Behavioral States Help Translate Dispersal Movements into Spatial Distribution Patterns of Floaters

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ABSTRACT: Within the field of spatial ecology, it is important to study animal movements in order to better understand population dynamics. Dispersal is a nonlinear process through which different behavioral mechanisms could affect movement patterns. One of the most common approaches to analyzing the trajectories of organisms within patches is to use random-walk models to describe movement features. These models express individual movements within a specific area in terms of random-walk parameters in an effort to relate movement patterns to the distributions of organisms in space. However, only using the movement trajectories of individuals to predict the spatial spread of animal populations may not fit the complex distribution of individuals across heterogeneous environments. When we empirically tested the results from a random-walk model (a residence index) used to predict the spatial equilibrium distribution of individuals, we found that the index severely underestimated the spatial spread of dispersing individuals. We believe this is because random-walk models only account for the effects of environmental conditions on individual movements, completely overlooking the crucial influence of behavior changes over time. In the future, both aspects should be accounted for when predicting general rules of (meta)population abundance, distribution, and dynamics from patterns of animal movements.

Keywords: Bubo bubo, dispersal, ideal free distribution, movement behavior, population dynamics, residence index.

The study of animal movement patterns, which represent individual- and population-level strategies, provides a window for understanding important aspects of ecology, such as home-range characteristics and social behaviors (Blackwell 1997; Moorcroft et al. 1999), space use and species conservation (Bélisle and St. Clair 2001; Block et al. 2001), biological invasions (Morgan et al. 2004), the coexistence of competitors (Keeling and Grenfell 1997), and general population dynamics (Kareiva 1990; Turchin 1991, 1998; Hanski 1998). Animal movements vary along heterogeneous temporal and spatial scales, and such variation can influence the complex patterns of population spatial structure (Turchin 1991, 1998; Wiens et al. 1995; Armsworth and Roughgarden 2005).

The analysis of movement patterns is a relatively new topic in ecology and has focused on only a few model organisms because of the difficulty of monitoring most animals in terms of their locations and displacements over extended time periods and ranges (Hancock and Millner-Gulland 2006). This is particularly true in the case of vertebrates during natal dispersal (hereafter termed "dispersal"), which is the movement of animals from their birthplace to their breeding location(s). Recent theoretical and empirical studies (e.g., Clobert et al. 2001; Bullock et al. 2002) have shown that dispersal is a fundamental process underlying population dynamics (Turchin 1998; Skalski and Gilliam 2003). However, while empirical studies have mainly focused on differences in dispersal patterns between the sexes or among populations, landscapes, or species (Van Dyck and Baguette 2005 and references therein), simplistic assumptions of the accompanying theoretical models regarding dispersal processes lack a great deal of realism (Travis and French 2000; Goodwin 2003; Gautestad and Mysterud 2005) and do not incorporate key behaviors affecting dispersal strategies (e.g., Hanski 1994; Doebeli 1995; Travis and Dytham 1999). The concept of dispersal, therefore, represents a good example of a widespread problem in ecology, namely that researchers have some knowledge of the observable patterns but do not yet understand the underlying process (Penteriani 2008). In fact, dispersal may be considered to be one of the most important yet least understood features of ecology, population biology, and evolution (Wiens 2001).

Dispersal is frequently considered to be a fixed species-

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specific strategy, even though it is a complex process involving the behavior of individuals. It can be subdivided into three sequential but behaviorally distinct phases (Andreassen et al. 2002; Clobert et al. 2004; Bowler and Benton 2005; Baguette and Van Dyck 2007): (1) the "start," when an individual leaves its place of birth; (2) "transfer" or "wandering," when a floating individual (sensu Penteriani et al. 2006*b*) explores other areas for a variable time period before definitively settling in a new area; and (3) the "stop," when an individual settles in a more stable zone, either as a temporary settlement during the dispersal process or ascension to ownership of a breeding territory (Penteriani et al. 2005*b*, 2005*c*, 2006*a*). Little information exists on animal movements during the wandering phase, and there are almost no empirical behavioral data on this topic in the vertebrate literature (Andreassen et al. 2002).

Selection of the settlement areas, dispersal distances, rates of dispersal success, and mortality rates during dispersal largely depend on the search strategy employed by floaters upon leaving their natal habitat (Conradt et al. 2003; Leon-Cortes et al. 2003; Doerr and Doerr 2004; Conradt and Roper 2006). Moreover, animal dispersal may represent an ecological process that is essential to understanding the effects of resource distribution on population distribution and structuring. In such a context, dispersal may be used to test modeled predictions of ideal free distribution (IFD; Fretwell and Lucas 1970), which have been used to describe the links between individual behavioral strategies and population dynamics (Sutherland 1996). In fact, the absence of territorial components in the dispersal strategies and spatial distribution of individuals before they enter the reproductive portion of a population as breeders can be considered a "real" IFD, that is, a density-dependent mechanism of animal settlement in heterogeneous habitats. The IFD model is based on the preference for higher-quality areas, which decreases with population density. This will generate differential spatial distributions of individuals depending on the movement strategies employed during dispersal.

To date, IFD modeling has generally been used to examine differences in breeding performance as a function of habitat heterogeneity. However, if the spatial distribution of individuals within a population begins with their dispersal movements, it is therefore not the exclusive consequence of individual interactions within breeding territories, as originally considered in the IFD and ideal despotic distribution models of Fretwell and Lucas (1970). Accordingly, we believe that the IFD should also be considered in terms of dispersal and dispersing individuals as a potential new approach to the study of animal population distribution.

Several approaches have been used in the analysis and modeling of animal displacement in space (see review in Turchin 1998). Although random-walk models and their diffusion approximations can be used to effectively predict the pattern of animal distribution over the short term, they tend to fail when longer periods are taken into consideration, potentially because these models fail to account for the influences of individual behaviors (Firle et al. 1998; Morales et al. 2004) and different habitat conditions (Jonsen and Taylor 2000; Frair et al. 2005) on movement patterns. In particular, on the basis of the ideas developed by Patlak (1953*a*, 1953*b*), the residence index is expressed in terms of random-walk parameters and can be used to generate predictions about the equilibrium distribution of organisms in specific areas. By measuring the time that elapses between when an individual enters and abandons a unit area, the residence index predicts that conspecific density within different patches follows an IFD, being positively related to the average time that organisms spend in the unit area mediated by the local availability of food resources (i.e., a continuous reaction-diffusion process; Okubo 1980; see also Bengtsson et al. 2002; Hannunen 2005). Because residence indices and density ratios in different patches are considered to be directly proportional, the highest densities of individuals should be found in areas where these individuals spend the most time. As an end result, the range of values of the residence index can be used to predict the equilibrium distribution of individuals on the basis of their movements between the different patches in an environment.

Here, we seek to characterize behavior during the wandering (searching) phase through analysis of the movement length, duration, and turning angles of radio-tagged eagle owls (*Bubo bubo*; for more details on the species, see Penteriani et al. 2005*a*). Although movement paths have been quantified in previous reports (Turchin 1991; Wiens et al. 1995), few prior studies have examined the behavioral patterns of animals moving over long distances (Morales et al. 2004; Frair et al. 2005). We then use the residence index of Turchin (1991) to compare the accuracy and realism of spatial-spread predictions obtained from random-walk models.

Material and Methods

Radio-Tracking Procedures

A radio-tracking study of eagle owl dispersal was started in 2003 in Sierra Norte (Sierra Morena massif), 20 km north of Seville, in southwestern Spain (see Penteriani et al. 2005*a*). Thirty-three owlets from 11 nest sites (primarily ground nests) were radio tagged when they were approximately 35 days old, 5–10 days prior to onset of fledging (2003: $n = 6$; 2004: $n = 10$; 2005: $n = 17$). Each bird was fitted with a 30-g harness-mounted backpack (Wareham

BH20 5AJ; Biotrack, Dorset, UK) and was followed from its natal nest until either death of the animal or failure of the battery transmitter (∼1.5–2 years). This species can first reproduce at 10–12 months of age under optimal conditions (i.e., an empty territory and a mate), meaning that the duration of radio tracking was relevant to the potential age of first reproduction. The locations of radio-marked individuals were determined by triangulation using 3-element handheld Yagi antennas (Biotrack) with Stabo portable receivers (XR-100, Osaka, Japan). The exact position of each bird was recorded weekly, typically when the owls were at their diurnal roosts. Topographical 1 : 25,000 maps and GPS were used to plot the locales, and triangulations were analyzed using the ArcView 3.2 GIS software.

Analysis of Movement Paths and Residence Index

In order to describe behaviors during the wandering phase, we first determined the start and stop of dispersal. 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 distances between the whole set of locations and the nest, with the latter value representing the global mean distance covered by each individual during the dispersal period. Prior to dispersal, the distance from the nest to each successive location should fluctuate around a low value because juveniles remain in the parental home range during this period. Following Palomares et al. (2000), we defined dispersal as starting when the distance of each location from the nest became larger than the global mean distance traveled to the nest (fig. 1A), that is, when the distance of each location from the nest started progressively increasing rather than fluctuating around a low value. The stop of dispersal for each individual was determined by plotting the length of successive moves against the average of the beeline distance they traveled through. We considered that owls reached the stop phase when the distances became smaller than the average distances of previous moves traveled by each dispersing owl (fig. 1B). Notably, several stop phases could occur during the dispersal process, which ended if/when the floater occupied a breeding territory. For the scope of this work, and following Andreassen et al. (2002), the stop phase was defined as settlement of a floating owl in a stable settlement area.

Our second step was to identify behaviors that differed among the individuals in the wandering phase. Data sets comprising the observed radio locations of each floater were separated into sequential monthlong blocks (this period length was arbitrarily chosen following Palomares et al. [2000]). We successively measured the total distances traveled between all locations in each of these blocks and calculated both the net distance traveled in each block and the net distance traveled from each block to the natal nest. We then used the relationship between the total and net distances traveled that were recorded during owl dispersal movements (fig. 2A) to generate a threshold that clearly separated all paths into two different behavioral states: (1) the "intensive behavioral state," when the observed total distance traveled was higher than the observed net distance traveled, indicating that the individual was moving within an established area (fig. 2A, panel a); and (2) the "extensive behavioral state," when the observed total distance traveled fluctuated around the observed net distance traveled from locations in each block or decreased below the net distance from the last location in each block to the nest, indicating that the owl crossed several different areas (fig. 2A, panel b). We estimated the minimum convex polygon to determine the overlap between individuals in each behavioral state and calculated the mean distance between the centers of the areas described by the two behavioral states. Moreover, to examine the relationships between movements and behavioral states, we analyzed the distributions of various movement variables (mean lengths, durations, and the mean cosine of turning angles between successive locations) for each behavioral state. An intensive behavioral state was defined by both small-scale movements of short lengths and many reversals and large turning angles, whereas an extensive behavioral state was characterized by longer movements and a low rate of turns, with angles smaller than those in the intensive behavioral state (Zollner and Lima 1999).

Finally, we used the residence index to compare the predicted versus real spatial distribution of dispersing owls. Because the paths describing the two above-cited behavioral states delineated two spatially segregated consecutive areas, we estimated several parameters for each one, namely: (1) the mean movement features, such as the mean move length ($\mu_j = 1/n_j \sum_{i=1}^{n_j} l_{ij}$), the mean squared move length ($M_j = 1/n_j \sum_{i=1}^{n_j} l_{ij}^2$), the mean move duration ($\tau_j = 1/n_j \sum_{i=1}^{n_j} t_{ij}$), and the mean cosine of turning angle ($\psi_j = 1/n_j \sum_{i=1}^{n_j} \cos \theta_{ij}$), where n_j is the total number of moves recorded for all paths in group j; (2) the quantities $\gamma = M/\mu^2$ and $\varphi_j = \gamma + (2 - \gamma)\psi_j$ to obtain the mean values of γ and φ necessary for index computation; and (3) the exponent $\alpha = 2\gamma(\mu_2 - \mu_1)/(2 - \gamma)(\varphi_1\mu_2 - \varphi_2\mu_1)$, which was necessary to obtain the Turchin's residence index (1991):

$$l_j = \tau_j \varphi_j^{\alpha} \mu_j^{-[(2-2\gamma)/(2-\gamma)+\alpha]}.$$

We computed the ratio of the residence indices calculated for the two areas delimited by the different behavioral states to obtain the predicted ratio (i.e., the distribution of organisms expected by the model). Then, we estimated
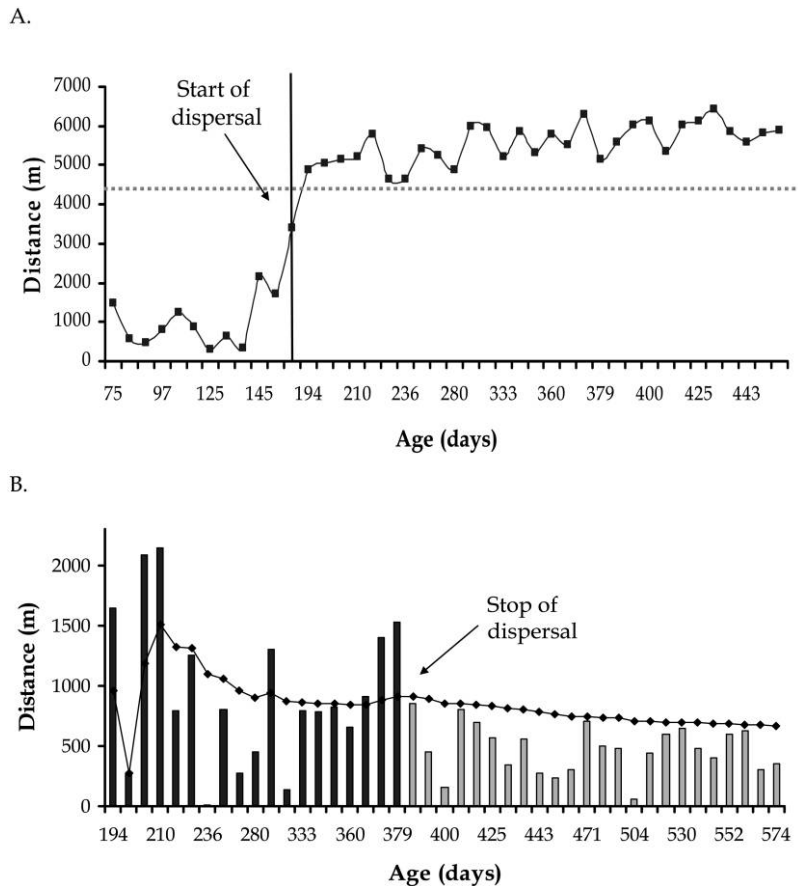
A.

B.

Figure 1: *A*, Analytical determination of the beginning of dispersal. *Black line*, the distances (meters) between successive moves. The reference line (*dotted line*) indicates the average distance covered by a dispersing individual to its nest. An individual was defined as having started dispersal when all recorded move distances were superior to the mean of all movements. *B*, Analytical determination of the stop of dispersal movements (see "Material and Methods" for more information). *Dark gray bars*, movement distances (meters) when owls were searching for a stable settlement area or breeding territory; *light gray bars*, the distances traveled after the stop of dispersal movements. The reference line (*black line*) indicates the average distance of the previous step covered by an individual. We designated that individuals found a stable settlement area or breeding territory when all recorded move distances were below the mean of all previous movements.

the observed distribution of floaters in the spatially segregated consecutive areas delimited by the two behavioral states, and we used these estimations to calculate the observed ratio. As explained above, the ratio of residence indices in different patches should be directly related to the ratio of densities in the patches (Turchin 1991).

Results

Dispersal Patterns and Movement Characteristics

Most juveniles started their dispersal at the end of August at a mean ($\pm$SD) age of 170 ± 20.51 days (range = 131–232 days). Although there was a high degree of in-

dividual variation, 30% of the eagle owls shifted from the wandering phase to the stop phase of dispersal (i.e., found a stable settlement area) in the middle of the following March at a mean ($\pm$SD) age of 395 ± 109.86 days (range = 181–640 days).

During the wandering phase, one-half of the floating owls ($n = 17$; 52% of all tagged owls) showed a biphasic movement behavior, that is, they switched from the intensive behavioral state typical of early dispersal to the extensive behavioral state (fig. 2). The time spent in the intensive behavioral state (mean $\pm$ SD $= 2.9 \pm 0.8$ months; range $= 2$–4 months) versus the extensive behavioral state (mean $\pm$ SD $= 9.1 \pm 4.7$ months; range $= 1$–19 months) varied significantly ($t = 8.9$, df $= 79$, $P < .001$; t-test). Eleven of the owls (33% of all
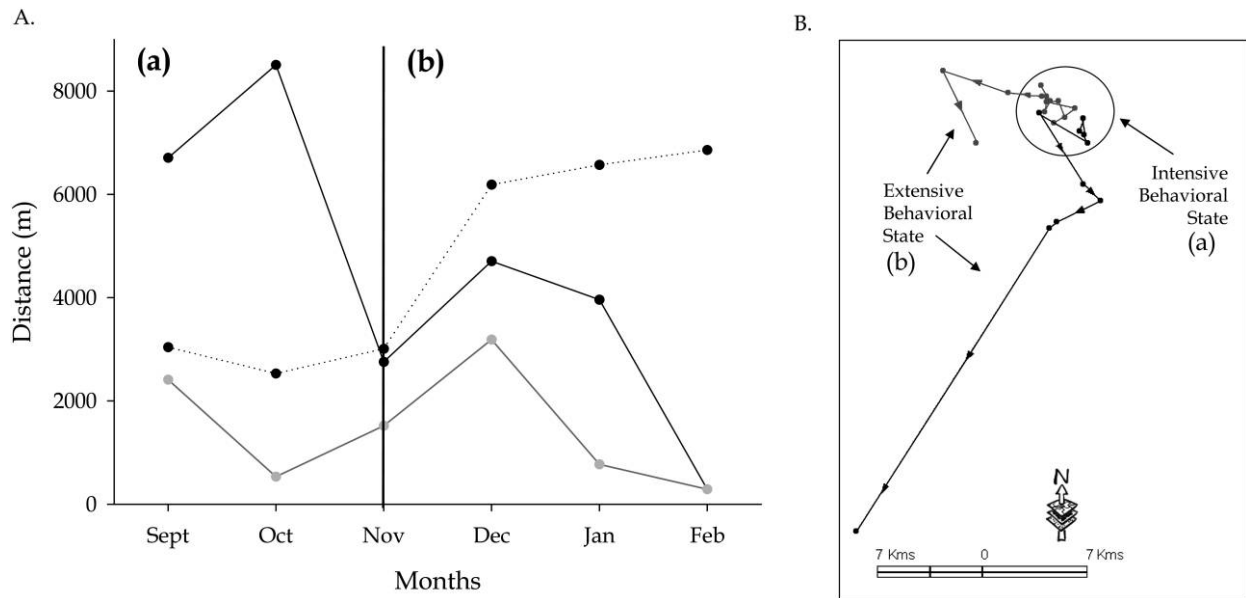
Figure 2: *A*, Analytical determination of the different behavioral states in a dispersing owl that was radio tracked during the wandering phase of dispersal. Reference lines indicate the total distance between all locations in each monthlong block (*solid black line*), the net distance in each monthlong block (*gray line*), and the net distance from each block to the nest (*dotted black line*). A floating owl was defined as being in an intensive behavioral state (*a*) when the observed total distance traveled was higher than the observed net distances traveled and in an extensive behavioral state (*b*) when the total distance traveled fluctuated around the observed net distance traveled from a location in each block or decreased below the net distance traveled from each block to the nest. *B*, Movement paths of a floating owl showing a biphasic movement behavior during the wandering phase (see the introduction to this article for more details). At the beginning of dispersal, displacements generally covered short distances and showed a high tendency for directional reversal. After a few weeks, floaters changed their movement behavior (*b*) and began showing straighter paths (i.e., extensive behavioral state). During this latter state, the areas used by dispersing owls did not overlap; the settlement areas were clearly separate from one another.

tagged owls) showed only the intensive behavioral state, whereas five individuals (15%) showed only the extensive behavioral state.

During the intensive behavioral state, the movement behavior of dispersing owls was characterized by small-scale movements along tortuous paths, with the majority of turning angles concentrated around $166.5° ± 12.5°$ (circular mean ± 95% confidence interval [CI]; Fisher 1993; Rayleigh's test of uniformity, $P < .001$; fig. 3*A*), indicating a high tendency to reverse direction. In this behavioral state, displacements generally occurred over short distances, showing zero modal movement lengths and a fat-tailed distribution (fig. 4), which indicates that most movements were close to 0. When floaters exhibited this behavior, their temporal settlement areas overlapped broadly (34% of the total area used during the intensive phase; fig. 2*B*). In contrast, owls in the extensive behavioral state followed straight pathways, with turning angles concentrated around $121.8° ± 31.6°$ (circular mean ± 95% CI; Rayleigh's test of uniformity, $P < .001$; fig. 3*B*). This state was described by a nonzero mode characteristic of a longer step-length distribution (fig. 4) and showed no

overlap of the settlement areas (15% of the total area used during the extensive phase; fig. 2*B*). The distributions of turning angles during the intensive and extensive behavioral states were significantly different ($Z = 23.77$, $P < .05$; Watson's two-sample test with ties; Zar 1999).

Comparison of Observed Distributions versus Those Predicted by the Residence Index

Because the settlement areas used during the two behavioral states were consecutively separated in space (mean distance ± SD = $4,036 ± 2,258$ m; range = 1,048–7,589 m; fig. 2*B*), we measured the observed and predicted spatial distributions of owls in each. The observed density shifted from 5 owls/10 km^2 (intensive behavioral state) to 1 owl/10 km^2 (extensive behavioral state), yielding an observed ratio of 0.2 between the extensive versus intensive phases. The predicted ratio of residence indices calculated for the two spatially segregated areas was 0.003, indicating that the residence index significantly underpredicted the density of individuals sharing the same settlement areas

for the extensive behavioral state (error $= -98\%$; table 1).

Discussion

Dispersal is mainly the result of "routine" movements associated with daily activities and "special" movements designed for net displacement away from the previous location. These groups of movements are clearly distinguishable from one another (Van Dyck and Baguette 2005) and may contribute to interpopulation movements. Understanding how animals make decisions regarding movement during the wandering phase represents an important step in predicting the trajectories of population dynamics (Hanski 1998, 1999; Clobert et al. 2001; Murrell et al. 2002). Because decision rules shaped by natural selection at the individual level are responsible for population-level dynamics (Folse et al. 1989), animal movement does not merely mirror behavioral choices but rather is the outcome of individuals following a strategy.

Our present analysis of the movement paths of juvenile eagle owls during the wandering phase of dispersal revealed different movement patterns, which engender important consequences in relation to (*a*) proximate factors, such as the spatial scale of displacements, the configuration of trajectories, the individual responses to conspecifics, and

individual-specific types of movement (see also Van Dyck and Baguette 2005); and (*b*) the intrinsic properties of the whole population resulting from the individual dynamics and fates across dispersal. Within our floating population, some individuals showed only a single movement behavior; 33% of the tagged owls showed only the intensive behavioral state and 15% showed only the extensive behavioral state. Within the possible range of behavioral choices, personality extremes in vertebrates (Dingemanse et al. 2003; Sih et al. 2004; Boon et al. 2007) were explained by Baguette and Van Dyck (2007) as reflecting the "shyness-boldness" dichotomy. Bold individuals are aggressive, are relatively insensitive to external stimuli, and are able to make rapid decisions, whereas shy individuals are cautious, are sensitive to external situations, and tend to adapt to their environment. Two prior empirical studies found that bolder individuals dispersed farther than shyer individuals (Fraser et al. 2001; Dingemanse et al. 2003). In our scenario, the bold individuals could be considered to be those owls showing a permanently extensive behavioral state, with larger and straighter movement trajectories, whereas the shy individuals could be seen as those exclusively showing the intensive behavioral state, with short movements and frequent reversals of direction.

Undoubtedly, other factors in addition to the bold-shy personality types are involved in determining dispersal
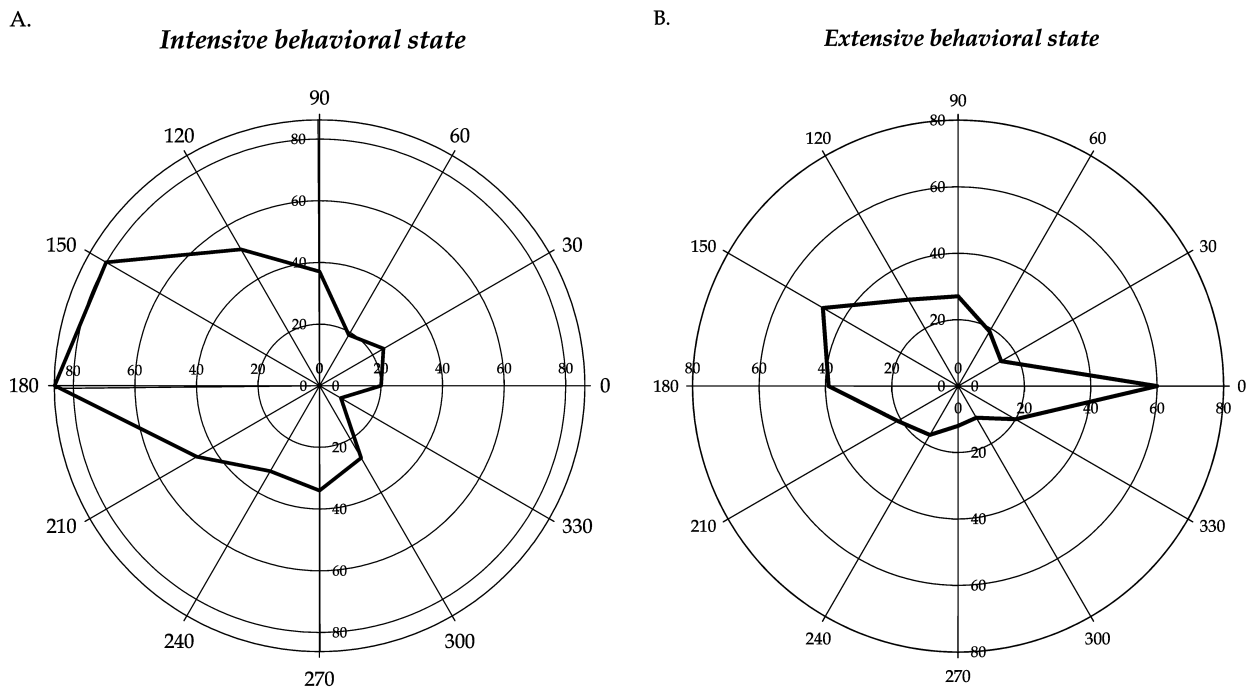

A.
Intensive behavioral state

B.
Extensive behavioral state

Figure 3: Proportions of turning angles shown by dispersing eagle owls in the two behavioral states: the intensive behavioral state (*A*) is characterized by large turning angles, whereas owls in the extensive behavioral state (*B*) show smaller turning angles.

movement. These might include various aspects of morphology, physiology, and behavior (see Dingemanse et al. 2003; Sih et al. 2004), the type of exploratory movement, and species-dependent and dispersal cause–dependent settlement choices. However, our finding that different proportions of individuals follow one of the two identified dispersal strategies may provide insight that animal population characteristics and viability may vary on the basis of the proportion of individuals following alternative strategies (i.e., showing different movement paths). For example, the biphasic strategy shown by one-half of our dispersing owls may be seen as evidence for intraspecific avoidance. Fifty-two percent of the floaters switched from the intensive behavioral state, which was characterized by high conspecific overlap, to the extensive behavioral state, wherein owls were relatively segregated and conspecific density was low. Thus, our findings are consistent with the notion that conditions of high conspecific density may prompt individuals of a territorial species to locate their own patches as quickly as possible, which can best be achieved by a nearly straight search (Zollner and Lima 1999), as with those individuals observed to be in the extensive behavioral state. From an adaptative perspective, it makes sense for individuals to adjust their movement behaviors according to current conditions. Thus, an individual might shift its behavioral choice from shy to bold given a change in external conditions.

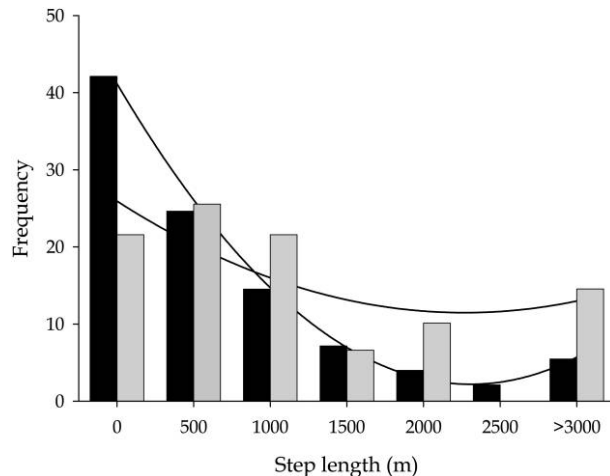The causes, consequences, costs, and benefits of dis-

Figure 4: Distribution of dispersing distances of eagle owls (represented by frequencies of traveled distances and their fitted curves) during the two different behavioral states identified during dispersal. *Black bars*, frequency of distances traveled in the intensive behavioral state, with short step lengths and a mode close to 0. The extensive behavioral state (*gray bars*) is characterized by longer step lengths and a nonzero modal distribution.

persal can vary not only among species (Bowler and Benton 2005), but also among individuals, generally yielding a plastic dispersal strategy. In our opinion, the between-behavior shifts observed herein may also correspond to the ability of a given individual to react to their actual experiences as they move (Dall et al. 2005). Across the dynamic process of dispersal, the diverse interactions that occur at the individual-individual and individual-habitat levels can be expected to continuously shape the behavioral responses of individuals. Notably, we were able to demonstrate that, within the same population, individuals can: (1) exhibit different behavioral personality types (i.e., bold or shy), which has more often been associated with differences between populations or species (Sih et al. 2004); and (2) change their behavioral personality type depending on social and environmental conditions. The former finding is pertinent within the limited behavioral plasticity that is implicit in the notion of behavioral personality types (Sih et al. 2004; Dall et al. 2005). Although the adaptive importance of behavioral personality typing is its stability over long periods during the life of an individual (Sih et al. 2004), we can hypothesize that the experiences accumulated by an individual moving across unfamiliar territories during dispersal may influence the individual's behavioral personality type.

Our empirical approach clearly supports the proposal of Van Dyck and Baguette (2005), who wrote that because no single strategy performs best in all conditions, dispersal can be considered to be a dimorphic trait wherein some sedentary individuals restrict their movements to intensive/routine types, whereas more dispersive individuals perform extensive movements. More generally, our results are consistent with recent empirical and theoretical studies that indicate that dispersal cannot be collapsed into a single parameter because it is composed of interdependent stages that may display different condition dependencies (Clobert et al. 2004; Bowler and Benton 2005; Baguette and Van Dyck 2007). Accumulating field studies, such as this one, increasingly suggest that the dispersal process is both dynamic and complex (Gautestad and Mysterud 2005), with different phases that may be strictly dependent on behavioral decision making.

The residence index states that a population whose redistribution obeys the Fokker-Planck equation should (*a*) have an equal ratio of individual densities in different patches, independent of the species, and (*b*) always match the environmental boundary conditions, such as the spatial distribution of resources (Turchin 1991, 1998). Thus, if the spatial distribution of individuals is the result of random-walk movements, the population distribution is in a state of IFD. However, when we applied the residence index to our study population, we found that this index severely underestimated the real distribution of individuals

Table 1: Estimated correlated random-walk parameters and comparison between the predicted and the observed models, as calculated by the residence index (Turchin 1991)

Behavioral state	μ	τ	ψ	γ	Observed ratio	Predicted ratio	Error (%)
Intensive	980	10	−.4	1.8	.19	.003	−98.4
Extensive	1,760	13.2	−.2	3.0			

Note: The observed ratio, defined as that between the numbers of dispersing owls recorded in the two spatially segregated areas delimited by the two behavioral states, represents the real spatial distribution of floaters. The predicted ratio was defined as that between the model-estimated residence indices of the two spatially segregated areas. Error = 100%(predicted ratio − observed ratio)/observed ratio. The units of μ and τ represent meters and days, respectively; μ = mean step length; τ = mean duration; ψ = mean cosine of turning angles; γ = coefficient between the mean squared length and the squared mean length.

in space, even though the final spatial distribution of individuals continued to fit an IFD. This is a crucial point, because the assumptions and constraints of the residence index are not necessary to predict population distribution under an IFD. In fact, following the main IFD predictions, owls seemed to move from a more aggregated distribution to a looser distribution, with no apparent constraints limiting their spatial explorations; they were allowed a free mobility that would ideally distribute them to various areas, thereby maximizing their fitness. Although our results suggest that an IFD-dependent spatial distribution of individuals may also arise when some of the basic assumptions of this model are violated, the opposite is generally a more common scenario. Individual patterns and population-distribution patterns may fail to follow an IFD when, for example: (*a*) extreme or more complex behaviors arise as a consequence of peculiar landscape configurations and compositions (Westerberg and Wennergren 2003); (*b*) individuals are not of equal competitive abilities and do not have perfect (i.e., "ideal") information on the availability of resources (Hugie and Grand 1998 and references therein; Humphries et al. 2001; but see Sutherland and Parker 1985); (*c*) individuals experience higher costs of movement among given patches (Levin et al. 1984 and references therein); and (*d*) small numbers of individuals switch between locations because of resource competition (Houston and McNamara 1987).

Notably, a given species may show both free and despotic distributions, depending on the status of its individuals (floater vs. breeder). During dispersal, owls are not territorial and may homogeneously distribute themselves in space, constrained only by the distribution of local resources. However, when individuals cease being floaters and become territory owners within the breeding population, their distribution becomes constrained by territoriality, following a within-population, despotic spatial redistribution.

Contrary to the index predictions, conspecific density within different patches was negatively related to the average time that individuals spent in a unit area. The highest densities of floating owls were found in areas where in-

dividuals spent shorter portions of their dispersal time, as revealed by the characteristics of their movements (i.e., the intensive behavioral state). Generally, diffusion models consider a passive strategy for dispersal, including local population growth but not density dependence or conspecific interferences, even though the latter factors are fundamental determinants of the spatial distribution of animals (Hancock and Millner-Gulland 2006; Cote and Clobert 2007). Because high population densities increase intraspecific competition for local resources, individual interactions can be greatly reduced by repulsive movements, which are typically biased in the direction of a decreasing population gradient (Rosenzweig 1991; Turchin 1998). Interestingly, our results showed an active strategy for dispersal, with balanced exchanges of floaters during the wandering phase in an inverse relation to individual densities (Doncaster et al. 1997). Dispersal movement decisions based on density dependence can reinforce the connection between populations and can homogenize population sizes; this is a fundamental factor that may make the spatial distribution of animal populations tend toward the IFD (Doncaster et al. 1997; Cote and Clobert 2007).

The random-walk model has been validated for a variety of small, passive organisms; however, it is debatable whether this approach is suitable for describing more complex situations or species, especially the dispersal behavior of individuals. Random-walk models assume that animals move with continuous but constant parameters over time; in the residence index calculation, the movement parameter γ is approximately the same in different patches (Turchin 1991). However, we found that the movement parameter γ varied significantly between the two patches we considered, probably as a consequence of changes in individual movement behavior observed during the wandering phase. When γ varies, the model predictions underestimate the degree of aggregation in the patch with the higher residence index. This possible violation to the assumption of the residence index was previously noted by Turchin (1991), who highlighted the need to extend the formula to cover cases where γ varies in space (e.g., when organisms change movement behavior over time).

Nevertheless, it is debatable whether the effect of dispersal behavior on the viability of spatially structured populations can be adequately described by a simple formula. When applied to our scenario, the residence index and random-walk theoretical models appear to fail because they only account for the effects of environmental conditions on individual movements and completely overlook the crucial influence of changes in behavioral state over time.

Our finding, that the random-walk model breaks down at the individual level, has implications for population-dynamic modeling approaches, suggesting that the future inclusion of individual behaviors could increase the predictive value of models incorporating animal movements. Although animal behavior is strongly influenced by landscape structure (Wiens 1989; Cresswell 1997), it may also be influenced by temporal scale. As time passes, behaviors other than locomotion may play increasingly important roles in influencing movement patterns. Consequently, analysis of movement behaviors at detailed temporal scales may also help us to understand how individuals respond to spatial composition (McIntyre and Wiens 1999; With et al. 1999; Morales and Ellner 2002; Nams 2005). Furthermore, the application of real, accurate information about floater dispersal, distribution, and abundance to ecological modeling of complex processes based on simple assumptions (i.e., random walks and diffusion processes) could facilitate the development of more realistic frameworks that reflect ecological realism. Gautestad and Mysterud (2005) noted that some aspects of the behavioral ecology of real animals defy the broad applicability of the classic random-walk approximations. These authors found that (*a*) the establishment of a home range implies nonrandom, memory-dependent revisiting of formerly visited areas (site fidelity and familiarity), and (*b*) such tactical and strategic habitat use may lead to the emergence of complex, multiscaled individual behaviors that will affect the efficacy of (meta)population modeling. Following the challenge of Gautestad and Mysterud (2005) to express population kinetics (i.e., a dynamic description of the factors underlying population dispersal and the consequential spatial distribution of individuals) in a multiscaled processing framework, our data on behavioral shifts in movement patterns add novel empirical support to new theories. In the context of an individual's spatial memory capacity influencing strategic displacements, our findings indicate that more realistic models on animal spatial distribution and abundance should include the possibility of changes in an organism's behavior during its lifetime. Thus, our results highlight the importance of understanding how animals make decisions regarding movements and the need to account for the effect of temporal variations in animal behavior. The application of these recommendations to future models will be an important step toward increasing biological realism when modeling dispersal.

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