vegetation with trees, scrublands, low vegetation, woody crops and herbaceous. We then calculated the proportion of these habitat types within the whole area explored by individuals during each night. The land cover areas in raster format (cell size, 0.5  $\times$  0.5 km) were used as a basic input data layer for measuring landscape metrics. We used the raster version of the FRAGSTATS 3.3 (McGarigal *et al.* 2002) to calculate the total landscape area, density and number of patches (defined as relatively homogeneous areas that differ from the surroundings), mean patch size, total amount of edge and edge density, mean patch fractal dimension, patch density, relative patch richness, Shannon's diversity and aggregation index. At a weekly scale, we only estimated the main habitat type (i.e. herbaceous, scrubland or forest) surrounding the diurnal roost. Differently from the nightly scale, we did not measure the structure of the landscape within the whole area crossed during dispersal. This was because it is difficult to relate each weekly movement decision with the landscape structure of the whole area crossed by each disperser, at such a coarse resolution.

*Individual heterogeneity when moving during dispersal: a natural experiment:* During dispersal, different owls explored the same areas before settling; this situation represented a natural experiment, allowing us to explore how much the environment affects owl movements. We compared both the movements of: (i) different owls while using the same surroundings and (ii) the same owl when both moving

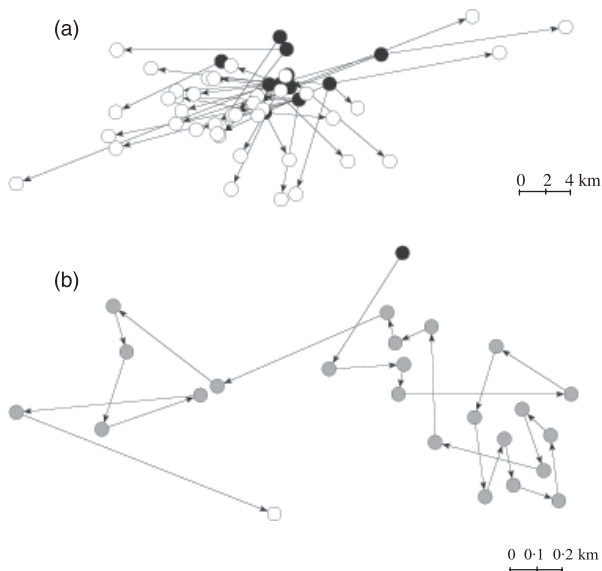
Table 1. Results of Generalized Linear Mixed Models exploring the effect of internal state and external factors on natal dispersal movements

Movement parameters	Distributions			Dispersal dependent									
	$\chi^2/z(\alpha)$	d.f.	P	Internal	Estimates ± SE	F	d.f.	P	External	Estimates ± SE	F	d.f.	P
Wandering phase													
Fine scale													
Total distance	6.77 (Lognormal)	11	0.45	gly HT heterop basop	-0.020 ± 0.003 -0.009 ± 0.005 -0.006 ± 0.003 -0.330 ± 0.150	53.15 3.40 3.44 4.84	178	** * * *	ta te pd ha hb ta	-0.001 ± 0.0001 -9.3E-6 ± 3.6E-6 -0.100 ± 0.0005 0.650 ± 0.068 0.700 ± 0.70 0.0005 ± 0.0002	148.03 6.83 333.79 89.59 86.53 5.10	178	* * ** ** ** *
Speed	7.09 (Lognormal)	11	0.79	ac uric HT basop No effect No effect	0.020 ± 0.005 -0.001 ± 0.002 -0.230 ± 0.087 - -	13.14 16.53 7.09 - -	942	** ** * > 0.5 > 0.5	pd No effect te	-0.070 ± 0.017 - -0.0043 ± 0.001	16.88 - 4.80	178	** > 0.5 *
Turning angles	(binomial)												
Fractal D	0.62 (Normal)		0.83										
Coarse scale													
Total distance	12.35 (Lognormal)	8	0.14	gly ac uric BCI No effect	-0.020 ± 0.004 -0.009 ± 0.004 10.55 ± 0.080 -	40.72 4.42 14.49 -	38	** * ** > 0.5	No effect	- - - -	- - - -	38	> 0.5 * * > 0.5
Speed	15.08 (Lognormal)	8	0.05										
Turning angles	(Binomial)												
Fractal D	0.88 (Normal)		0.42										
Settlement phase													
Coarse scale													
Net distance	4.27 (Lognormal)	8	0.83	gly Urea heterop Sex BCI Urea mono HT Age Dispersal	0.030 ± 0.003 0.030 ± 0.003 0.010 ± 0.001 0.130 ± 0.060 -1.150 ± 0.300 -0.010 ± 0.002 -0.009 ± 0.002 0.020 ± 0.002 0.010 ± 0.006	54.10 95.83 45.79 4.67 14.74 24.70 22.17 125.10 371.47	38	** ** ** * * ** ** ** **	Habitat type Habitat type No effect	habitat type <sup>a</sup> - -	19.81 - -	38	** * * * * * * * **
Timing to settle	0.79 (Normal)		0.56				13	*	No effect	-	-		> 0.5

Gly, glycerol concentration; ac uric, uric acid concentration; HT, haematocrit value; heterop, proportion of heterophiles; basop, proportion of basophiles; lymop, proportion of lymphocytes; mono, proportion of monocytes; BCI, body condition index; ta, total area; te, total number of edges; pd, patch density; ha, percentage of scrubland habitat; hb, percentage of forest habitat.  
<sup>a</sup>Categorical variable: urban areas, water bodies, forest, scrublands with trees, sparse vegetation with trees, scrublands, low vegetation, woody crops, and herbaceous.  
\*  $P < 0.05$ ; \*\*  $P < 0.0001$ .

within the same area and when moving among different ones. If environmental conditions do affect animal movements, then movement paths of the individuals using the same areas should be more similar than those of individuals using different ones. We characterized movement paths by estimating: (i) path tortuosity (measured by fractal  $D$ ); (ii) the overall speed of nightly movement; and (iii) the deviation from a correlated random walk (measured by  $CRW_{Diff}$ ; scaling test, Nams 2006; Delgado, Penteriani & Nams 2009). Fractal  $D$  and speed measure parameters of a specific movement mechanism, while  $CRW_{Diff}$  tests for the movement mechanism. We assessed the similarity of areas by the distance between the mean locations of nightly movements (central points). Then we calculated the distance between the mean locations of all possible pairs of owl nights, with shorter distances between them meaning that owls used more similar environmental surroundings. We also estimated the difference in each movement path characteristic for each combination of two owls.

To test for the effects of the environment on movement characteristics, we compared the movements of different owls using a procedure analogous to correlograms, as follows. To compare movements of different individuals, we first sorted all possible pairs of owl nights (different owls) according to distances between nightly movements, and then grouped them into 500 m distance categories. The 500 m distance intervals were chosen because the settlement areas explored by dispersers generally were < 1 km in diameter (M.M. Delgado & V. Penteriani, unpublished data), and so owls with activity centres separated by < 500 m were likely exploring overlapping areas. Within each distance category, we estimated the mean difference in each movement path characteristic (fractal  $D$ ,  $CRW_{Diff}$  and overall speed) between the two owls. A lower difference for shorter distances would indicate that owls closer together have more similar movement paths. Note that the distances are not simultaneous; that is, two owls could be using the same area but on different nights. To compare movements of the same individual, we compared individuals



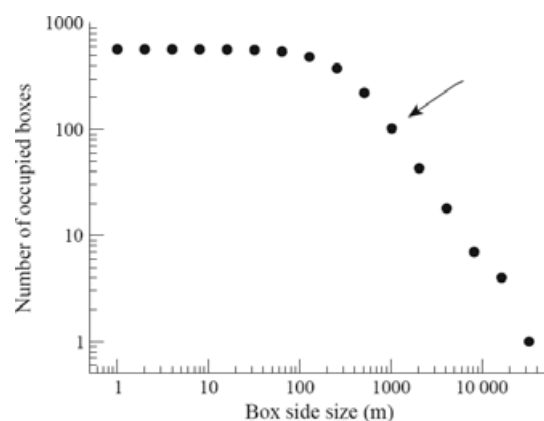
**Fig. 1.** (a) Spatial locations of the nests (black circles,  $n = 11$ ) from which the juvenile eagle owls were radiotagged, and the settlement/breeding areas (white circles,  $n = 42$ ) in which they fixed themselves during dispersal. Arrows indicate the dispersal routes followed from the natal sites to the settlement areas. (b) An example of a real route followed by one owl during dispersal. Grey circles represent weekly spatial locations during this period. Arrows indicate the direction of movements.

travelling in the same area among nights (distance between the mean locations of nightly pairs  $\leq 500$  m) to individuals travelling in different areas (distance  $> 500$  m) using GLMMs. We considered individuals as a random effect and the within-individual effects as a fixed factor. The dependent variables (i.e. fractal  $D$ ,  $CRW_{Diff}$  and overall speed) showed a normal distribution and therefore they were modelled using the identity link function (Littell *et al.* 1996).

**Effects of habitat connectivity:** Wandering is one of the most risky stages of dispersal because individuals spend most of the time moving across unknown habitats (Baker & Rao 2004). However, dispersal does not only depend on habitat patches, but also on the connectivity of the intervening habitat through which organisms disperse (Ricketts 2001). The complexity of a landscape can be simplified by considering the landscape as a set of habitat patches linked by the dispersal movements of the species. This approach defines the landscape as a graph (as in graph theory; Minor & Urban 2008). Graph theory provides a simple means of depicting the overall structure of a habitat mosaic in terms of metapopulation structure and dispersal (for more details, see the review of Urban *et al.* 2009). Because graphs are models of landscapes, they are appropriate to analyse the spatial connectivity of the areas crossed during dispersal.

To build the graph spatial network associated with our dispersal system, we first translated the individual weekly locations during the wandering phase of dispersal into a patch occupancy pattern (see Fig. 1a; see Fig. 1b as an example of an individual dispersal route). In order to do this, we first defined the spatial scale that maximized variation in patch occupancies (Schroeder 1991). To do this, we superimposed a set of grids on the landscape, using increasing grid scales in successive steps. Then, including only those squares with at least one individual, we selected the spatial scale that comprised the highest number of individuals visiting each grid square – in our case a grid square of 1 km<sup>2</sup> (Fig. 2). At smaller spatial scales, many patches were occupied by just one individual, whereas at larger scales few patches were occupied. The landscape was hence divided in areas of 1 km<sup>2</sup>, and hereafter a habitat patch is defined as an area of 1 km<sup>2</sup>. We then used network analyses to build the spatial network of dispersers, where the nodes represented the habitat patches visited by owls and the arrows corresponded to their movements among successive patches (Fig. 3).

We analysed this network in three ways. We first evaluated how important each visited node (habitat patch) was as a dispersal stepping-stone, by considering the number of individual owls visiting it. For this, we (i) analysed the degree of occupied patches by different



**Fig. 2.** Box-counting analysis. The arrow indicates the selected spatial pattern, i.e. the patch size used to build the dispersal spatial network.

number of dispersing owls; and (ii) regressed the cumulative degree distribution (i.e. the number of patches visited by at least one individual or more, patches visited by two individuals or more, until the maximum number of different owls we found visiting the same patch, that was 10) to both an exponential and power-law functions. All patches, except the natal and the final settlement patches, have the same number of incoming and outgoing arrows; that is, when an individual arrived in a patch, it always left it. We were interested in characterizing the importance of a habitat patch to the dispersal of the population. For this reason, we assessed the role of the patches as a function of the number of different owls visiting them. Therefore, multiple visits of the same individual to a given patch were not added as additional arrows and they did not affect the measure of patch degree.

Secondly, we characterized the dispersal routes of owls by measuring the number of different patches each owl visited. In order to gain information on the features of dispersal routes, we compared the real dispersal route to optimized and randomized ones (100 randomized ones for each owl). An optimized route is the route that, crossing the minimum number of patches and following the real (i.e. the observed) directions carried out by any owl in its movements between patches, links the natal site to the settlement/breeding area. A randomized route uses randomly chosen owl directions. Both of these routes are restricted by only choosing those patches visited by owls. Thus, the null models for random or optimal movement are the most conservative; the removal of either of these two restrictions would increase the chance of finding differences between real routes and either optimized or randomized ones.

Finally, we analysed the direction of the dispersal trajectories, that is, the direction of the net movement from the natal site to the settlement/breeding area, to test for asymmetry in the dispersal process. We tested for (i) differences between dispersal directions and random directions; and (ii) a relationship between dispersal direction and the predominant wind direction at the start of dispersal (from July to September, when dispersal starts, and for the years of study; Agencia Estatal de Meteorología). These comparisons were performed by

$\chi^2$ -tests of the distribution of numbers of owls in each angle grouping (directions were rounded to the nearest 45°).

#### THE SETTLEMENT PHASE

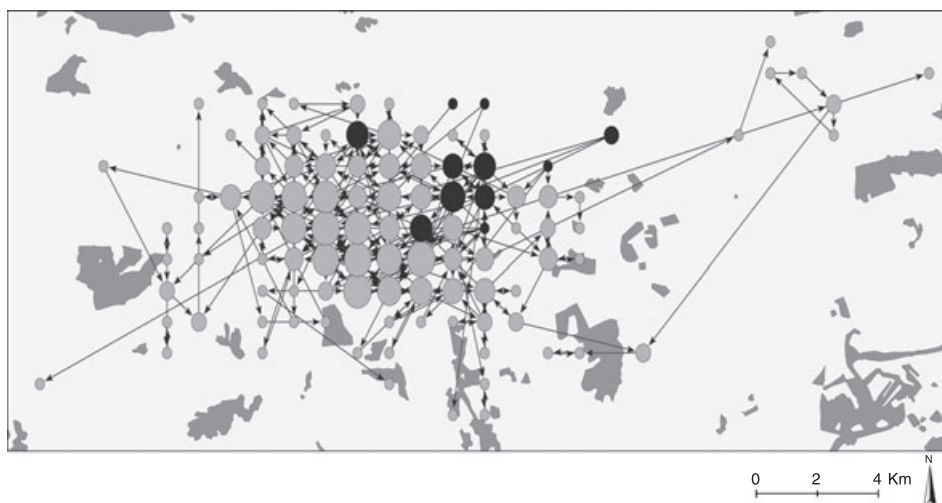
Similar to what we did during the wandering phase, we focus here on the phenotypic traits and external cues explaining the different settlement patterns (i.e. individual settlement decision, measured as both distance and timing to settle). Given that the behavioural decisions during one stage of dispersal have the potential to affect the individual performances during the successive phases, we also evaluated how the patterns of movement during the wandering phase could be related to the subsequent settlement patterns.

#### Internal state of dispersers

We analysed the effects of the individual physiological and movement behaviours on both distance and timing to settle. In most movement models, path variables are intrinsically related, e.g. longer paths are associated with travel for longer periods of time. In order to separate these effects, we first carried out a principal components analysis on dispersal time, net distance and total distance travelled, and then regressed the behavioural movement properties against the first principal component. This gave us the effects of the search strategies on overall path performance. In order to see the effects of each path component independently of the others, we removed the possible effects of those variables and used the residuals. For example, for the effects on time, our dependent variable was the residuals of the regression of time vs. net and total distances. This gave us the unique effects on time by itself, not a by-product of an effect on distance or total path length.

#### External cues acting on dispersers

We explored how individuals were able to assess the quality of their biotic and abiotic environment as input for settlement strategies –



**Fig. 3.** The spatial patterns described by dispersing eagle owls in a graph space, in which the real routes followed by owls from the natal site to the final settlement/breeding area are represented. Nodes represent the crossed habitat patches and their sizes are proportional to the number of different individuals that occupied them. In black are represented those nodes also containing the nests in which juveniles were radiotagged. Light grey background represents the habitat in where at least one owl was localized at least once. Dark grey background encompassed those habitats never occupied during dispersal.

when individuals decide to stop wandering, and where they settle when moving in a new environment. To test whether the selection of settlement areas differed from the area used within the natal home range or from areas used by dispersers during the wandering phase, we estimated, for each individual, the natal, wandering and settlement areas, using 95% minimum convex polygons with weekly locations from those life stages. Both landscape structure and composition of those areas were evaluated in relation to external cues and movement decisions during the wandering phase.

## Results

### GENERAL PATTERNS OF OWL DISPERSAL

Most of the tagged juveniles (6 of the 74 radiotagged owls, i.e. 8%, died during the postfledging dependence period) started their dispersal at the end of August (mean age at the beginning of dispersal =  $170 \pm 20.5$  days, range = 131–232 days). Despite the high degree of individual variation, we found that 35% ( $n = 24$ ) of the 68 eagle owls found a stable settlement area (i.e. shifted from the wandering to the settlement phase of dispersal) in the middle of March (mean dispersal age at the settlement phase =  $395 \pm 109.9$  days, range = 181–40 days). Ten (42%) of the settlers became territory owners and started breeding. Of the 68 dispersing individuals, 21 (31%) were found dead (all tagged birds that died were recovered in the field): 13 (19%) died during their first year of life and during the wandering phase, and 8 after settlement. Thirteen (19%) of dispersing owls were lost (or their transmitter failed during the dispersal period). Ten owls (15%) were in the wandering phase when their transmitters run out. Dispersal distances (the net distance from the natal to the last location) ranged from 1.5 to 34.3 km (mean  $\pm$  SD =  $6.0 \pm 4.2$  km).

When analysing the individual heterogeneity among dispersers, we detected two main features. First, movement speed of dispersers changed during the whole dispersal process ( $F = 4.51$ , d.f. = 534,  $P = 0.03$ ); i.e. individuals can show different strategies throughout dispersal. This result strengthens the need to analyse all steps of dispersal in order to understand the whole process dynamics. Second, we found that the individual (as a random factor) explained 52% of the variability observed. This suggests that, independently of the physical condition of dispersers and the effect of the external factors that we measured, each individual behaves in a characteristic manner (i.e. there are consistent behavioural differences between individuals).

### THE WANDERING PHASE

#### Nightly scale

Individual health and habitat characteristics significantly affected some of the movement path parameters during the wandering phase of dispersal (Table 1). Owls in poorer physical condition (i.e. those with high levels of glycerol and white blood cells) travelled shorter total distances and moved slower during the night, especially when crossing

heterogeneous habitats (i.e. characterized by high numbers of edges and patches). Moreover, individuals showed the straightest trajectories when crossing heterogeneous habitats with high numbers of edges.

#### Individual heterogeneity when moving during dispersal: a natural experiment

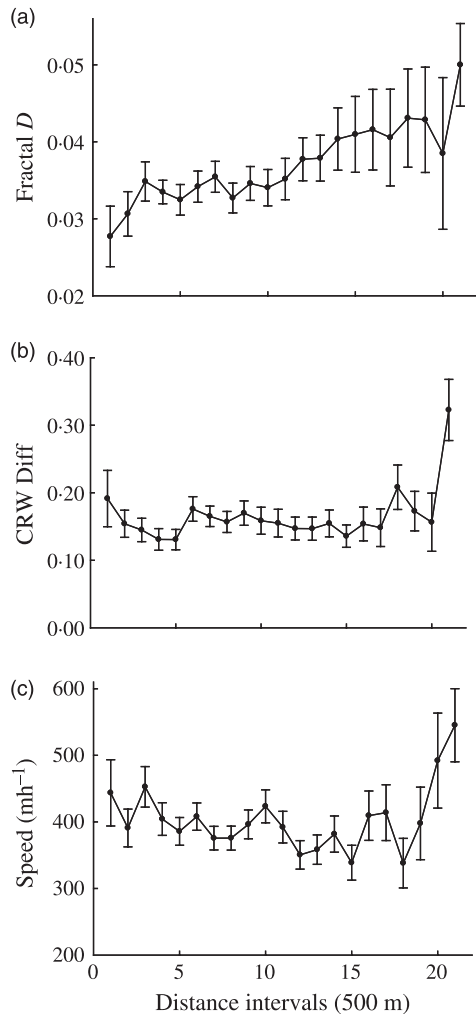
Tortuosity of movement paths during nights (i.e. at the nightly scale) was more similar (i.e. the differences between tortuosity values being closer to zero) when owls were closer together (i.e. they used the same area, but not necessarily at the same time; Fig. 4a;  $r = 0.90$ ,  $P < 0.001$ ). However, neither  $CRW_{Diff}$  (Fig. 4b;  $r = 0.23$ ,  $P = 0.27$ ) nor speed (Fig. 4c;  $r = 0.0$ ,  $P = 0.80$ ) showed a significant relationship with distance between areas explored by owls. When comparing tortuosity within the same owl vs. between different owls, we found that the variation in tortuosity between owls was higher (GLMMs:  $R^2 = 0.17$ ,  $P < 0.0005$ ) than within the same owl when moved in the same surrounding (i.e. the same individual showed similar movement trajectories). However, when individuals shifted among different areas the change in their movement patterns decreased the variation in tortuosity between owls (GLMMs:  $R^2 = 0.02$ ,  $P = 0.99$ ). That is, the variation in path tortuosity between different owls was now less than the variation of the same owl moving between different areas. Finally,  $CRW_{Diff}$  and speed were more similar within than among individuals, both when the same owl shifted among different environmental surroundings ( $CRW_{Diff}$ :  $R^2 = 0.24$ ,  $P < 0.0175$ ; speed:  $R^2 = 0.44$ ,  $P < 0.0001$ ) and when it remained in the same area ( $CRW_{Diff}$ :  $R^2 = 0.13$ ,  $P = 0.0066$ ; speed:  $R^2 = 0.27$ ,  $P < 0.0001$ ).

#### Weekly scale

Landscape significantly affected movement path characteristics during the wandering phase of dispersal (Table 1). On the one hand, owls with higher values of lymphocytes (i.e. individuals in poorer body condition) and travelling across habitats characterized by high numbers of edges moved straighter (lower fractal  $D$ ). On the other hand, individuals in poorer condition moved shorter weekly total distances. We did not detect any significant effects of habitat composition or physiological condition measurements (all  $P > 0.5$ ) on the speed of movement at the weekly scale.

#### Effects of habitat connectivity

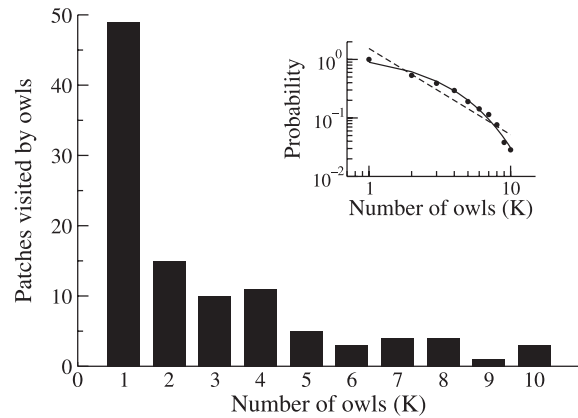
Dispersing eagle owls showed a heterogeneous pattern of patch (node) occupancy during dispersal: (a) only a fraction of the available landscape was used (Fig. 3) and (b) the degree distribution of the patches was heterogeneous (Fig. 5). That is, most patches were visited by just one individual, while few patches were visited by almost 25% of all the radiotagged individuals. However, the probability of



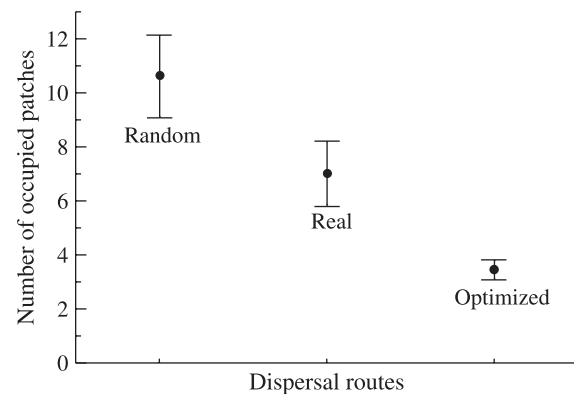
**Fig. 4.** The effects of distance between nightly areas used by all pairs of wandering owls and the differences in their movement path characteristics. Each distance interval represents 500 m. The significant increase in Fractal  $D$  differences vs. distance (a) showed that path tortuosity was more similar for owls using areas closer together than farther apart. Differences in CRW<sub>Diff</sub> (b) and speed (c) did not vary significantly with distance, suggesting that these two parameters were not related with landscape structure.

finding a patch decays exponentially with the numbers of individuals ( $F_{1,8} = 684.22$ ,  $R^2 = 0.988$ ,  $P < 0.001$ ; this was the result of fitting the cumulative degree distribution to an exponential function; regression analysis; see inset Fig. 5).

The mean number of visited patches per owl was  $7.0 \pm 3.7$  for real routes,  $3.5 \pm 1.1$  for optimized routes and  $10.9 \pm 5.1$  for randomized routes. Real routes contained fewer patches than did randomized ones ( $t = -4.98$ ,  $n = 42$ ,  $P < 0.001$ ; paired  $t$ -test); showing that owls do not move randomly among habitat patches during dispersal, using fewer habitat patches than expected by chance. However, real routes also contained more patches than did optimized routes ( $t = 6.83$ ,  $n = 42$ ,  $P < 0.001$ ; paired  $t$ -test), showing that dispersing owls also do not follow optimal routes that minimize displacements (see Fig. 6).



**Fig. 5.** Degree distribution of occupied patches by dispersing owls. Inset: the cumulative degree distribution fitted to an exponential function (solid line) and power-law function (dashed line).



**Fig. 6.** Number of nodes occupied by dispersing owls, as well as randomized and optimized routes. Mean values and 95% confidence intervals are shown.

During dispersal, the directions followed by dispersing owls ( $\chi^2_7 = 35.33$ ,  $P < 0.001$ ) did not follow a homogeneous distribution. More than 61% of the dispersal trajectories were oriented within  $45^\circ$  of  $247.5^\circ$  (i.e. along a W–S–W direction), indicating a marked directionality (Fig. 7a). The direction of the wind was significantly different from the one expected by chance ( $\chi^2_7 = 297.94$ ,  $P < 0.001$ ): during more than 71% of the days, the wind blew down from  $202.5^\circ$  (between  $157.5^\circ$  and  $247.5^\circ$ , i.e. along a well-defined S–W direction; Fig. 7b). But, still more surprising and non-intuitive, the direction followed by the eagle owls and the direction of the wind during dispersal were statistically associated ( $\chi^2_7 = 35.97$ ,  $P < 0.001$ ).

#### THE SETTLEMENT PHASE

The distance between the settlement area and the natal territory travelled by dispersing owls ranged from 1.5 to 34.3 km (mean  $\pm$  SD =  $6.0 \pm 4.2$  km). The first principal component explained 66% of the variation in movement paths, and this component was almost equally composed of time,



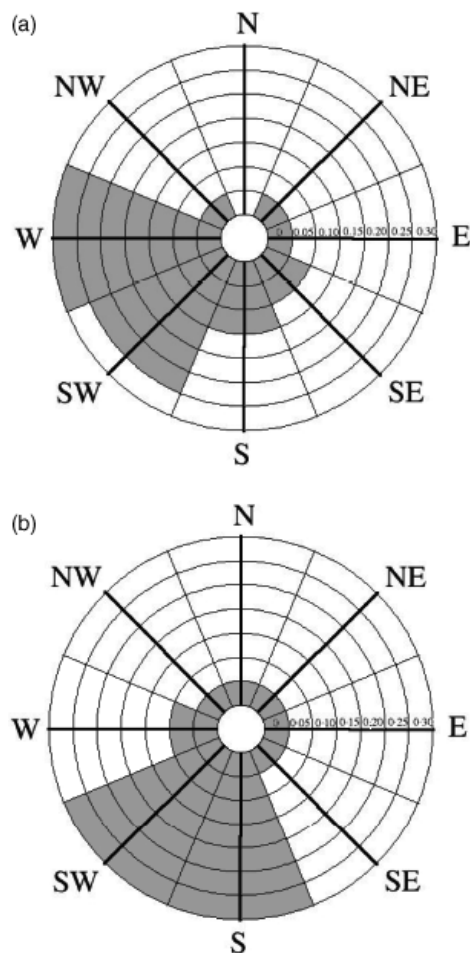


Fig. 7. (a) The direction of owl dispersal movements and (b) the direction of the wind in the study area when dispersal started. Grey areas indicate the fraction in each direction. Owl dispersal was in broad correspondence with the direction of local winds.

distance and total distance. This component describes the overall effect of travel distance/time, where longer paths took more time and went a greater net distance from the nest site. This principal component ( $R^2 = 0.26$ ) was affected by individual movement behaviour (fractal  $D$  at weekly scale:  $B = -2.84$ ,  $P < 0.029$ ). Those owls travelling quite tortuously at a weekly scale find settlement areas sooner, and at a shorter distance from the starting point. This search behaviour allows animals to locate a new territory sooner.

After removing the effects of the other variables, by regressing residuals, dispersal distance was significantly affected by fractal  $D$  at both the nightly scale ( $B = -19900$ ,  $P < 0.022$ ) and at the weekly scale ( $B = -12700$ ,  $P < 0.009$ ). The negative components mean that owls travelling with more tortuous paths at both nightly and weekly scales find settlement areas at shorter distances from the nests, independently of time travelled. Net distance was also affected by the disperser physiological state and landscape (Table 1). Even though poorer individuals travelled shorter total distances because they followed straighter paths, they also travelled larger net distances (i.e. distance from settlement

area to the natal site), especially if they travelled across habitats mainly composed by open vegetation. Net distances were also sex-biased, with females settling generally at further net distances.

Time to settle was significantly affected by the individual internal state: owls in worse condition, especially females, took longer times to find settlement areas. Moreover, those owls starting dispersal later took longer times to settle.

Finally, when analysing the habitat selection of dispersers among their natal, wandering and settlement areas, we observed that: (i) natal territories differed substantially from wandering and settlement areas (*water bodies*:  $\chi^2 = 5.41$ ,  $P = 0.002$ ; *scrubland with trees*:  $\chi^2 = 4.03$ ,  $P = 0.05$ ; *woody crops*:  $\chi^2 = 5.21$ ,  $P = 0.02$ ); and (ii) wandering and settlement areas were quite similar to each other, the only difference between them being the presence of urban zones in the areas crossed during the wandering phase ( $\chi^2 = 6.87$ ,  $P = 0.0009$ ). As a consequence, we can hypothesize that dispersing individuals do not seem to explore wandering and settlement areas by using a search image of their natal surroundings.

## Discussion

Dispersal is a life-history trait shaped by complex interactions between external factors/constraints and the internal state of individuals. Our findings suggest the existence of two non-mutually exclusive sources of heterogeneity. First is individual heterogeneity among dispersers. Even though previous studies traditionally considered individual variability as a statistical noise, today it is well recognized that consistent behavioural differences between individuals have important ecological and evolutionary implications (Sih, Alison & Johnson 2004). Indeed, we found that variation between individual makes up more than 50% of the explained variation; this could be also related to a heritable component in its broadest sense, thus explaining transgenerational effects on similarity in dispersal (V. Penteriani & M.M. Delgado, unpublished data). We argue that individual behaviour may provide enough variability between individuals to favour the evolution of dispersal strategies.

The second is heterogeneity of behavioural responses among the different stages of dispersal. The costs and benefits of dispersal can vary during the different phases (Van Dyck & Baguette 2005), generally yielding a plastic dispersal behaviour. Observed shifts among different behaviours during the different phases may correspond to the ability of a given individual to react to their actual experiences as they move (Dall *et al.* 2005). Across the process of dispersal, the diverse interactions that occur at the individual-individual and individual-habitat levels can be expected to continuously shape the dispersal decisions of individuals. This implies that short-term information on dispersal patterns, e.g. studying individual behaviours during only one phase, may lead us to a partial perception of the entire process. This is particularly important because of the sequential nature of the behavioural phases of dispersal

and the potential cascading effect of subsequent decisions on dispersal strategies and disperser fitness.

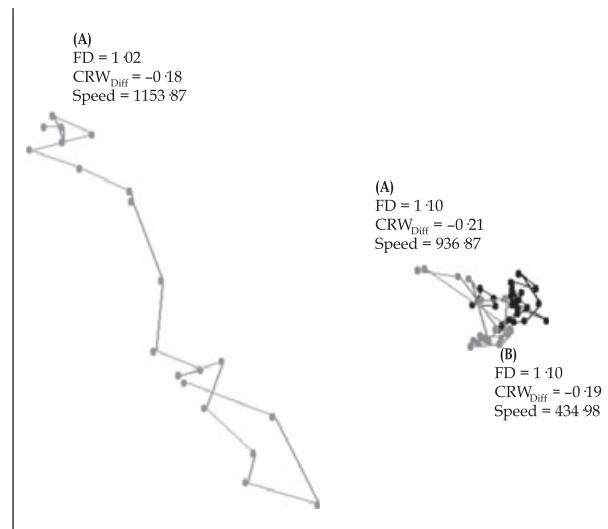
#### THE WANDERING PHASE

Our results demonstrated the importance of the internal state on the behaviour of an animal that seeks a new habitat. Those individuals in poorer condition described straighter trajectories over shorter total distances, moving slower during their 'routine' movements. Phenotypic traits, as claimed by Clobert *et al.* (2009), can generate a range of plastic search strategies, successively determining that not all individuals are equal competitors. But the individual internal state is not the only source of variation; we found that environmental factors are also. For example, individuals moving across unknown habitats and crossing heterogeneous habitats travelled shorter total distances at both nightly and weekly scales. When the costs of movements (e.g. risk of mortality, intraspecific competition) are high, a strategy may evolve to reduce the number of steps with the aim to avoid the amount of time spent in an inhospitable environment. Indeed, we found that straighter movements were more frequent in heterogeneous landscapes rich in patch boundaries and open areas. In our study area, open areas are represented by large patches of cultivated areas, an inhospitable environment for owls. Both the quality and the physical structure of habitats may engender diverse costs and benefits, and consequently noticeable differences in behaviours (Diffendorfer, Gaines & Holt 1995).

#### *Individual heterogeneity when moving during dispersal: a natural experiment*

The analysis of the relationship between fractal  $D$  and distance allowed us to make inference about the importance of external cues as one of the key factors affecting movement behaviours of dispersers. Previous work has highlighted the importance of landscape properties on movement decisions (e.g. Haynes & Cronin 2006). Most of these studies have considered the effect of only one factor at a time, such as habitat fragmentation, patch distribution and composition, or resources abundance and distribution. However, the most common situation in nature is that animals are affected simultaneously by multiple factors that may be involved in individual movement decisions. As individuals moving within the same area vs. different ones showed similar vs. different movement patterns respectively, our findings highlight the overall effect of habitat on movement paths.

The three movement path statistics that we used relate to two different aspects of animal movement: the mechanism, and the parameters of that mechanism. The  $CRW_{Diff}$  statistic considers movement mechanisms (Nams 2006), comparing them to correlated random walk models, which have been widely considered as the null hypothesis for animal movement.  $CRW_{Diff}$  detects if a movement pattern changes from being a correlated random walk to not being one – thus



**Fig. 8.** Owls using the same area present a more similar path tortuosity (FD) than owls moving on different surroundings. We illustrate the typical change in the movement path structure of an individual (owl A, dark grey) when moving within two different areas. When owl (A) uses the same area as owl (B) (black; on the right of the figure), their movement paths are more similar (as reflected by the values of FD).

$CRW_{Diff}$  can detect the changes in movement mechanisms. Speed and fractal  $D$  are specific parameters of that mechanism. For example, if many individuals travel according to a correlated random walk, each one may travel with different speeds or path tortuosities, but they all would still use the same basic movement mechanism. The  $CRW_{Diff}$  analysis showed an interesting feature: the similarities in  $CRW_{Diff}$  between owls did not significantly change with distance between explored areas. This suggests that the areas where owls moved did not affect the movement path mechanism. Additionally, although the distance between explored areas did not affect the travelling speed, it had an evident effect on fractal  $D$ , which was more similar the closer together the areas were. In particular, when path tortuosity is explicitly analysed as a function of the physical surroundings: (i) the same individual showed different movement paths when shifting among different areas, but similar when moving in the same surrounding; and (ii) path tortuosity was more similar between different owls moving within the same area than those moving in different ones (see also Fig. 8).

To conclude, our natural experiment: (i) suggests that movement mechanisms are not as plastic as the parameters of those mechanisms; and (ii) provides empirical support to the theoretical work that identifies the landscape as the major factor driving animal movement patterns (e.g. Nathan *et al.* 2008).

#### *Effects of habitat connectivity*

Connectivity affects metapopulation stability mainly via migration rates among habitat patches (Moilanen & Nieminen 2002). This means that not all patches are of equal

connectivity. Our results showed a clear anisotropic flow of individuals; that is, owl dispersal was polarized along both a specific axis and direction – i.e. asymmetric dispersal. Recently, graph models of landscape structure have been used (Bunn, Urban & Keitt 2000; Urban & Keitt 2001), allowing both to incorporate information regarding the dispersal abilities of focal species and to highlight the importance of individual patches in a landscape (e.g. effects of patch losses due to habitat destruction or other types of disturbance). Our field study has offered a unique opportunity to depict a real scenario during dispersal and to highlight the importance of focal nodes and arrows of the dispersal paths, as well as the possible consequences of their loss on the probability of reaching given temporary settlement areas and on population equilibrium and persistence (Vuilleumier & Possingham 2006; Revilla & Wiegand 2008). Because the number of connected patches largely determines metapopulation viability in an asymmetric system (Vuilleumier & Possingham 2006), we could expect a serious decline of our population if the most frequented patches or arrows connecting breeding territories to settlement areas would disappear or will be affected by environmental stochasticity (Penteriani, Otalora & Ferrer 2005b; Penteriani *et al.* 2005c).

Anisotropic dispersal may result from variations in the ease of moving in different directions (Bélisle 2005). In our scenario, winds affected the direction of dispersal, even when the homogeneity that characterizes our study area would have allowed the owls to disperse in any direction. This is not the first time that birds mix up active and passive dispersal strategies, their patterns of dispersal being largely influenced by dominant winds (Ferrer 1993; Walls, Kenward & Holloway 2005). Depending on: (i) the species-specific importance of the wind direction in shaping dispersal routes and the directionality of local winds at the start of dispersal; and (ii) the structure and characteristics of the spatial network, we can probably find the answers to several ecological puzzles concerning species distributions, colonization and persistence.

#### THE SETTLEMENT PHASE

Individual internal states and habitat features significantly affected settlement patterns; owls in the poorest condition that started dispersal later (i.e. the less competitive individuals; Barbraud, Johnson & Bertault 2003) were those that settled further away and after longer times. This supports previous works showing that individuals making longer distance movements represent a non-random sample of the dispersal population (Clobert *et al.* 2004; Van Dyck & Baguette 2005). In general, environmentally specific characteristics (i.e. population density or habitat characteristics) frequently provide good predictors of dispersal rate at the population level. However, there is often considerable individual variation in dispersal propensity within populations. This could be explained, at least partially, by different internal conditions. It is crucial for individuals to be able to match their own internal condition (i.e. phenotype) against the current

environmental conditions. Thus, the interaction between the internal state of each individual and the local density of conspecifics may explain these settlement patterns.

In our system, many dispersing owls are concentrated in a common area close to the birth population (Delgado & Penteriani 2008). This crowding may explain part of the variation in dispersal strategies as an additional component in the selective pressure on dispersal, i.e. to avoid staying in saturated areas (density-dependent dispersal decisions; Delgado & Penteriani 2008). This could be the reason why poorer quality individuals, faced with intense intraspecific competition in the settlement areas closest to the breeding population, will benefit from moving further away. However, we cannot discard the influence of other factors influencing the variation in the observed dispersal patterns of individuals, e.g. presence of breeders, interspecific interactions such as with other predators or prey, which could co-vary with environmental factors.

Different empirical studies on the effect of phenotypic traits on dispersal decisions have found seemingly contradictory outcomes (Ims & Hjerermann 2001). Some found that a good body condition allows individuals to disperse longer distances without increasing the risk of mortality, while others found that a poor body condition forces individuals to disperse longer distances due to high intraspecific competition. This inconsistency could be explained by the large set of factors affecting dispersal. As these factors may affect individual survival and/or reproduction, it is expected that individual phenotypes are flexible and adaptive to face up to the current environmental conditions. We observed dispersers to be heterogeneous, including both high and poor quality individuals, with the poor ones dispersing longer distances.

However, even if longer distances and longer times before settling are energetically expensive and increase the costs of dispersal, an adaptive behavioural strategy may avoid the negative effects of longer dispersal. Dispersers in poorer condition can still have a good chance of surviving to the early dispersal stage if they perform straighter movements. These movements allow individuals to cover shorter total distances by reducing the number of steps (Bartón *et al.* 2009) and searching more rapidly and over larger net distances (Zollner & Lima 1999). Such a strategy could be considered as ‘the best of a bad situation’, which would increase the settlement probability more rapidly than if they had to find this same, or a further one, settlement area by travelling with more tortuous movement paths.

We also found a significant effect of sex, with females moving longer distances than males. Even though this could be explained by the well-known hypothesis that, in birds, males increase their chance to acquire and defend territories by remaining close to their natal area (Martín *et al.* 2008), the inter-sexual differences in dispersal distances were very small [mean dispersal distance ( $\pm$ SD): males = 6094  $\pm$  4783 m; females = 5849  $\pm$  2767 m]. Thus, it is difficult for us to justify dispersal sex bias in the context of mating system.

In our study system, although dispersing owls remain close to and float around their native population, we never

recorded an individual returning to its natal territory to: (i) check for the availability of an empty territory or a mate; or (ii) to obtain evident benefits from its familiarity with the breeding site (which it has been proposed as a possible reason why natural selection may have selected for fidelity to the natal site; Davis & Stamps 2004). Unfortunately, we cannot make inference about which sex in eagle owls decides to acquire and establish a new territory. The ascension of a disperser as an owner of a territory seems to be more determined by chance. Only those individuals who, by chance, crossed an empty territory or came close to an available mate while wandering, settled and became breeders. In fact, after dispersers encountered a stable settlement area and decided to settle, they remained there for several years without breeding (also if they were mature and shared the settlement area with a conspecific of the opposite sex).

Finally, our results highlight that the individual internal states and behaviours are not the only factors that affect dispersal, as the nature of the intervening landscape can also affect the movement during the wandering phase and, therefore, the different settlement patterns. Our results showed that most owls settled in areas more similar to those that they previously explored during the wandering phase of dispersal, but less similar to their natal habitat. Some early works have found that the previous experience of dispersers in its natal habitat seems able to provide information that increases their level of preference for postdispersal habitats that shares cues with the natal ones (Davis & Stamps 2004; Stamps 2001). However, we found that individuals may prefer to settle in habitats similar to those visited during the wandering phase. This could be explained because: (i) this behaviour may reduce the costs of assessing suitable habitats (e.g. costs of gathering information, energy and time costs, etc.); or (ii) experience in pre-dispersal habitat improves performance if an animal settles in the same type of habitat after dispersing. Therefore, dispersal varies not only among species and individuals but also among landscapes, and the final settlement pattern is therefore affected by a combination of different behavioural decisions, resulting from both physiological state of dispersers and the spatial configuration of the landscape.

## Conclusions

Dispersal can undoubtedly be considered as one of the most intriguing and multifaceted ecological processes. The high complexity and heterogeneity of the patterns we observe result from the non-exclusive combination of many internal and external factors and constraints that continuously recombine in a highly dynamic cascading sequence. Although dispersal has been one of the most studied topics in ecology, it remains still relatively poorly understood. Its theoretical explorations have allowed us to both learn about possible mechanisms underlying dispersal patterns, although in a *virtual world*, and translate this information on the background of empirical studies. But when in a *real world*, one of the most attractive aspects of dispersal, its dynamic

complexity determining simple patterns, has frequently limited our understanding of the whole process, mainly because real individuals in the field are difficult to study. However, empirical information is the basis on which to build sound theoretical models. To our knowledge, our results could represent an important empirical support to several predictions on the multiple and complex interactions between individual phenotypic traits and external cues, acting at various temporal and spatial scales during the different stages of dispersal (Clobert *et al.* 2009). However, because life-history traits represent another constraint to generalizations, we consider it highly probable that similar analyses on dispersal patterns of other species or group of species will increase our knowledge. The combination of the information coming from the relationships among a large set of factors acting and integrating at different spatial and temporal scales, under the perspective of heterogeneous life histories, are a fertile ground for future exploration of natal dispersal.

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