Estudio de la Dispersión Natal de una Especie de Larga Vida
Análisis de los Patrones de Movimiento Animal

María del Mar Delgado
Tesis Doctoral
2008
Estudio de la Dispersión Natal de
una Especie de larga Vida.
Análisis de los patrones de Movimiento Animal

Exploring Natal Dispersal under the
Perspective of Animal Movement
Analysis.
A Behavioural Study on the Dispersal of a Long-lived Species

Memoria presentada por María del Mar Delgado Sánchez,
Licenciada en Biología para optar al título de Doctor en Biología
por la Universidad de Sevilla

Fdo. María del Mar Delgado Sánchez

Director: Tutor:

Dr. Vincenzo Penteriani
Estación Biológica de Doñana (CSIC)

Lourdes Encina
Universidad de Sevilla
Doy mi autorización a la Biblioteca de esta Facultad para que mi Tesis Doctoral:

"FUNDIO DE LA DISPERSIÓN NITAR DE UNA ESPECIE DE LAGRA VIVA. ANÁLISIS DE LAS RELACIONES DE MOVIMIENTO ANIMAL"

Sea consultada, según la modalidad/es indicadas:

- [X] Consulta en depósito.
- [X] Préstamo interbibliotecario.
- Reproducción parcial.
- Reproducción total.
- Tipo de usuarios.
- Otros términos.

Firmado: MARÍA DE LA MAR DE AGUADO SÁNCHEZ

Sevilla, a ___ de ___ de ___ de 2003
Exploring Natal Dispersal under the Perspective of Animal Movement Analysis.

A Behavioural Study on the Dispersal of a Long-lived Species

María del Mar Delgado

PhD Thesis

Sevilla, 2008
# CONTENTS

1 Introduction

1.1 The dynamic of the dispersal process and animal movements

1.2 Floaters, the Light and the Dark Side of Animal Populations

2 Methodological considerations

3 How Fledglings Explore Surroundings from Fledging to Dispersal?

4 Behavioural States Help Translate Dispersal Movements into Spatial Distribution Patterns of Floaters

5 Key Factors Driving Animal Movements

6 Routes Towards Animal Dispersal: Extending the Graph-Theory Approach

7 Dispersal Behavioural Tactics, Physiological and Environmental Factors Determine Settlement Patterns

8 Levels of Familiarity through Natal Dispersal

9 Conclusions

Resúmenes de los Capítulos

Agradecimientos

Referentes
Introduction

1.1
The dynamic of the dispersal process and animal movements
During the last 30 years, the study of animal populations has shifted from a less complex science, mainly based on the breeding portion of single units or populations, to a more refined discipline which explicitly recognizes that populations are composed of multiple fractions (the metapopulations), whose complex dynamics and individual behaviours determine their characteristics and fates.

At the beginning, the most crucial mechanisms regulating animal populations were intrinsic properties of breeders only. On the one hand, we were exclusively focusing on the ecology of those individuals that reproduce and, on the other, when immigration by natal dispersal was considered, nongbreeding individuals were purely considered as a numeric entity without identity, whose main interest was their immigration rates. The nineties represent a very fertile decade of explorations on animal populations, revealing to us part of the previously undetected ecological complexity of populations. The Metapopulation Ecology by Hanski (1999) offers an example of the complexity of animal populations by analysing them as a complex unit composed of different pieces, the metapopulations. Coupled with the fractioning of the original concept of a population as a single unit, nongbreeders started then to acquire their legitimate, important role in the equilibrium of (meta)populations. Through simply moving from one location to another, the process of natal dispersal (i.e. the movements between the natal area and the area where breeding first takes place; Clobert et al. 2001) and dispersing individuals have become crucial elements regulating population dynamics, trajectories, spatiotemporal distributions and stability, as well as their likelihood of extinction.

However, despite its importance, the dispersal process still represents a significant gap in our understanding of animal ecology (Doerr and Doerr 2005). This is very surprising, given the amazing number of studies on this topic and the huge amount of literature that has been written on the subject. For example, by simply introducing the term dispersal in one of the most important and complete tables of bibliographic information from the scientific world's (the Current Contents Connect) we can find more than 20000 studies on such topic. So, where is the origin of the dispersal "black hole", i.e. why do we still
have an incomplete understanding of dispersal? As remarked by several authors, the combination of the lack of empirical data (especially on vertebrate species) with the difficulties of considering dispersal as a complex, dynamic process, could be one of the main reasons for this setback. Moreover, during the last decades, dispersal studies have mainly focused on the cues used in the first steps (i.e. when individuals take the decision to leave their natal site) and the last stages (i.e. when dispersing select a stable settlement area), while little is still unknown about the intermediate, wandering phase.

In spite of these constraints, a greater understanding of the dispersal process has been achieved by approaching it under the perspective of the animal movement patterns. In fact, several novel facts were highlighted on the: (a) causes and consequences of dispersal (Clobert et al. 2001); (b) variation in time and in space of its costs and benefits (Deno et al. 1989, Waser et al. 1994); (c) beneficial and detrimental effects of dispersal patterns on the persistence of spatially structured systems (Hanski 1999, Heino 1997, Penteriani 2008); as well as (d) on the behavioural basis underlying individual decisions during such process (Bowler & Benton 2003, Delgado & Penteriani, in revision). Several approaches have been used in the analysis and modelling of animal displacement in space. Initially, diffusion theory (Okubo 1980, Kareiva 1983, Andow 1990) was useful in describing animal movement patterns, providing a natural spatial extension of Lotka-Volterra models. Ordinary (i.e. Fickian) diffusion models assume that particles (e.g. biological organisms) move independently and execute a simple random walk. A theoretical diffusion models largely used to evaluate movement pathways have been the correlated and biased random walk, which assume independent distributions of move lengths and move angles having a net directional bias (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, McCulloch and Cain 1989, Bergman et al. 2000, Bartumeus et al. 2005). Although random walk models (and their diffusion approximations) have been particularly useful in situations where movement behaviours were difficult to observe and can effectively predict the pattern of animal distribution on short time scales (Turchin 1998), they also showed important limitations (Pialaik 1998, Turchin 1989, 1991, Johnson et al. 1992, Holmes 1993). For example, random walk models tend to fail when longer time horizons are taken
into consideration, mainly due to not considering the occurrence of behavioural changes during the life-span of an individual and their influences on movement patterns (Firle et al. 1998, Morales et al. 2006), as well as the possible changes of movement patterns when different habitat conditions are encountered (Jonsen and Taylor 2000, Faip et al. 2005). To solve some of the problems of diffusion models (mainly directional biases during movement), more recent diffusion models have incorporated directed movements, i.e. patterns of moves characterized by persistence of direction and variations in the medium that the animal is travelling in (e.g. net bias, Okubo 1980; prey taxis; Banks et al. 1987; or advection terms, Turchin 1989). Lately, because movement pathways are strongly influenced by environmental structures, the importance of spatial scale has been emphasized by these studies. Therefore, models on animal movements have been extended to heterogeneous landscapes by simulating movements in percolation networks (i.e. the probabilities of movements is a direct function of landscape patterns, Gardner et al. 1989, Johnson et al. 1992). More recently, several authors have applied fractal methods (Wiens et al. 1995, Nams 1996, Bascompte and Vilá 1997, Nams and Bourgeois 2004, Doerr and Doerr 2004) and Lévy walks (Bartumeus et al. 2005) to assess organism responses to spatial heterogeneity.

Although several empirical supports exist for some of these models, they generally come from experimental studies or data on short-term movements of invertebrates, which may be expected to show less complexity and variability than dispersal in vertebrates moving through a heterogeneous and complex natural world. When considering an animal searching for suitable habitat patches while dispersing through a matrix landscape, we have to take into account that, during the travel from the natal to the breeding patch, the movements will be influenced by, for example, matrix habitat variability, density, competition, predation and food availability. All these factors may generate different movement behaviours and search strategies. Moreover, these factors cannot be considered independently of the potential effect of animal cognitive abilities (With & Crist 1995, With et al. 1997, 1999) and learning capabilities (Stamps & Krishnan 1999). Animals can use significant powers of spatial memory and learning to move through their landscape as efficiently as possible (Saarenmaa et al. 1988, Vuilleumier &
Perrin 2006). That is, animal movement ability and therefore, the dispersal process, is the result of multiple complex interactions of external and internal factors acting at various spatial and temporal scales.

On the one hand, my personal curiosities towards the complex ‘world’ of animal dispersal and the different behavioural strategies have guided my scientific interest towards such a process. On the other, I had been always fascinated by those species and systems that are less commonly studied and that, consequently, may also offer new and unexpected insights into ecological questions, giving us the possibility to find novel results. As an ending result, in the course of this thesis my co-authors and I have investigated the effects of the landscape’s characteristics, individual fitness and the organism’s cognitive and learning abilities on the dispersal movement behaviours of a long-lived species, the eagle owl (Bubo bubo). I have started my personal voyage across dispersal and the main component of this process, the floaters, with a detailed revision in which I resumed and discussed the different effects that floaters can have on the structure, dynamics and persistence of bird populations (Introduction 1.2). Because the potential influence that the postfledging dependence period, an intensive phase of experience and learning, may have on individuals’ behavioural strategies during the later crucial dispersal period, I have devoted the first episode (chapter 3) to describing and analysing the patterns of movement during this phase. Subsequently, I become wrapped up in the dispersal process. First of all, I characterised the behaviour during the wandering (searching) phase of dispersal through the analysis of movement characteristics. Keeping in mind the complexity of behavioural dispersal strategies, I compared the accuracy and realism of the predictions of random walk models on the spatial spread of animal populations (chapter 4). The following chapter has been especially focused on the effect of the interaction between the surrounding environment and features of individual animals (chapter 5). As a natural consequence of such a direction in my research, I was especially intrigued by the dispersal spatial network. I analysed it by comparing the real dispersal routes with optimized and randomized routes in order to gain information on the movement dispersal strategies of juveniles and the importance of connectivity on the dispersal process (Chapter 6). Because the individual variations in movement behaviour, the costs of dispersal and landscape structure can lead to variation in settlement patterns, I also explored (chapter 7) when, where and
how individuals search for settlement areas. Finally, I investigated how the learning abilities and the increase of the level of familiarity with the surroundings can cause a radical change in the movement patterns of dispersing individuals (chapter 8).

This thesis is based on 7 original manuscripts, all of them currently under review (first and second revisions) in SCI journals. I have contributed to the conception and planning of the studies, the acquisition, analyses and interpretation of data, and writing of all the articles.
Introduction

1.2
Floaters, the Light and the Dark Side of Animal Populations

by

Vincenzo Penteriani, Miguel Ferrer & María del Mar Delgado
Floaters are dispersing individuals able to enter as breeders in the reproductive population when a breeding territory or a potential mate (i.e. an owner of a suitable breeding territory) becomes available. In a time in which the study of animal populations has shifted from a fairly simple science, mainly focused on breeding populations, to a more complex and refined discipline based on metapopulation sub-units (breeders and floaters), we resume and discuss here the different effects that the floater pools can have on the structure, dynamics and persistence of bird populations. Across our voyage within the underworld of floaters, we will discover that they are an indispensable, but sometimes hostile, component of each bird population. Under some natural scenarios, floaters are able to shift from secretive presences, contributing to reduce the extinction risk of a given (meta)population, to active intruders that may seriously alter the breeding performance and the behavioural traits of territory owners.

**KEYWORDS**: animal population, dispersal, floater, metapopulation, non-breeding
Over the past 30 years, the study of animal populations has shifted from a fairly simple science, mainly comprising analysis of the breeding portion of single units or populations, to a more complex and refined discipline that evolved as researchers recognized that populations are composed of multiple fractions (metapopulations) with characteristics and fates that are determined by complex dynamics and individual behaviours.

The early studies, which assumed that the most crucial mechanisms responsible for regulating animal populations were the intrinsic properties of breeders, exclusively focused on the ecology of reproductive individuals. When immigration by natal dispersal was considered, non-breeding individuals were typically included as an unidentified numeric entity reflecting only the immigration rate. Dispersing individuals were reduced to the level of 'animal seeds' that had lost any spatiotemporal contact with the original population. This centralised effort to capture the dynamics of breeding populations severely limited our capacity to examine the effects of non-breeders on populations.

In the 1990s, however, numerous publications exploring animal populations revealed previously undetected ecological complexities. The Metapopulation Ecology by Hanski (1999) introduced the complexity of animal populations by analysing them as an intricate unit composed of different pieces (designated metapopulations). Not only did this theory fragment the original concept of a population as a single unit, it also suggested that non-breeders play a legitimate, important role in the equilibrium of (meta)populations. Furthermore, the dispersing individuals themselves were taken as crucial elements in the regulation of population dynamics, trajectories, spatiotemporal distributions and stability, as well as the likelihood of extinction.

Based on this and numerous other studies, the field then moved a step further towards a greater understanding of animal populations and their dynamics by explicitly recognizing the value and importance of the non-breeding portions of animal populations: the so-called floaters.

While floaters were first defined as surplus individuals or members of a population reserve (Brown 1969), they are now defined as dispersing individuals able to enter as breeders in the reproductive population when a breeding territory or a potential mate (i.e. an owner of a suitable breeding territory) becomes available (Penteriani et al. 2006a). However, this is only one piece of the floater puzzle. In reality, surplus individuals and population reserves can reflect two different realities. In the first, floaters may become a crucial population reserve for filling empty territories when breeding dispersal or breeder mortality open up previously occupied territories. Under this scenario, floaters represent a positive input to the stability of breeding populations. In the second scenario, however, floaters may also represent a serious threat to breeders (or an additional pressure, at the very least), by competing with owners for their territories.

Thus, as creatures of Star Wars, wherein the light side (associated with creation and life) was separated by a very short distance from the dark side (associated with death and
destruction) (Decker et al. 2005), floaters may depart from their positive role for population persistence (buffering mortality in the breeding sector) to become, depending on circumstances and scenarios, inconvenient competitors of breeders by intruding on their territories or fighting for matings. As noted by López-Sepulcre and Kokko (2005), although floaters may compensate for decreases in the breeder pool, this benefit is associated with such a large list of negative fitness consequences for breeders that floaters could also represent a potential menace for population stability and persistence.

In this review, we will take a voyage across the “underworld of floaters” (sensu Smith 1978). However, before departing, we would like to emphasize that: (a) we will take into account bird populations only, because little information on non-breeding individuals exists for other animal populations; and (b) we exclude helpers and cooperatively breeding species from our analyses because non-breeding individuals of such social organisations cannot be considered floaters sensu strictu, since actual floaters do not participate in the care of alien offspring.

The Origin of Floaters: Territoriality, Habitat Saturation and Adaptative Strategies

In the late 1970s and early 1980s, when specific research on floaters first began (see Smith 1978, 1984 and references therein), floaters were perceived as renegade individuals that did not fit into the behaviour and social systems of the “regular” members of the species (i.e. the breeders). In fact, non-breeder were essentially considered to lead a wandering existence with no fixed areas of residence or social organization, due to their subordinate social status and competitive inferiority (Errington 1956, Delius 1965, Krebs 1971, Stutchbury and Robertson 1985). Similarly, the term ‘ floater’ has been also used to describe persons without a permanent residence or a regular job (Webster’s 9th in Zack and Stutchbury 1992).

Probably because the first, indirect evidences for the existence of floaters were the rapid replacement rates of territorial owners following removal experiments (e.g. Stewart and Aldrich 1961, Orians 1961, Krebs 1971, Knapton and Krebs 1974), they were initially considered to be subordinate individuals who passively wait for opportunities and use resources in an entirely opportunistic way.

Floaters were also considered to represent unsuccessful competitors who had been excluded from breeding territories by higher-ranked individuals (Eckert and Weatherhead 1987), implying that they were competitively inferior to owners. This would seem logical given that territory owners usually win almost all conflicts with intruders (Krebs 1982). However, theoretical analyses of animal contests (e.g. Maynard Smith 1982) predict that territory owners will be more successful fighters than intruding floaters simply because of asymmetries that are independent of fighting abilities (e.g. knowledge of the territory, importance of the defended resources, arbitrary conventions), suggesting that the floaters might not necessarily be unsuccessful competitors.

The ‘negative’ image surrounding floaters, along with difficulties in localising and studying them, could explain why floaters
aroused less interest at the beginning of their appearance in the study of bird populations, i.e. "...they have been simply dismissed as strays, or even migrants, and thus ignored" (Smith 1984:97). However, this idea was challenged in the early 1980s (Smith 1978, 1984), and thereafter the floater concept came to mean individuals living within a different but highly structured social system, who are ruled by unusual tactics and waiting strategies, but are able to compete and fight for a territory and mate when necessary.

Although Darwin (1871) was the first to note the presence of wandering males and the rapid replacements of lost males, the idea that floaters are a consequence of the territorial spacing of breeding pairs was first expressed by Moffat (1903:137), who wrote about the stable number of chaffinches nesting every spring in an orchard around his home in rural Ireland. He wrote: "...it appears to follow that we must have a very large number of non-breeding birds of both sexes, preventing from breeding simply by the fact that they have no suitable ground."

Initially, floaters were defined as sexually mature birds prevented from breeding by territoriality or other spacing behaviours (Brown 1969, Smith 1978, Eckert and Weatherhead 1987, Newton 1992, see also the conceptual review of Winker 1998). In other words: (1) resource availability limits the number of breeders; and (2) territory competition makes some individuals become floaters when all suitable breeding habitats are occupied by territory owners. In support of this, the creation of new breeding habitats has been shown to decrease the number of floaters (Hunter 1987 Smith 1987), with new individuals (i.e. former floaters) sometimes settling in and beginning to defend new nest sites within hours (Smith 1978, Stutchbury and Robertson 1985, Smith and Arcese 1989, Hunt 1998, Penteriani et al. 2003).

Thus, the saturation of suitable breeding sites and subsequent competition for breeding generates two main categories of individuals within the same population, namely territory owners and non-territorial floaters. Because intrasexual competition for breeding opportunities is stronger among males than females, floating population of males were recognized first (e.g. Stewart and Aldrich 1981, Delsis 1965, Smith 1978). However, if breeding opportunities are limited, females can also be excluded from breeding and surplus females may originate floating populations (Stutchbury and Robertson 1985 and references therein; Stutchbury and Robertson 1987, Sandell and Diemer 1999, Pilz and Smith 2004).

However, while such 'individual-saturated' scenarios are true and may feed the pool of floaters, the reality can sometimes be more complex. For example: (a) the floater stage in an individual's life could be an alternative strategy for juveniles, leading to higher fitness than that seen with early breeding (e.g. Smith and Arcese 1989); or (b) a trade-off may exist between current investment and future survival, meaning that delayed maturation may be more successful for long-lived species (life history theory, Stearns 1992). Floaters can be also considered to represent individuals who have rejected all vacant breeding locations they have encountered because they increase their fitness by doing so, i.e. there may be a threshold quality level necessary for an individual to accept a breeding site as being worth the energy investment to hold the site and take a mate, as opposed to waiting for a higher

As underlined by Austad (1984), we can regard territory owners and floaters as two distinct kinds of individuals exhibiting alternative reproductive behaviours. Three scenarios are possible (Smith and Arcese 1989), with the alternative reproductive behaviours being: (1) condition-dependent, i.e. only the best individuals of a population become territory owners; (2) a mixture of evolutionarily-stable strategies, whereby each individual has the same opportunity to show a given strategy or a population consists of a stochastic mix of both categories of individuals (Dominey 1984); and (3) alternative evolutionarily-stable strategies, whereby genetically diverse individuals show different behaviours in a negatively frequency-dependent manner (Gross 1982, Dominey 1984). Alternative reproductive behaviours are the result of local environmental conditions and local population density conditions: in this case, floaters appear to be the by-product of the regulation of population numbers by territorial behaviour, rather than low-ranked individuals (the doomed surplus sensu Errington 1956). Thus, although floating may be perceived as an unattractive option ("the best of a bad job," as suggested by Dunbar 1982 and Hogetad 1990) determined by high population densities that make it difficult to gain and hold breeding (Smith and Arcese 1989), the acquisition of a vacant breeding site can also be a matter of chance, and the behavioural strategies, genetic features and individual fitness of floaters is not necessarily less desirable than those of their breeding counterparts (Jamieson and Zwickel 1983).

Our initial limited perception of the floater "underworld" was no doubt due largely to the difficulties in localising, recognising and studying these individuals. In fact, the existence of this "shadow population" (Rohner 1986) is difficult to demonstrate using the common census techniques of counting displaying or singing males, occupied nests or nest-boxes. However, based on the theory that a floater in a fixed or restricted territory would benefit from knowledge of the area and its neighbours (including potential mates), perhaps allowing them to establish social relationships with other floaters that might decrease fighting in the aftermath of an owner's disappearance, Smith (1978) published the first striking results showing that rufous-collared sparrow (Zonotrichia capensis) floaters have a well-defined social system and do not wander randomly. Since then, we have learned that floaters may live in very restricted areas that resemble real territories (e.g. exclusive use of an area), and have relationships showing a clear dominance of females over males. Thus, the so-called "underworld" of floaters is in fact a highly organised social system characterised by sex-based dominance hierarchies and lifestyles. The dominance relationships among floaters represent a mechanism similar to the one giving territory owners a high resource-holding potential; the investment of a floater in a given year and territory can confer an advantage during future contest for that space following the disappearance of the previous owner (Zack and Stutchbury 1992).

Matthysen (1989) showed that it is possible to distinguish up to three types of floaters: (1) solitary individuals with a home range overlapping several territories or parts of them; (2) paired birds moving across several
breeding territories; and (3) satellite individuals that may live within a specific occupied territory but never engage in overt conflicts with the owner. More than one satellite (of different sexes) may be found in a given territory, and the territory quality may determine the presence of satellite individuals, who may be tolerated by owners only in situations of abundant resources (Davies and Huston 1981).

Because floaters do not need to defend a territory or provide parental care, they may spend most of their time visiting breeding territories and searching for reproductive opportunities (e.g. finding a mate or an empty/potentially challengeable territory). When floaters are close to or within an owner-occupied territory, they are typically secretive and either fly away or remain motionless when owners are nearby or performing territorial displays, likely because owners are typically aggressive towards floaters (Arcese 1987). Regardless, floaters typically settle close to the activity centres of breeders and overlap their home ranges with the territory of one or more owners (Jamieson and Zwickel 1983, Arcese 1987, Walls and Kenward 1995, Rohner 1997, Walls and Kenward 1998). Floaters may show stable home ranges with occasional movements beyond their normal area; their increased mobility compared to that of a territory owner means that floater home ranges may be much bigger than breeder territories (e.g. Ferrer 1993, Rohner 1997, see also Brotons 2000 for wintering spacing in a population of the coal tit, Parus ater), and the home ranges of different floaters may broadly overlap. The larger home ranges and broadly overlapping ranges of floaters may be considered a direct consequence of the absence of territorial behaviours in non-breeders. The increased number of territories that they can check for vacancies (which in turn affects the probability of securing a vacancy as it occurs) represents a species- and density-specific trade-off (Zack and Stutchbury 1992, Rohner 1997). The nature of this trade-off varies with some species characteristics, such as longevity; in short-lived species the high mortality rate of owners confers a high probability that any prospected nest site will become available. Nest density may also influence the movement behaviour of floaters, with small clumped nest sites being easier to monitor than large, scattered territories.

Juvenile floaters seem to be more easily tolerated by territory owners due to their dull plumage, which is easily distinguishable from that of the adults (Smith 1978, Lyon and Montgomery 1986). In the context of this close coexistence between floaters and breeders, it has been hypothesised that juvenile plumage could reduce the risk of territorial aggression by owners (Stutchbury and Robertson 1987), and may thus represent an evolutionary strategy that allow floaters to prospect the best opportunities (potential territories and mates) and establish dominant relationships with other floaters (see also Zack and Stutchbury 1992). Juvenile floaters of various species may therefore gain easier access to breeding territories, allowing them to judge the: (1) quality of different territories; (2) local available hierarchies of dominance (e.g. a floater may first try to join the hierarchy of the best territory); (3) potential mates; and (4) health state of rival owners. Under this perspective, it seems reasonable to expect that floaters of species with juvenile plumage may more frequently prospect the breeding areas of their/neighbouring (meta)populations and overlap with the home ranges of one or more
breeders, perhaps leading to more rapid filling of a given vacancy. However, other explanations (e.g. the physiological costs due to the production of the adult plumage) should be taken into account before to accept the above-cited possibility.

Faced with evidence of a floater organization living in the shade of territorial owners, one can ask: why would an owner allow an alien individual to share the same resources? This decision may arise from the balance among three elements (Smith 1978), namely: (a) the owner's benefit of having floaters nearby, e.g. extra-pair copulation with neighbouring individuals, fast mate replacement and reduced risk of predation (Morton et al. 1990, Stutchbury 1991); (b) the disadvantages of sharing the same territorial resources with non-related individuals; and (c) the investment in time and energy required to keep floaters out of the territory. From a floater perspective, it may be a good strategy to live in the owner's sphere of influence when potential future gains (e.g. access to high-quality resources, availability of a potential mate, knowledge of terrain) are superior to the level of owner defence. The four key elements that allow the emergence of such a delayed breeding strategy are (see the review in Zack and Stutchbury 1992, Eins et al. 1995 for a detailed description of the phenomenon, as well as Kokko and Sutherland 1998 and Pen and Wessing 2000 for theoretical discussions on queuing): (1) floaters queuing for a focal territory (e.g. nonbreeders restrict their movements to limited home ranges, mainly those with older owners); (2) owner tolerance towards the individuals floating within its territory; (3) site competition among floaters; and (4) the acquisition of a high-quality territory as a result of delayed breeding. Queuing and delayed breeding, two strategies where individuals forgo current reproductive opportunities to wait for better breeding vacancies to be available, are phenomena similar to delayed dispersal. Postponed dispersal and breeding are both linked to fitness benefits and may originate from variations in the quality of breeding territories (Ekman et al. 1999).

Before this information became available, floaters were considered a density-dependent population response. However, the more current findings seem to suggest that becoming a floater may be not always be a necessary response of population saturation; rather it may be a choice to wait for the best breeding opportunity (i.e. obtain a high-quality territory) available in the natal population or a new population created through dispersal. Recently, Bruinzeel and van de Pol (2004) showed that the probability of a floater entering as a new breeder in a particular area increased as a function of previous presence in and knowledge of that area, stressing the importance of familiarity. Under this perspective, floaters are not the periphery of populations, but rather cagey individuals who use sophisticated strategies to augment their future breeding benefits (in agreement with Zack and Stutchbury 1992, see also the importance of public information on best territory establishment in Sergio and Pantani 2005). Because of the influence of territory quality on this type of strategy, we should not be surprised that floater tactics show within-population variations representing different responses to the diverse options available at the local level of each (meta)population. Just as variations of territory quality play a fundamental role in avian
habitat selection, mating, breeding performance and social systems (Zack and Stutchbury 1992, Ferrer and Donázar 1996, Ferrer and Penteriani 2003 and references therein), both the properties of the breeding population and the attributes of territory will contribute to shaping the behaviours and fate of floaters.

The studies of Ekman and his colleagues on willow tits (Parus montanus) and crested tits (P. cristatus) extended the term floater to individuals in the non-breeding season (i.e. winter floaters; Ekman 1979a,b; Ekman et al. 1981; see also Høgelad 1990, Winker 1998 and Brotons 2000). Breeders holding territories during reproductive periods often spend wintertime in flocks; they generally frequent only one flock, although some species also show inter-flock movements (Smith 1984 and references therein, Smith 1987). The complex organisations seen among breeding-season floaters also characterise winter floaters (Smith 1984), in that: (a) dominant wanderers may move in pairs among different flocks with no apparent aggressive interactions among individuals of the different flocks; (b) low-ranked birds may switch singly among flocks; (c) the status of floaters may change based on opportunities, with increased aggressive interactions seen when a high-ranking male is replaced by a previously subordinate bird (among females, shifts in dominance are typically accomplished with less aggression).

Such different interpretations, views and results originating from studies of the same phenomenon (i.e. the floating life) are essentially asking for more studies on floater dynamics within species with different life-histories (e.g. short versus long-lived species, migrants versus resident versus whole-year territorial species), in order to help us understand the different factors responsible for determining the occurrence and numbers of non-breeding individuals. Life-history characteristics may engender specific needs and choices, originating floaters under different scenarios, motivations and pressures. For example, in short-lived species, high recruitment rates may benefit both owners and floaters who share the same territory, but this scenario changes in a long-lived species, as birds with a life expectancy of twenty or thirty years will not gain the same benefit from sharing territorial resources with alien individuals. Furthermore, weapons can determine different floating strategies (e.g. shadow lives versus aggressive intrusions); passerine disputes may not lead to the same results as eagle or owl fights. Thus, the complexity of the floater underworld first described by Smith (1978) appears to only represent a fraction of the complex social interactions among floaters and between floaters and breeders. Such a perspective is also supported by the fact that important differences may be seen within species that are expected to have similar life histories. For example, different floating behaviours are seen for the rufous-collared sparrow (Smith 1978), whose floaters wander within the territories of breeders, and the song sparrow, Melospiza melodia (Arcese 1987, Smith and Arcese 1989), whose floaters do not wait passively for territories to become available, but rather actively challenge territory owners.

From Living in an Underworld
To Becoming a Territory Owner
The way in which a young bird may become a member of the breeding population strictly
depends on the specific-features of its floater organisation and the choice the individual makes during the dispersal process. This undoubtedly complex process is still poorly understood at present. As emphasised by Stutchbury and Robertson (1987), one of the essential elements in understanding reproductive strategies is the knowledge of the behavioural strategies that floaters are able to perform when faced with breeders. Because floaters may show different alternative reproductive tactics (depending on species and local conditions) to achieve a breeding territory and/or a mate, their intrusive behaviours and tactics may also play an important role in shaping the territorial behaviour of territory owners. The diversity of species’ life-histories further complicates this scenario, with different species or groups of species differing in their dispersal patterns, winter survival strategies, social organisations, territorial behaviours and so on.

In addition, different tactics may also arise within the floaters of a single species. For example, Smith (1984) reported that two main strategies were employed by juvenile black-capped chickadees (Parus atricapillus) attempting to insert themselves into the social system imposed by older, higher-ranked conspecific birds, with the goal of obtaining a breeding territory and mate as quickly as possible. Because of the alternating social system of this species (i.e. non-breeding winter flocks become territorial pairs during the breeding season), a truly successful floater must first position itself within the winter flock system such that it will have an opportunity to obtain a place in the breeding population the following spring. The young chickadee thus chooses between attempting to find a mate rapidly right after dispersal (at the time of winter flock formation), or opting for a simpler solution of wandering among flocks and entering the social system at a lower rank. Under the latter scenario, the pathways of integration from floater to breeder will be longer and more complex, with the youngster attaining higher rank in the flock only when a high-ranked individual of the same sex disappears.

Thus, the floating strategy is clearly a mix of more or less fixed factors (e.g. individual quality and fitness) and aleatory events (e.g. stochastic winter mortality affecting either the young entering the flock, or the older and higher-ranked individuals and breeding pairs). Because successful individuals (i.e. juveniles obtaining a breeding territory the following spring) will determine the structure and characteristics of the next breeding population, floater fraction dynamics are critical to the population at large. In other words, all factors (biotic and abiotic, individual- or habitat-dependent, random events) affecting the fate of floaters before they become an active part of the population by contributing to annual reproductive outcome will shape the features (e.g. health, age structure, breeding performance) of the breeding population they enter.

Ens et al. (1995: 646-647) noted that "...the observed distribution of territorial birds cannot be understood from measurements on the territorial owners only but must include their years of battle as non-breeders." This clearly underscores the importance and strength of the floater underworld in determining the characteristics of breeding populations, especially since recruitment is shaped by the events that characterised the life of a floater before it becomes a breeder. The
link between floaters and breeders is therefore not purely that of immigrations and emigrations rates; each breeder was previously a floater, and its experiences during its wandering existence will influence the characteristics of the breeding population it enters as a new territory owner. This leads to a new understanding of how two populations of the same species can show important differences, i.e. because their floaters experienced very diverse existences before their settlement as breeders.

FLOATERS ON THE DARK SIDE:
Competitive Relationships between Territory Owners and Floaters, Territorial Contests from a Floater Perspective

A study by Arcese (1987) was one of first detailed reports on the behavioural relationships between floaters and owners among a passerine bird, i.e. the song sparrow. The findings differed from the prior reports of Orians (1961), Delius (1965), and Smith (1978), in that Arcese (1987) found that floaters intruded more often into territories inhabited by young (e.g. inexperienced in resource defence), old (e.g. less vigorous) and handicapped (i.e. less able to defend themselves) individuals of the breeding population. Notably, such patterns of aggression also seemed to suggest that, in contrast to the frequently-accepted paradigm, territory ownership was not necessarily restricted the best individuals of a population. The challenge of territorial males could also represent a floater strategy designed to evaluate the reaction (and strength) of owners (Arcese 1987), allowing for an honest system of assessment (Zahavi 1977) in which the owner is unable to mask weaknesses in his defensive ability.

Depending on species-specific characteristics and local conditions, several differences have also been detected in the temporal patterns of intrusion. Due to the fact that colonisation rates of empty territories were highest in the morning for the great tit (Parus major), Kacelnick and Krebs (1983) hypothesised that the dawn chorus of territorial tits could be a consequence of a daily peak in floater intrusion (although in this case the colonising birds were not real floaters but probably owners of neighbouring, lower quality territories). Such an idea was not supported by Arcees (1987), who did not find any predictable time of day in territorial intrusions. Another singular example of temporal patterns of intrusions was detected in nightingales (Luscinia megarhynchos) by Amrhein et al. (2004), who found that non-breeding males intruded most often into breeding territories at dawn, probably because they were attracted by singing breeders. During these intrusions, floaters could have been assessing the quality of the singing male and his territory, as well as the presence or absence of a female.

Seasonal variations in intrusion pressure also showed variability, with some floaters intruding only during the breeding period, while others intruded throughout the year (Orians 1961, Smith 1978, Arcese 1987, 1989, Stutchbury 1991, Stutchbury and Robertson 1987, Ferrer 1993, Tobler and Smith 2004); however, this may simply reflect the territoriality of a given species (Arcese 1987, 1989). In species that are territorial year-round, owners may be challenged at any point by
intruding floaters engaged in opportunistic strategies for territory acquisition, particularly with respect to high value, stable territories with well-known neighbours. In contrast, seasonally territorial species may gain less benefit from acquiring a territory during the non-breeding period, due to complications such as high winter mortality and the associated low probability of breeding, and/or the possible appearance of dominant/higher-quality competitors in the next breeding season, leading to territory loss. Furthermore, the pattern of seasonal intrusion can also be affected by ability of a given species to reproduce more than once per year. For example, Stutchbury and Robertson (1985) showed that although female tree swallows (Tachycineta bicolor) reproducing early in the breeding season, their floaters nested late because their access to breeding territory was prevented at the beginning of the reproductive period. This type of situation would be likely to engender late patterns of territory intrusion and/or establishment. Moreover, when breeding seasons are long, floaters that persist in intruding behaviours may produce more young than floaters who wait for a territory to become vacant (Arcese 1989). This could be especially true for species in which territory turnover is slow, i.e. those with high survival expectancies and strong territory and mate fidelity. Finally, seasonal changes in floater behaviour and tactics may be also related to seasonal changes in the costs and benefits of searching for breeding opportunities (Stutchbury and Robertson 1985). Since the level of breeder aggression towards intruders decreases over the season (see also Sandell and Smith 1997), the cost to visit a nest site late in the breeding season is relatively small for a floater. Late in the season, therefore, floaters may collect information on the quality of nest sites, improving their competitive ability in the next breeding season (Tobler and Smith 2004; Sergio and Penteriani 2005).

A special case is the one described by Meek and Robertson (1992), in which floating male eastern bluebirds (Sialia sialis) obtained new territories when the young of the previous male owners were still present in the nests. This strategy allowed the replacement males to gain matings and father second broods. Interestingly, the replacement males showed lower territory and nest defence than the previous owners, probably because: (a) the new owners did not adopt or defend the young; (b) the new owners might have had lower resource-holding potential; and/or (c) the new owners may have been less willing to defend the territory because they had less invested in the territory compared to the previous male owners. Above all, raising the offspring of an unrelated individual suggest a fitness reward, i.e. the acquisition of a territory, mate and future reproductions.

Floaters may be continuously challenging territory owners in a sort of “war of attrition,” wherein the win goes to the individual who persists longest (Parker and Rubenstein 1981). For example, in song sparrows (Arceae 1987, 1989) and purple martins (Progne subis; Stutchbury 1991), such a strategy of challenges and retreats seems to pay off, with the most persistent floaters being the most likely to achieve territories. This could also explain why floater intrusions (or their association with only a few territories; Jamieson and Zwickel 1983; Smith 1987) are mainly directed toward specific owners; if the war of attrition may be a successful strategy for obtaining a territory, a floater may be able to sustain this continuous
challenging only if he restricts disputes to a small portion of the available territory owners.

The above-cited scenarios depict complex and diversified territorial dynamics and strategies, and underline why it is important to understand the conditions that determine the different types of territorial behaviours (Arcese 1989). However, it should be noted that some of the assumptions inherent in the current models of territorial dynamics may be untrue, particularly when considering the interactions of floaters with the breeding portion of a population. Although modern science often encourages short-term field studies and easy biological models in the interest of rapidly obtaining publishable results, the solving of some ecological questions like territorial dynamics will require longer-term studies. Although the selection of easy-to-study biological models may facilitate experiments and allow the acquisition of large sample sizes, there is a significant risk of discovering only partial truths and revealing only those rules that govern the biological cycles and actions of similar organisms. Thus, we must not forget that general models of population dynamics should account for important variations among species in regard to territorial strategies (Arcese 1989).

Asymmetries and Competitive Abilities of Floaters vs Breeders: Are Floaters Really Losers?

Yasukawa (1979), in studying a population of red-winged blackbirds (Agelaius phoeniceus), found no difference in body size or aggressive behaviour between males who were and were not successful in establishing a territory. Similarly, Eckert and Weatherhead (1987) showed that the (inferior) status of floaters was not due (at least entirely) to the fact that they were substandard individuals. When several male owners were experimentally removed from the population, the replacing individuals did not show the morphologies of low-ranked individuals (i.e., smaller bodies or shorter epaulettes). Similarly, Matthysen (1989) for European nuthatches (Sitta europaea) and Hogstad (1990) for willow tits found no differences in body size and condition between residents and floaters, and concluded that floaters are not necessarily second-rate birds, but may instead simply be birds born too late to find a vacant territory. Moreover, these authors observed that a considerable proportion of owners were deposed by intruding floaters, suggesting that floater were not necessarily inferior individuals. Indeed, Arcese (1987) found that intruding floaters could also be individuals of higher quality and health than territory owners. The age and territory turnover revealed by Arcese (1989) for a population of song sparrows represents an interesting case of how floater versus owner asymmetries may influence some aspects of population structures. Probably due to the higher competitive abilities of 2-3 year-old males over 1 and 4 year-old territory owners, the former (middle-aged males) were more likely to gain additional territories during intrusions. By replacing the more inexperienced or oldest individuals of a population, the intrusions thereby refreshed the breeding stock. In this case, the non-breeding individuals not only filled vacant territories, they helped preserve the highest reproductive output for the population.

The resource-holding potential (RHP) hypothesis (Parker 1974), which suggests that owners have physical or behavioural advantages over floaters, initially seemed to
explain the successes of territory holders during owners versus floater interactions. However, as noted above, it is frequently difficult to distinguish between owners and floaters on the basis of size, secondary traits, weaponry or displays, meaning that the RHP hypothesis does not always explain why some individuals win contests. In this case, the high success rate of territory owners during territorial contests could be due differences in expected benefits (value asymmetry hypothesis, Maynard Smith and Parker 1976), irrespective of small differences in RHP. In other words, the territory has a greater future value to the owner than to an intruder, so the owner invests more in the territorial contest and is consequently more likely to win. The asymmetry in value may arise (see also conceptual syntheses in Shutler and Weatherhead 1991, 1992) because the owner: (a) is more familiar with the location of resources (e.g. food, escape routes from predators), territory characteristics and neighbours (e.g. disputes with familiar neighbours can be less expensive than boundary renegotiation with new individuals); and (b) will have more reproductive advantage than an intruder in maintaining the territory. In making these investments based on future potential gains, owners create an asymmetry in knowledge that increases their valuation of the territory. An example of such a situation was described by Shutler and Weatherhead (1991; but see Shutler and Weatherhead 1992) in a population of red-winged blackbirds, where owners and floater adults involved in territorial contests did not differ in RHP. Because the process of territory acquisition may also have an aleatory and chance component (e.g. the first floater to discover a vacant territory may become a territory owner and enter as a breeder in the population; Ferrer and Penteriani 2003), a new owner may preserve the territory even if subsequent challengers are similar in RHP (Eckert and Weatherhead 1987).

Additionally, if floaters were always subordinate or lower-quality individuals, we could expect that they would have little or no chance to engage in extra-pair copulation, because females are unlikely to accept copulations with substandard males. Peer et al. (2000) clearly demonstrated that the reproductive organs of floater male tree swallows were just as developed as those of the territory owners, also showing that floaters cannot be generally lumped into the category of non-reproductive young birds. Moreover, the full development of their reproductive organs and other hallmarks of good physiological condition indicated that the floaters were not lower-quality individuals with no chance to obtain extra-pair copulations. Thus, male floaters can be considered reproductively active individuals with the potential to best resident males in sperm competition (Peer et al. 2000).

Interestingly, these works seemed to contradict the findings of Rohwer (1982), who performed removal experiments with a population of red-winged blackbirds and found that territory owners seemed to be competitively superior to the floaters that replaced them. In this case, we should note (as underlined by Eckert and Weatherhead 1987) that although competitive asymmetries (as well as local and specific situations) may contribute to determining the owner/floater status within a population, they should not be taken as the only factors shaping social status among the individuals of a given population. More recently, Pryke and Andersson (2003) provided new information supporting the
competitive inferiority of floaters compared to territory owners among red-shouldered widowbirds (Euplectes axillaries), with epaulette size and hue differing significantly between floaters and breeders. Although we probably still lack of sufficient information for definitive answers, the variability of both life-histories and natural scenarios account for such an intriguing diversity in study results.

Active vs Passive Floaters, Weaponry and Risks of Death

Challenging and evicting a breeding resident is one of the possible strategies that a floater can use to enter in the breeding population. Some species, however, seem to prefer a more passive tactic, that of “waiting” floaters. For example, the behavioural tactics of floater female tree swallows (Stutchbury and Robertson 1987) include extensive explorations of the reproductive sectors of the population early in the breeding season. The inexperience of sub-adult females, in combination with their smaller wing length compared to adult females, may reduce their competitive ability and promote a less aggressive waiting strategy of territory acquisition. Sometimes, such waiting floaters may engage in brief, low-access intrusions, but these seem to be mainly aimed at assessing the status of a nest site (vacant or occupied) or the fighting ability of the owner (Stutchbury and Robertson 1987). Indeed, Bruinzeel and van de Pol (2004) proposed that intrusion behaviour could not be uniquely interpreted as intended to evict an owner, but could also be an attempt to become familiar with an area and its occupants. However, under different conditions, floating females of this same species have been shown to evict owner females through direct aggression (Leffelaar and Robertson 1985, Sandell and Smith 1997), with consequently higher risks of mortality or serious injury (e.g., Leffelaar and Robertson 1985).

If this is the case for a species without obvious fighting weapons, we might wonder what strategies would be employed by species with potentially mortal weapons (e.g., birds of prey and owls). In cases where fighting is risky and territory owners may be difficult to expel, we would expect that floaters would generally opt for a waiting strategy and search for vacancies rather than challenging residents (Walls and Kenward 1995). Consistent with this hypothesis, Rohner (1996) found that owl floaters: (a) did not declare their presence by calling, especially when in the proximity of territory owners; and (b) moved away when faced with owners displaying territorial behaviours. This secretive behaviour allowed the floaters to overlap broadly with defended territories (Rohner 1996). As reported by Rohner (1997), typically floaters of birds of prey and owls settle: (1) on nesting territories not occupied by a breeding pair; (2) in the interstices among different breeding territories; (3) in habitats unsuitable for breeding; and (4) unobtrusively within the home range of territory owners.

Weapon-bearing species may also show differences in some floater versus owner contexts (Hunt 1998). For example, vulnerability to nest predation or disruption of nesting activities (e.g., brood parasitism) are less evident in weapon-bearing species compared to unarmed species. The forceful territorial defence shown by armed species also appears to insulate resources from density-influenced degradation more effectively than the strategies of unarmed species; in armed species, the minimum territory size, density of
breeding pairs and the sizes of annual cohorts appears to more directly mirror the habitat quality and characteristics compared to those of unarmed species (Hunt 1998).

**When Floaters Become ‘Inconvenient’ Competitors by Hounding Owners**

Under some circumstances and in several species, floaters may shift from satellite or secretive presences within owners’ territories, to active intruders that seriously threaten the owners’ permanence (e.g., Birkhead and Clarkson 1985, Arcese 1987).

Evidence exists showing that there are situations in which: (a) owners may spend a great deal of time and energy chasing floaters from their territories (Myers et al. 1979, Hixon 1980 and references therein); (b) high levels of floater pressure may oblige owners to reduce the size of their territories (Norton et al. 1982), yielding the remainder to floating individuals (Tompa 1964, Birkhead and Clarkson 1985, López-Sepulcre and Kokko 2005); (c) floater intrusions can represent an additional reproductive cost for owners, probably decreasing their lifetime reproductive success (Arcese 1987), increasing the time spent in mate guarding (Beecher and Beecher 1979, Morton 1987, Birkhead 1982), and increasing the risk of extra-pair copulations/fertilizations (Morton et al. 1990, Ewen et al. 1999) and divorce (Penteriani and Ferrer 2004); (d) the presence of floaters may increase the risk of parasite transmission (Brown and Brown 1986); (e) the presence of female floaters close to breeding territories may engender or increase territorial defence by females (Searcy and Yasukawa 1983, Hurly and Robertson 1984, Eens and Pinxten 1996, Sandell and Smith 1997, Pilz and Smith 2004); (f) aggression towards female floater may increase the egg yolk androgen levels of female owners (Pilz and Smith 2004), which can be detrimental to offspring fitness; (g) floating females can parasitize owners’ nests (Cowaty 1985, Sandell and Diemer 1999); and (h) floater intrusions may alter seasonal patterns in territorial behaviour (Weatherhead and Robertson 1980, Cowaty 1981).

Such competitive aspects of floaters inform three important considerations regarding floaters and animal populations. First, the presence of floaters wandering close to breeding territories represents a strong pressure for owners, and can alter some of their behavioural traits. One of the most striking examples of the behavioural changes determined by prospecting floaters are the attempts of female European starling (Sturnus vulgaris) try distracting their males from the presence of floating females, in order to prevent such prospecting individuals from copulating with their mate (Eens and Pinxten 1996). During such intrusions, owner females may develop particularly aggressive behaviours against intruding females attempting to solicit copulations from their mate, such as blocking the nest entrance and increasing singing rates. Another example of intrusion-generated change is the surprising modification of offspring phenotype due to floater female intrusions in breeding territories of starlings (Pilz and Smith 2004). In this species, territorial intrusions by floaters increase the levels of yolk androgen, which appears to determine some important changes in offspring dispersal, producing a trans-generational mechanism for density-dependent dispersal and enhancing offspring competitiveness (e.g. increased growth, which can be an advantage in high-density
conditions). Such information underscores the importance of considering both floaters and breeders when we seek to fully understand the behaviour patterns shown by individuals of a population. For example, observations of increased aggressiveness and copulation rates among territorial females might be misconstrued without information on the presence of intruding females. In reality, mating systems are the result of various pressures acting from both inside and outside of the breeding population.

The second important consideration regarding floaters and animal populations is the notion that non-breeding individuals are not simply substandard individuals excluded from the competition for a breeding territory. When a floater decides to exert intrusion pressure against an owner, it likely does so because it has some hope of winning (i.e. the floater is at least competitively equal to the owner).

Third and finally, the types and results of the intrusion pressures of and defence against floaters by territorial breeders represent important factors that help determine the characteristics and social organisation of local populations. Local conditions and population structures shape the relationships between floaters and breeders and contribute to determining the various observed patterns, as in the case of a male-biased population in which the increased competition for females makes extra-pair fertilization by male floaters a successful alternative reproductive strategy (Ewen et al. 1999).

When floaters do not passively wait to fill a vacant territory, but rather play an active role in the turnover of individuals in breeding territories, the nature of the floater-owner interactions may also determine the spatial distribution of floaters. For example, floaters may concentrate mainly near high-quality territories or habitats (e.g. to await the death of breeders; Smith 1978, Arcese 1987), within or near the territories of males in a particular age class, or near fertile females who may be more likely to engage in extra-pair copulations (Ford 1983, Flood 1985). This means that: (a) the majority of aggressive interactions likely affect only a portion of breeders; and (b) the pool of floaters will show a heterogeneous distribution in the space, with the end result that a stochastic event affecting floater survival in specific areas could have a detrimental effect on the whole pool of floaters.

** Floaters Dynamics and Choices under Constraints **

The origins of population responses are best understood when we integrate the dynamics of floaters and breeders of the same (meta)population. This was highlighted by Rohner's (1996) study of a Canadian population of great horned owls (*Bubo virginianus*), wherein prey declines triggered important effects on both contingents, including: (a) immediate reduction in population growth due to both increased emigration and lowered production of recruits in the breeding territories and (b) increased mortality, particularly within the floater pool; this led to (c) limited availability of new breeders.

As an additional note in the predator-prey relationship, we think it is important to emphasize that, due to the large numbers of floaters (e.g. 40-50% of the whole population in Rohner 1996; see also revision on non-breeder pools in raptor populations in Kenward et al. 2000), studies evaluating the impact of
predators on prey populations must account for the potential impact of the floater population. Because predator-prey interactions are mainly studied with reference to the more visible and easily located breeding populations, real predation pressure on prey would have been severely underestimated, as highlighted by Rohner (1996) and Kenward et al. (2000). Similarly, we can expect a potentially strong floater impact to be missed in breeder-only studies on the patterns of intra-guild predation, which is the phenomenon by which a species acts as both predator and competitor for other species at the same or similar trophic level. Intra-guild predation has generally been studied within breeding populations (e.g. Sergio et al. 2003), but floaters of predatory species may also act as ‘invisible’ intra-guild predators, their presence being generally unperceived. Thus, estimations of the effects of intra-guild predations that do not account for the impact of floaters on their intra-guild prey may strongly underestimate intra-guild predatory interactions within avian communities.

Although an individual’s ultimate goal is often the acquisition of a breeding territory and mate, habitat quality and its gradients may represent a constraint when that individual decides whether or not to settle as a territory owner, since territory ownership and breeding are fraught with serious difficulties and risks. Because territory acceptance is often a subtle process with complex rules (Kokko and Sutherland 1998, Pen and Weissing 2000, Rutz and Bijlsma 2006), floating can be considered a viable alternative to immediate breeding when, for example, the individual must choose between making a potentially lifelong commitment to a poor-quality territory, or continuing to float and wait for a better opportunity later (queuing behaviour; Ens et al. 1995, Zack and Stutchbury 1992, Kokko and Sutherland 1998). However, the importance of habitat quality in shaping the relationships between floaters and population stability and persistence goes beyond a ‘game theory’ modelling of the behavioural choices showed by floaters. As shown by Kokko and Sutherland (1998), in cases of habitat loss, the relative quality of lost habitat may represent a major determinant of population declines. While the loss of low-quality habitats allows the population to maintain a healthy buffer of floaters, despite reduction in the less productive breeding territories, loss of high-quality habitats reduces the most productive territories and triggers an even greater and risky reduction in the floater pool (Ferrer and Donázar 1996).

When there is considerable variation in territory quality due to habitat heterogeneity, meaning that the owner is at increased risk of losing the territory to a usurper, the time taken in choosing a mate might represent another major constraint. Thus, the mating tactics evolved under this scenario may differ from those involving solely sexual selection, and the access of floaters to the breeding population may also show different patterns; both of these aspects may affect the process of pair formation. In birds, the notion that territory quality helps shape mating systems is generally supported by two observations: (1) many individuals select for the characteristics of breeding sites, not those of the potential partners occupying such sites; and (2) mate fidelity can be a by-product of nest site fidelity, with individuals accepting a vacancy in an established territory with a bird of the opposite sex already present. Many territorial species despastically and pre-emptively occupy sites with good suitability for reproduction and/or survival, thus relegating other individuals to
lower-quality sites. For these species, a mating strategy based on maximizing the probability of choosing the best available mate may not be profitable. Similarly, rapid mating may suggest temporal constraints for sexual selection opportunities, as reported for several species of raptors observed mating within just one day (see review in Penterian et al. 2003). In these cases, mate replacement occurred within such a short time that we may hypothesize that temporal constraints prevented assessment of multiple partners. Consistent with this notion, lack of sexual selection due to temporal constraints in raptors has been shown in studies on Spanish imperial eagles (Aquila adalberti); Penterian et al. (2003) reported 20 independent mating events of marked individuals occurring within 8–24 hr of previous mate loss. These rapid changes always occurred in the highest quality territories. In contrast, mate changes occurred more slowly (e.g., over several months) in lower quality territories or in years in which the population had reached its saturation threshold. In the former case (rapid mate selection), sexual selection was infeasible because: (a) the vacancy was not filled by a floater who was regularly or intermittently present on that territory, even though some such individuals were older than the one who eventually filled the vacancy; and (b) two prospecting individuals were never observed simultaneously in the same territory during a mating event. However, it is possible that sexual selection acts in more subtle and indirect manners in these cases. For example, in many avian species, males compete for access to territories or for proximity to a female (Ligon 1999). This could compensate for the reduced intensity of sexual selection during rapid mate acquisition, suggesting that indirect sexual selection may occur through increased male-male competition when female choice is reduced. However, in the Spanish imperial eagle, the absence of fighting or territorial/sexual displays between male floaters near breeding areas (Ferrer 2001) suggests that male-male competition does not occur when female choice is constrained, meaning that some males are prevented from being among the available males. In addition, during the above-cited mating events, there were no observations of two adult males fighting within a breeding territory to obtain a lone female. Because divorces exist in several taxonomic bird groups (Black 1996), the risk of territory loss may be minimized by an individual simply accepting the first new mate encountered. In addition, the rapid acquisition of a new mate will reduce or eliminate the potential costs associated with mate change, such as the need to fight rivals and search for a new mate. In birds of prey, which are characterized by a protracted breeding cycle, taking a long time to select a mate may also prevent reproduction or delay egg laying for the current year. Late laying in these species is usually associated with low breeding success and low survival prospects for the offspring (Newton 1979). Again, such results clearly show that a deep understanding of animal population patterns requires a comprehensive analysis of the interactions among all portions of a population. When considering one of the classic predictions of the theory of sexual selection, namely the existence of mating preferences in many bird species (assortative mating by secondary male sexual traits and by age), several kinds of evidence should be taken into account when analyzing the age-assortative mating processes and patterns. The remarkable amount of research on sexual selection over the last few decades has mainly been directed at determining
which mates are chosen and why, largely ignoring the process behind the observed pattern, and the possible influence of individuals floating around the breeding sites. As discussed above, if individuals of the same population inhabit territories that differ in quality and experience habitat-specific demographic rates, then the landscape features and the distribution of individuals become major determinants of overall population characteristics. Therefore, social behaviour (including mate selection) could be highly responsive to the features of heterogeneous habitats and different turnover rates between territories (e.g. mortality, migration, frequency and duration of vacancies). In this case, territory quality can represent a possible confounding factor affecting the mating process (i.e. the encounter of potential mates) and determine a positive assortement in mating pairs independent of mate preferences (Ferrer and Penteriani 2003). When considering the behaviour of the floaters in a population of Spanish imperial eagles and their interactions with both habitat heterogeneity and breeders, a theoretical approach based on empirical data allowed us demonstrate the crucial role played by a mix of these factors in the age-assortative mating showed by eagles, namely that selective mating might occur passively because successful floaters occupied certain territories more often than others. Therefore, no assumption about age or plumage selection is needed to generate a distribution similar to the observed one, which may be produced by simply considering the existence of differences between territories in the probability of occupancy by floaters (Ferrer and Bissón 2008). Therefore, a direct correspondence between the pattern of individual mating preferences and the population-level mating pattern is not necessary by itself to demonstrate age-assortative mating. However, analyses that ignore floaters may yield equivocal interpretation of the patterns observed in a population, because it is likely impossible to both: (a) make definitive statements about the mating preferences of individuals by solely observing the mating pattern of a population; and, vice-versa (b) predict the mating pattern of a population simply by using the mating preferences of its constituent individuals. This example shows that we need to carefully consider all the possible processes that can be responsible for the patterns observed in an animal population, because floater behaviours and interactions with breeders and habitat may engender mistakes in our perception of population dynamics. Above all, the possibility that excluding floaters could bias our understanding of animal populations should be seen as an impetus to continue improving our analyses of animal populations, potentially leading to the discovery of unexpected factors (both intrinsic and extrinsic to a population) that help determine the observed patterns (Penteriani in press).

FLOATERS ON THE LIGHT SIDE:
Floaters Dynamics Determine Population Viability and Persistence
More than thirty years ago, Brown (1969:284) was the first to explicitly recognise the value and contribution of floaters within bird populations, stating that the "...net reproductive rate for the whole population, Rn, can be expressed as the total number of young produced to maturity...divided
by the total number of mature adults there, including breeders and floaters." The author also highlighted the importance of considering floaters not only as the individuals who rapidly replace lost territory owners or mates, but as a well-defined fraction of animal populations characterised by specific sizes, distributions and dynamics from year-to-year (Brown 1969).

More than a decade later, although relatively few studies had focused on animal population recruits, floaters were already recognised as a necessary component of a population, and their study was accepted as being important for a complete understanding of population dynamics (Jenison and Zwickel 1983). Over the following ten years, two essential concepts involving floaters were developed: (1) Wilcove and Terborg (1984) hypothesised that population declines affecting floaters may be difficult to detect in studies limited to breeding populations; and (2) Franklin (1992) showed that temporal lags may exist in the detection of population declines, depending on the unknown size of the floater portion. However, if floaters were considered an essential part of a population through the early 1990s, why were they frequently excluded from later studies focusing on the dynamics and stability of breeding populations? Likely because, as stated by Newton and Rothery (2001), we still lack accurate information on the interactions between floaters and breeders, two strictly related components of avian populations.

Floaters have widespread implications in the multi-level characterisation of bird populations (see review in López-Sepulcre and Kokko 2005). Above, we discussed the importance of floaters in shaping the territorial and reproductive strategies of breeders. Now, our interest will be mainly directed towards the role that floaters play in shaping population structure, dynamics and persistence.

How the Fate of Floaters May Affect the Stability of Breeding Populations

As we mentioned previously, Wilcove and Terborg (1984) and Franklin (1992) were the first to show a crucial link between the dynamics of the floater pool of a population and the stability of its breeding portion. Moreover, population responses may be only partially reflected by and within breeding territories (Rohner 1996). Such seminal works were the first to recognize that there is a link of dependence, in terms of the survival and stability of a population, between floaters and breeders.

From the perspective of conservation biology, the absence of information on floaters may yield dangerous conclusions regarding population health and persistence. Franklin (1992) was one of the first to show that numerical declines in the floater sector of a declining population (in this case the spotted owl, Strix occidentalis) may take several years to be detected in the breeding population. Moreover, decreases among floater populations may not be detected by traditional monitoring programs, which are typically based on breeding territory censuses (Wilcove and Terborg 1984, Rohner 1996).

An important concept that was first introduced by Newton (1998) and later discussed by Hunt (1998) is the floater-
breeder ratio, a crucial parameter of animal populations that allows researchers to assess the health of a population and its potential to act as a source of recruits to other populations. Newton (1988) observed that a ratio of one (or more) to one could be expected for healthy populations, and that larger pools of floaters were associated with more stable breeding portions, even in cases where breeding output could be impacted by floater interference (Hunt 1998). This concept suggested that two trade-off scenarios may shape floater versus breeder relationships. First, when floaters show intrusive behaviours, we can expect a trade-off between the population's need for a floater pool (for persistence) and the negative impact of continuous intrusions (i.e. frequent fights, increased reproductive costs, and risks of eviction) and owner resource partitioning with intruders. In the second scenario, when floaters mainly wait for vacancies in the breeding sector, the trade-off scenario will account for the population's need for floaters compared to the cost of resource partitioning. The end results of both these scenarios are density-dependent, but unlike most general paradigms of bird populations, this density-dependence is not exclusively that of breeders. It is a property of the floater population too, in that the larger the reserve of floaters (i.e. more floaters wandering close to breeding territories), the more impact they will exert on breeders (see also Hunt 1998). A third factor may mediate the above-described trade-offs, namely the availability of habitat suitable for survival (e.g. abundant cover and food resources) in areas without nest sites, more or less separate from the breeding sector of the population. Complex but still unexplored interactions are expected to govern the entrance of floaters as territory owners in this situation, mainly dependent on species life history, dispersal patterns and philopatry.

More recently, theoretical approaches to the study of bird population dynamics have highlighted several interesting, novel aspects of the links existing between floaters and breeders of the same population, suggesting that floater decisions may play a fundamental role in some basic population features, such as the strength of competition for breeding sites, dispersal and migration (Kokko and Lundberg 2001; Kokko and Elman 2002). Kokko and Sutherland (1998) were among the first to show that floaters may represent a problem in conservation, not only because floating as a deliberate choice to delay breeding leads to wasted breeding opportunities, but also because such an important buffering pool of individuals is very difficult to quantify. This impacts not only our understanding of how and why animal populations fluctuate, decrease and disappear, but also our knowledge of where extinction factors act on a population.

Most population dynamics research to date has focused on the mortality in the breeding sectors and the impact of persecution and habitat loss on the dynamics of breeding communities, whereas the temporary settling zones used during dispersal by non-breeders and the dynamics of dispersers are poorly understood for most species. The effects of habitat loss, mortality rates, extinction probability and environmental stochasticity are typically considered less important or ignored for settlement areas. As a consequence, conservation measures tend to overlook such sites, potentially leading to increased mortality risks for dispersing individuals. Because dispersal displaces
individuals across unfamiliar terrain, losses during dispersal are likely to be considerable. As a result, habitat destruction and decline in survival rates within settlement areas could be critical factors affecting the persistence of the whole population, potentially making the species more vulnerable to extinction by demographic and environmental stochasticity. Fenton et al. (2005a) drew attention to a sort of ‘pervasive butterfly effect’ due to an increase of floater mortality impacting the breeding population. Because productivity is density-dependent, this parameter tends to be less sensitive to an initial increase in floater mortality, which reduces the saturation of the breeding population. For this reason, an initial decline in pair numbers should not affect productivity. For a population of Spanish imperial eagles, increased floater mortality was shown to appreciably impact the breeding sector of the population after more than 20 years, when the declining trend accelerated. When considering the more extreme scenarios (i.e., species with high ages at first reproduction and elevated rates of floater mortality), we see a positive correlation between pair numbers and productivity. This could explain the long latency before the definitive decline of breeding performance; when mortality is low in the settlement areas, the demographic contribution of dispersers compensates for breeder mortality and reduces the risk of extinction, but when mortality is high in the settlement areas, pair formation becomes increasingly difficult due to the lack of new individuals available to replace a lost mate. The worst consequence of this scenario is that, at the beginning of a population decline due to a major loss of floaters, relatively stable breeding performance could generate the false impression that the population is healthy, even if some breeding territories are lost. Moreover, because the less frequently occupied and most easily deserted territories are generally the low-quality ones, such an early warning signal could easily go unnoticed. This implies that it could be dangerous to monitor only the breeding portion of a population, because of the potential delay in decline detection, underestimation of decline extent, and overestimation of recovery levels (see Kokko and Sutherland 1998, Kenward et al. 2000).

This ‘butterfly effect’ only represents a specific situation clearly showing the deep link between floaters and breeders of the same population. More generally Fenton et al. (2005b, 2006b) found that: (a) the survival of dispersing individuals (the numbers of which depend on the productivity in breeding areas) is highly dependent on the number of available settlement areas and their resources; (b) environmental stochasticity has a stronger influence on the entire population (breeders + floaters) when variations in environmental conditions occur in a synchronous way (i.e., simultaneously in both the settlement and breeding areas); (c) increased floater mortality within settlement areas negatively impacts the stability and dynamics of breeders within the reproductive areas.

Many factors influencing population dynamics have their origin in local processes acting on subunits of the whole population, and several of them can be linked to the way dispersal affects demography in breeding territories, showing a profound impact on the persistence of the entire population. Therefore, a population should be viewed as a stratified system divided into a network of smaller subunits (e.g., dispersers and breeders, or settlement and breeding areas), the persistence of which is not only dependent on the local
dynamics within each breeding unit, but also on the probability that floaters survive dispersal each year and are integrated into the reproductive portion of the population, relative to the number of individuals that die in both settlement and breeding areas.

Under specific local conditions, the breeder and floater segments of a population may decline in concert (Rutz and Bijlsma 2006). Decreased food resources over large areas that include both breeding territories and settlement areas may be a typical example of such a joint decline of breeders and floaters. Human-induced mortality could also represent a locally severe constraint to an avian population. When direct persecution or more subtle destabilisations of a population (e.g., mortality induced by power lines, Sergio et al. 2004) acts within the breeding population, the availability of a healthy floater pool is crucial for the persistence of the whole population. In fact, the availability of floaters may make the difference between a stable population and a decreasing population that come close to the extinction threshold.

However, under the perspective that most bird species exhibit age-specific patterns of breeding performance, with fecundity generally increasing with age (Sæther 1983, Newton 1989, Forslund and Pärt 1995), the sudden entrance of numerous juveniles into a breeding population characterised by high anthropogenic mortality may also decrease its breeding performance (Balbontín et al. 2005). Among the hypotheses that have been suggested to explain the differences in breeding performance among age classes (see reviews in Curio 1993, Forslund and Pärt 1995), the constraint hypothesis proposes that age-related changes in competence during a bird’s lifetime may improve skills that are essential to high reproductive performance. The selection hypothesis, in contrast, proposes that natural selection yields an age-related decrease in the proportion of lower-quality individuals, meaning that breeding success increases with age at the population level. Essentially, natural selection may remove lower-quality individuals at higher rate from younger cohorts than from older ones, leading to a progressive increase of better-quality phenotypes among the breeding-age cohorts. Under such a perspective, stochastic events such as human impact could change the proportion of high- versus low-quality individuals, working against the selection of high-fitness individuals (Balbontín et al. 2005). If human-induced mortality in breeding sectors is very high, therefore, a massive increase of young (inexperienced and formerly non-breeding) individuals into the breeding population could lower the overall quality of the genetic pool, negatively impacting the reproductive output of the whole population. We can hypothesise that such an effect should be really evident only in cases of large-scale breeder replacements, because under non-critical breeding population requirements: (a) the effects of relatively few individuals from the youngest cohorts on reproductive performance should remain unperceived; and (b) natural selection should eliminate the lowest-quality floaters during their first years of life.

Floaters and Density-Dependent Regulation of Bird Populations

A great deal of research has been devoted toward improving our understanding of the mechanisms regulating population ecology, and the possible implication that floater
dynamics may have on the density-dependent regulation of populations.

One of the first findings related to the impact of floaters on density dependence was the observation that some floaters decide not to breed if, for example, the available breeding territories are under a necessary quality threshold (e.g., End et al. 1992, 1995, Kokko and Sutherland 1998; but see also Pen and Weissing 2000 for their discussion on the possible variability in the territory acceptance rules due to the approach of the breeding season). In fact, the decision of some birds to wait for breeding, even when environmental conditions and available mates would allow them to do so, may have important consequences for population ecology (Gordon 1997, Kokko and Sutherland 1998). This sort of voluntary delay in breeding reduces the reproductive output of a population; furthermore, because it appears to be influenced by population size, it will alter the density dependence within the breeding sector. Such an effect of floaters on density-dependent regulation of breeders is determined by an intentional decision, and consequently may be considered a ‘direct adjustment’ of density dependence. The term ‘direct’ here refers to the fact that a ‘deliberate’ decision of floaters (e.g., queuing) can alter the shape of density dependence.

However, adjustments and patterns in the density-dependent regulations of breeders are more frequently the results of ‘involuntary’ dynamic decisions that can occur in both the breeders and floaters of the same population. Density dependence affects life-history traits and is one of the key processes in bird population dynamics (see review in Penteriani et al. 2006a) in the following ways: (a) in stable, saturated populations living in homogeneous habitats, density-dependent reproduction generally shows a negative relationship with population density, i.e. the higher the density the lower the fecundity; and (b) there are many causes of density-dependence, and these can act simultaneously at different spatial scales.

Previously, we reported a crucial link between the population dynamics of birds in their settlement and breeding areas (Penteriani et al. 2005a,b); such a strong relationship between floaters and breeders of the same population suggests that floater dynamics within settlement areas may affect breeding population properties such as density dependence. However, most studies on density dependence have mainly focused on the breeding portion of animal populations, and have generally ignored the possible influences of floaters, i.e. that non-breeder mortality has the potential to be a crucial ecological mechanism by which density can affect demographic rates. Consequently, similarly to the previously cited scenario involving the patterns of assortative mating of a population, studies that ignore floater dynamics may fail to understand all of the factors influencing density-dependent population patterns. Two important points may be raised from the long-term field study-based theoretical approach of Penteriani et al. (2006a): (1) high floater mortality may decrease the number of breeders due to low availability of replacement mates, meaning that a positive density-fecundity relationship exists in the breeding portion of the population (i.e. the Allee effect, see reviews in Penteriani et al. in press) and (2) in the same way that population dynamics within breeding areas have a strong influence on dispersal, it is crucial to consider floater dynamics and behaviours when modelling population dynamics for the whole
population. Floaters are not ‘animal seeds’ randomly wandering in an infinite space; instead, their behaviours and movement patterns are key factors helping determine the structure of the whole population. As such, the study of population dynamics in dispersal areas warrants the same level of interest and awareness as breeding population studies. Indeed, floaters may be the answer to our unsolved questions on population regulation and changes, and demographic tendencies in breeding territories.

As for the previous cited Allee effect, a floater perspective may be a novel way to approach such a property of declining populations (Penteriani et al. in press). In fact, the study of floater dynamics can help us gain additional information on the causes of (and their origins) a typical Allee scenario, in which small populations show a positive relationship between population growth rate and population size, increasing their likelihood of extinction through decreased reproduction and/or survival. Although the Allee effect relates to the breeding portion of a population, the extinction process itself, which starts because of the scarcity of available mates (the difficulty of finding a partner represents the most frequently mentioned cause of the Allee effect), can originate from or be increased by high floater mortalities within settlement areas. Thus, simply knowing that an Allee effect is threatening a population may not help reverse its fate; conservationists must also understand where (e.g. floater settlement areas) to direct protection efforts in order to most effectively increase the species/(meta)population density.

Age Cohorts of Bird Populations:
Increasing Rates of Floaters’ Acquisition of Breeding Territories as a Warning Signal of Population Decreases

Early in the study of animal (meta)populations, we appreciated the importance of floater age and their potential as available recruits for the response of natural populations to environmental changes (see review in Rohner 1996). For example, some species have been able to recover from human-induced mortalities through high recruitment of juveniles floating around the breeding (meta)populations (e.g. Wyllie and Newton 1991). Little information is available on the age composition of floaters, but it is generally accepted that non-breeding populations are mainly composed of juveniles (Newton 1991, 1992, Rohner 1996). Consequently, pools of juvenile floaters are especially important in species for which the age at first breeding is early or can decrease when the availability of breeding territories increases (Ferrer et al. 2004). For a floating individual, age also represents the residual reproductive value that will determine the acceptance or rejection of a breeding opportunity. This means that the adaptive acceptance of risk for reproductive promise depends not only on the quality of the available breeding territories or mates, but also on the expectation of surviving to breed in future years (see Hunt 1998). Individuals near the end of their longevity may be more likely than juveniles to accept breeding opportunities in substandard situations, or attempt to intrude into a territory with potentially dangerous owners. Likewise, factors such as high winter mortality, prior experience and
current physical conditions can determine different local patterns of floater entrance into reproductive territories as new breeders.

Franklin (1992), in his work on northern spotted owls, provided what appears to be the first evidence that a change in the age of breeders can function as a warning signal of an imminent decline in the territorial population, underscoring the importance of monitoring not just the numbers and locations of breeders, but also the age of breeding populations. This is an essential concept in conservation biology, because monitoring the composition of recruits from the floating population may allow us to predict future population declines in the early stages, when it might be possible to prevent such declines. Indeed, considerable increases in the proportion of juvenile floaters within breeding populations were reported by Kenward et al. (1999, 2000), Balboni et al. (2003) and Ferrer et al. (2003). Such increases in the proportion of juveniles in the breeding sector of a population may be due to increases in the pre-adult and/or adult mortality rates, or in the availability of resources such as nest sites or food. Indeed, for both the Bonelli’s *Hieraaetus fasciatus* (Balboni et al. 2003) and Spanish imperial eagle (Ferrer et al. 2003), the observed decreases in age at first breeding were due to increased adult mortality rates. These results highlight the importance of long-term studies of demographic traits, especially age at first breeding and productivity, in long-lived territorial avian species characterised by deferred maturity. Furthermore, regular monitoring of the age-structures of territorial pairs can be a potentially reliable method for forecasting changes in population viability. Such methods may have better predictive power than the simpler and more common surveys counting the number of pairs present in the breeding territories each year, as highlighted by Franklin in the early 1990s. In this way, the monitoring of “early warning signals” that can foretell population declines, along with analyses examining specific features of the floater population (e.g. increased access to breeding sites), provide useful tools for improved conservation biology.

Finally, an interesting conclusion may be drawn from floater recruitment in populations undergoing breeding populations decline. Franklin (1992) proposed that if breeder numbers decrease significantly, the floating population could become exhausted through increased recruitment to the reproductive component. More than fifteen years later, Ferrer and Penteriani (in press) supported this thought in their report on the temporal trends of the Spanish imperial eagle population in the Doñana National Park. The history of this eagle population constitutes a well-documented example of how a population that began on the increase and then reached stability could later approach extinction due to the dual effect of increased breeder mortality and a consequently low availability of floaters. A high recruitment rate of immature eagles would have the same effect on the population as a hypothetical increase of floater mortality, i.e. the appearance of a positive relationship between density and fecundity (Penteriani et al. 2005a) due to the increasing difficulty of replacing a lost mate. In fact, although floaters entered the eagle reproductive population as new breeders when breeder mortality increased, this recruitment never allowed the population to increase to a stable or saturated level, due to high adult mortality (i.e. floaters were not sufficient to replace all of the lost mates among the breeding population). To our knowledge,
this is the first time that the study of both portions of an avian population allowed detection of a new mechanism capable of engendering the Allee effect (see review in Penteriani et al. in press), supporting Franklin’s idea that the floating population could become exhausted through increased recruitments within breeders.

Breeding areas vs Temporary Settlement Areas: A Lesson for Conservation Biology

The dispersal behaviours and patterns of floaters are crucial elements in conservation biology. For species needing recovery plans, an accurate knowledge of dispersal behaviour can be a key factor of conservation success, since efficient reintroduction/restocking requires accurate knowledge of the animals’ movement patterns (e.g., Walls and Kenward 1998).

Because the areas where dispersers settle are unknown or difficult to detect, fewer efforts are typically devoted to the conservation of these sites compared to breeding territories; however, this can decrease the effectiveness of conservation plans and action. Population studies, analyses of population viability and extinction risk assessments that ignore the dynamics of dispersers within settlement areas may fail to understand how and why animal populations decrease, and may support inappropriate or ineffective conservation action.

Increasing evidence indicates that (a) dispersers may frequently use areas in which high levels of anthropogenic disturbance result in high mortality rates; and (b) settlement areas can look very different from breeding areas (Fig. 1). Thus, while apparently low-value areas are not typically considered in conservation plans, they may be inhabited by the majority of floaters waiting for breeding opportunities (e.g., Ferrer and Harte 1997, Delgado and Penteriani 2005; see also Fig. 1). Therefore, because conservation efforts targeting endangered species and/or populations focus on breeding areas or nesting sites, they may be ineffective if the real problem is located in the settlement areas. As a result, human and economic efforts are wasted in locations other than those in which conservation measures are really necessary. In fact, declines in breeding population size could divert attention from critical problems in the floater pool. Along the same lines, the reserve design theory and the idea of creating reserves to ensure species and population persistence usually focuses on the areas occupied by breeders only (e.g., Rodrigues et al. 2000, Araújo et al. 2002); in the future, such plans should also account for non-breeding habitats that play a critical role in the larger-scale persistence of the species (e.g., Williams 1998). Conversely, we risk underestimating the threat when the main problem affecting a species/population is not located in its breeding territories, where the effects of floater mortality only appear dozens of years later than their beginning. Therefore, the absence of information on the location of settlement areas and the dynamics of individuals within them (for the majority of species) may catch us unprepared to halt population declines.

CONCLUSIONS: Floaters, Necessary but Sometimes Hostile

Over the past decades, researchers have increasingly focused on understanding the behavioural mechanisms underlying the
floaters' life and the relationships between floaters and territory owners. The earliest studies essentially painted a portrait of the individuals that occupied the floater portion of a population, mostly in terms of the floater's age class, individual quality and hierarchical position within the population of floating individuals. Thereafter, researchers began to investigate the characteristics of floater home ranges, their strategies for becoming breeders, and the nature of the contests that can arise when an owner detects an intruder or a floater actively tries to force an owner to leave its territory. Over time, it became accepted that floaters can buffer, regulate, and stabilise populations, not just beat up and disturb owners in their reproductive tasks.

The words of one of the first persons to be fascinated by floaters (Brown 1989:313-314), resume their complex world and mission: "...the surplus becomes a predictable feature of the environment of the population and the possibility of evolutionary adaptation to it emerges." That is, the (breeding) population may show specific adaptations to the presence of a persistent floater pool close to or within breeding areas, meaning that floaters can be a fundamental evolutionary force shaping the attributes of the entire population. In general, floaters should be considered a necessary but sometime hostile component of almost all bird populations (Brown 1969). Delayed maturation and changes of plumages from juvenile to sexually mature individuals, migration habits and rate of philopatry, clutch sizes and sex ratios, year-round territoriality, territory size and home range overlaps (as a trade-off between the capability of defending a territory from intruders and having sufficient resources within them), group territoriality (where additional members of family groups aid in the detection and chasing of intruders), degrees of mate fidelity and polygon (as an evolutive adaptation to the contemporaneous availability of surplus potential mates) may represent some of the characteristics of bird population that could also mirror different forms of adaptations towards this 'invisible' but strong component of populations, the floater.
Figure 1. BREEDING vs. SETTLEMENT AREAS
The world of breeders and the world of floaters can be extremely unlike. This reality is mirrored by the impressive difference in landscape structure and habitat quality between these two examples of a breeding site (1A) and a floater settlement area (1B) of the same species, the eagle owl. Such differences may engender dangerous mistakes in species conservation: breeding areas, both for major wilderness and because breeders are generally simpler to detect than floaters, are generally easier to protect than the frequently human-altered habitats of settlement areas, in which mortality rates may be extremely high (e.g., electrocution, car collision, shooting).
Figure 2. The complexity of the 'Underworld' of Floaters: Their Origins and Effects on Breeders and Breeding Populations

Floaters are mainly the result of several not mutually exclusive factors, which can also interact at the individual level within the same population. Factors originating floaters can be grouped in three main blocks: (1) external factors, as the levels of saturation within breeding areas and the despotic distribution of territory owners; (2) a deliberative choice, when delay breeding increases fitness; and (3) a miscellaneous of very different causes, from the chance to stay in the right site at the right moment (e.g., to fill a vacancy in a territory) to the dominance status. Both the features of the breeding population and the decision to start or not breeding are the result of habitat quality. As a consequence of the heterogeneous distribution of high- and low-quality patches, floaters are not uniformly distributed in space. This means that their positive effect on the stability of (main)populations, or their negative pressures on breeders, as well as the impact of environmental stochasticity on floater pools, follow an heterogeneous distribution strictly related to the spatial distribution of resources. Finally, in their role of indispensable (the 'light side') but frequently inopportune (the 'dark side') component of animal populations, floaters may have very diverse effects on the behaviors and dynamics of the breeding portions of populations.
2
Methodological Considerations
THE SPECIES AND STUDY AREA

One of the greatest challenges in science is the search for general rules to explain the high variability of different patterns and behaviors that we observe in biological systems. But this pursuit is rendered difficult due to the amazing diversity and richness of life histories of animal species. Moreover, due to the productivity needs of modern science, ever and ever easier (and similar) limited range of species has been considered as good biological models to study, to experimentally manipulate and to rapidly obtain publishable results. Although the selection of such biological models undoubtedly allows easy manipulations and experiments, as well as large samples, there is a significant risk of discovering only partial truths. In other words, we only reveal the rules that govern the biological cycles and actions of these easy-to-study organisms. But we cannot envisage deeply understanding and explaining natural diversity by a narrow range of biological models. What about the other sides of the truth? We forget that the variety of forms and traits of animal species is an organism’s response to a complex and structured world that cannot be exclusively solved in aviaries, aquariums or, more generally, controlled environments. For this reason, the choice of good biological models is crucial. But what is a good biological model? The complexity of patterns that we observe in biological phenomena, strategies and evolutionary routes have naturally guided my “scientific curiosity” towards those species and systems that were unusual and less studied. They are more difficult to study, but they may also offer new and unexpected sights of ecological questions, giving us the possibility to present original and novel results. Also when approaching biological themes on which researchers have focused their attention from several decades:
The Eagle owl (Bubo bubo), the largest owl in the world, is a sexually plumage-monomorphic and socially monogamous long-lived species. It is a sedentary and territorial owl, with a low reproductive rate (Penteriani 1996). It is a generalist both in diet (e.g., Mikkola 1994, Lourenço 2006) and nest choice (e.g., Mikkola 1994, Penteriani et al. 2001, 2002, Marchesi et al. 2002, Martinez et al. 2003), having an important impact on bird communities (Sergio et al. 2003). This top predator, with a vulnerable conservation status (Sergio et al. 2004), is widely distributed throughout Palearctic Regions (Mikkola 1994, Penteriani 1996). It occurs in a variety of habitats, ranging from boreal forests to Mediterranean scrubland and steppes, including rocky and sandy deserts (Mikkola 1994, Penteriani 1996).

This study was conducted in the Sierra Norte (Sierra Morena massif), 20 Km north of Seville (southwestern Spain). The area comprises an artificial lake (Embalse del Gergal, 250 ha), two river valleys (Cala and Huelva rivers) and its surrounding hills, ranging between 60 and 200 m in altitude. The landscape is dominated by sparse woodlands composed of Holm Oaks Quercus ilex, Gall Oaks Quercus faginea, Stone Pine Pinus pinea, Olive Trees Olea europaea, Lentisk Pistacia lentiscus and small plantations of Eucalyptus Eucalyptus sideroxylon. In many areas, scrubland has replaced woodland. Most of the areas, is managed for game species (mainly Red-Legged Partridges Alectoris rufa and European Rabbit Oryctolagus cuniculus).
DATA COLLECTION

From 2003 to 2006 we radiotagged 74 owlets (2003: n = 8; 2004: n = 18; 2005: n = 26; 2006: n = 22) from 12 nest sites when they were approximately 35 days old. Individuals were fitted with a teflon ribbon backpack harness that carried a 30 g radio-transmitters (Biotrack Ltd, Wareham BH20 5AJ, Dorset, UK), with a mercury posture sensor that allowed us to discriminate rhythms of activity by changes in the radio signal of the transmitters. The backpacks were attached to owl wings. Each transmitter backpack and harness weighed less than 3% of the weight of the smallest adult (1500 g) of our eagle owl population (1761 ± 231.7 g, n = 17 adult owls), as recommended by the U. S. Geological Survey Bird Banding Laboratory. Because young were still growing, backpacks were adjusted so that the teflon ribbon could expand. After 4 years of continuous radiotracking of 17 breeders and 74 dispersing owls, we never recorded a possible adverse affect that could be directly attributed to backpacks on birds (Delgado & Penteriani, unpublished data; see also Sunde 2006 and references therein). We manipulated and marked owls under the Junta de Andalucía – Consejería de Medio Ambiente permits No. SCFF5-AFR/GGG RS-260/02 and SCFF5-AFR/CMM RS-1904/02.

INDIVIDUAL QUALITY AND SEX

Owls were aged following Penteriani et al. (2005d) and were sexed by molecular procedures using DNA extracted from blood (Griffiths et al. 1998). To determine individual physical condition, we measured morphological, biometrical, biochemical and blood parameters when owls were approximately 35 days old. Morphological and biometrical measurements were summarized into a body condition index (BCI) estimated by a reduced major axis (RMA) regression (Green 2001), using
logarithm of both body mass (to the nearest 10 g, with 1 kg Pesola scales) and tarsus length (using a digital calliper, ± 0.1 mm). The principal aim of the BCI is to separate aspects of body mass related to structural size from aspects reflecting fats and other energy stores. Thus, BCI measures animal’s fitness, with higher values meaning higher fitness (Green 2001).

To obtain biochemical measurements, blood samples were collected and stored in tubes with heparin at 4°C until arrival at the laboratory, where they were centrifuged for 10 min at 4000 rpm and the plasma was separated and stored at -78°C. From plasma samples, cholesterol, triglycerides, uric acid, urea, glycerol and total proteins concentrations were determined using a spectrophotometer (Screenpoint 2, COR SRL, Ginestra Florentina, Italy), using commercial kits (BIOLABO). These biochemical parameters have been shown to be good indices of body condition in birds (e.g. Alonso-Alvarez et al. 2002).

Blood smears (fixed with the GIEMSA method) were used to measure both the immunodefense and the levels of stress and health. For such propose, and following Figuerola et al. (1999), we estimated: (a) the total leucocyte count, by scanning 20 fields at 40 x, and then extrapolating the total number of leucocytes counted to 100 fields. This number is assumed to be equivalent to the number of leucocytes per μl of blood; (b) the proportion of the different types of white blood cells (eosinophils, lymphocytes, monocytes and heterophils) by counting 100 of white blood cells in each smears by microscopy (x 100) and under oil immersion (Ortho & Espada 2007); and (3) the intensity of the parasite Leucocytozoon spp. The presence of the blood parasite Leucocytozoon spp was ascertained during white blood cells counts.
INDIVIDUAL TRACKS

We defined the different life phases as follows. The postfledging dependence period (hereafter PFDP) started when the first juveniles left the nest. Because the majority of nests in our study area were on the ground or on small cliffs this happened approx. at an age of 40-45 days (late March in our study area; see Penteriani et al. 2005c). During the PFDP we performed periods of intensive radiotracking two times per week, from one hour before sunset to one hour after sunrise. In these radiotracking sessions we visited all the nests and radiolocated owlets from all family units simultaneously. Family units were monitored with an hour time interval between successive locations during the whole nights. Night locations of radio-marked animals were carried out via triangulation. In total we obtained 1962 locations of 41 tagged owlets.

Such a period lasted until the beginning of the natal dispersal. Natal dispersal started when the distance between successive moves became larger than the average distance travelled by each animal (Palomares et al. 2000; see chapter 5). This happened at the end of August in our study area, when birds were $170 \pm 20.51$ days old (range = 131 - 232 days). We consider two different temporal scales: (a) during the nightly activity periods: owls were tracked individually in 163 continuous radiotracking sessions, with a total time duration of 1840.25 hrs, from when the owls started to disperse until they either died or their battery transmitters failed. A continuous radiotracking session is the following of a focal individual during the whole night (i.e. from 1 h before sunset to 1 h after sunrise; mean time duration of a radiotracking session $\pm$ SD = 11.28 $\pm$ 2.13 hrs). We recorded a location ($n = 2934$) each time that we detected a change in either individual posture or position (mean number of locations per
radiotracking session ± SD = 18 ± 4.62). Such changes were detected by a fixed antenna located on the roof of a car. Locations were done using triangulation with a 3-element hand-held Yagi-antenna connected to ICOM (IC-R20) portable receivers (www.icom.co.jp); and (b) for the weekly type of radiolocations: when they were at their diurnal roost sites. We used ArcView v 3.2 and ArcGis v 9.0 geographic information system (GIS) softwares (ESRI) to obtain map representations (1:25 000) of the different move paths.
3
How Fledglings Explore Surroundings from Fledging to Dispersal

by

María del Mar Delgado, Vincenzo Penteriani & Vilis O. Nams
Movement is a primary mechanism underlying animal distributions. The movement process affects individuals’ search success and, subsequently, the dynamics and persistence of populations. Little, however, is known about the characteristics of movements during the postfledging dependence period, a phase of the biological cycle of bird species during many of them can show important displacement around the natal nest. We studied path search strategies employed by eagle owls (Bubo bubo) during this period. Our results reveal that during the postfledging dependence period animals show dynamic movement behaviour that might be related to the development degree of individuals’ mobility and cognitive abilities. Immediately after leaving the nest individuals moved with short steps and focused their activities very close to the nest, but after a few weeks individuals travelled further and faster. Moreover, using fractal analysis we demonstrated how an organism's can change search path during the postfledging dependence period.

KEYWORDS: eagle owl, fractal analysis, path search strategies, perceptual range, postfledging dependence period
The study of animal movement patterns allows us to understand ecological processes at various spatial and temporal scales (Kareiva and Shigesada 1983, Wiens et al. 1995, Blackwell 1997). Animal movements can be influenced by many abiotic and biotic factors, such as landscape scales and features (Wiens and Milne 1989, Zoller and Lima 2003, Heinz and Strand 2006), interspecific and intra-specific interactions (e.g., density of conspecifics, competition and predation; Wiens et al. 1995, Turchin 1996, Bowler and Benton 2005) and food availability (Boyd 1996, Garcia et al. 2005). Such elements generate different movement behaviours and search strategies among individuals and species under different conditions, providing clues to understanding how animals respond to landscape scale and structure. These factors, however, cannot be considered independently of the potential effects of animal cognitive abilities (With and Crist 1996, With 1997, With et al. 1999). Animals' spatial memory and learning allow them to move through their landscape as efficiently as possible (Saarela et al. 1988, Vuilleumier and Perrin 2000). The abilities of animals to move between fragmented habitats are an important factor driving the structure and distribution of organisms (Zoller and Lima 1999). Moreover, ecologists have identified animal movement as an important determinant of population dynamics (Turchin 1986, Hanski 1996, 1999, Morales et al. 2004).

Until now, most movement studies have focused on: (a) movements within the home range (e.g. Worton 1987, Sunde and Redpath 2006); (b) search strategies directed toward favourable habitat patches (Zoller and Lima 1999); (c) the response to fragmented habitat (e.g., Crist et al. 1992, With and Crist 1995, Wiens et al. 1997); and (d) foraging movements in heterogeneous landscapes (e.g., Turchin 1991, Crist et al. 2002, Bailey and Thompson 2006). Due to the impact on floaters on breeding (meta)population dynamics (Hanski 1999, Heino et al. 1997, Penteriani et al. 2005a, b, 2006), dispersal has also become a main focus of much current research on animal movements (Bowler and Benton 2005). However, few studies have analysed the temporal and spatial movement patterns before dispersal.

In avian species, the period from fledging to independence is known as the postfledging dependence period (hereafter, PFDP). During this stage, juveniles gradually have to, for example, develop flight abilities, and acquire skills and learning about their close environment (Sullivan 1989). The different behavioural options of search strategy in this critical period might affect the fate of individuals.

This period is a crucial phase of avian breeding cycle because it represents the time in which individuals reach the necessary body condition for dispersal. All the reproductive efforts put by parents during the previous stages, i.e. territory defence, copulation, incubation and nesting, risk being lost if the PFDP occurs in hostile or uncertain environments/conditions for fledglings. The PFDP is also a dynamic phase, in which juveniles increase their mobility (Bogner and Baldassarre 2002, Kershner et al. 2004, Myers and Vaughan 2004, Penteriani et al. 2005c, Wiens et al. 2006); if the increased
travel occurs in hostile or uncertain habitats, mortality could increase (e.g. predation; Sundel 2003; electrocution, Sergio et al. 2004). In addition, because juvenile mobility increases, parental protection decreases. This increase in juvenile mortality affects breeding populations because of the reduction of the floater sector of a population (Delibes et al. 2001; Penteriani et al. 2005a, b, 2006). Finally, PFDP is a crucial phase because individuals have to: (1) enhance muscular development, (2) experiment with the external world and conspecifics without the protection of the nest, and (3) learn essential skills to survive as an adult.

Despite its importance, information on this phase is scarce and considered one of the missing links in our understanding of avian life-histories (Sullivan 1989, Weatherhead and McRae 1990, Rappole 1995). A knowledge of movement patterns during PFDP is one of the most useful tools to understand this final phase of the breeding cycle, as well as to be aware of the possible risks to which the fledglings are confronted. This is particularly important in the case of endangered species (as many raptor species), which during their exploratory moves during the PFDP may encounter various stochastic events.

Until now, the few studies analysing the PFDP have mainly focused on survival (e.g. Monros et al. 2002, Sundel 2005, Hylton et al. 2006, Adams et al. 2005) and the length of the dependence period (Ferrer 1992, Amato et al. 2000, Minguez et al. 2001). Little is known about the spatial and temporal movement patterns of juveniles. Although some studies have measured movements, they mainly reported some characteristics of juvenile movements, such as the displacements from the nest or the area used by juveniles (Kershner et al. 2004, Myers and Vaughan 2004, McClaren et al. 2005, Penteriani et al. 2005c; Wiens et al. 2006).

Our objective in this study was, by means of a radio-tracking study on the postfledging dependence period of the eagle owl Bubo bubo, to describe and analyse the patterns of movement during this phase. In particular, we focused our attention on: (1) the essential characteristics of movements, family unit interactions and territory use throughout the PFDP; and (2) finding out how movement patterns change during this stage of the breeding cycle.

Materials and methods

DATA COLLECTION
We conducted field research from late March to early August 2004 and 2005 on 41 eagle owl fledglings (24 males; 17 females) from 13 different nests.

We defined the different life phases as follows. The PFDP started when the first juveniles left the nest. Because the majority of nests in our study area were on the ground or on small cliffs this happened approx. at an age of 40-45 days (late March in our study area; see Penteriani et al. 2005c); such a period lasted until the beginning of the natal dispersal. Natal dispersal started when the distance between successive moves became larger than the average distance travelled by each animal (Palomares et al. 2000, Delgado and Penteriani, in revision). This happened at
the end of August in our study area, when birds were 170 ± 20.51 days old (range = 131 - 232 days).

During the PFDP we performed periods of intensive radiotracking two times per week, from one hour before sunset to one hour after sunrise. In these radiotracking sessions we visited all the nests and radiolocated owlets from all family units simultaneously. Family units were monitored with an hour time interval between successive locations during the whole nights. In total we obtained 1962 locations of the 41 tagged owlets.

**POSTFLEDGING PATHS ANALYSIS**

We divided the PFDP into 6 periods of 20 days, following Penteriani et al. (2005c) and Delgado and Penteriani (2007).

**Characteristics of movements, territory use and family unit interactions**

To study the essential characteristics of movements, for each of the 20-days period we calculated the mean distance between successive locations, and the mean distance between the nest and each location point collected during the nights of radiotracking. To evaluate the interactions between siblings (i.e. family unit interactions) we estimated the mean distance between owlets from the same family unit (by using individual locations recorded simultaneously). Finally, to understand how the fledglings explore surroundings of the nest, we estimated the postfledging areas (hereafter PFAs) using 95% minimum convex polygons (MCP; Hayne 1949). These areas were calculated for each individual and during the different nights; then, we computed the mean of these areas in each 20-days period.

**Spatial and temporal movement patterns**

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

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

STATISTICAL ANALYSES

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

The original fractal D was non-normal, but its logarithm fitted a Gaussian distribution (Katz and George 1985). Then, we used Pearson’s bivariate correlation to analyze the degree of tortuosity of the search paths among 20 days-periods.

Results

Movement characteristics, territory use and family unit interactions

Average step length, distance from the nest, between-sibling distances and PFAs size all increased with time throughout the postfledging dependence period (Fig. 1). Step lengths were short [mean = 543.6 ± 32.0 m (95% CI)] when juveniles left the nest and until 20 days after fledge. In the next 60 days, the distance travelled between successive moves significantly increased (F_2,66 = 6.66, p < 0.0001; Fig. 1a), reaching the highest values before start of dispersal [mean = 754.2 ± 160.8 m (95% CI)]. Also, juveniles were closer to the nest during the first 20 days-period [394.8 ± 25.5 m (95% CI)], travelling further from the nest during the rest of the PFDP (F_2 = 61.65, p < 0.0001), reaching a maximum distance just before dispersal (Fig. 1b). There were no significant effects on any of the movement characteristics of owlet sex, year, nor their interactions (all p > 0.40).

Between-sibling distances showed a significant interaction between the effects of sex and time (F_1,5 = 28.73, p < 0.0001). Until owlets were 20 days since they left the nest, family units were closer together and, independently of the sex of juveniles, were all together [mean = 197.3 ± 30.3 m (95% CI)]. Between-sibling distances increased with time as individuals became increasingly mobile (Fig. 1c). The closest proximity was between siblings of different sex [mean = 237.8 ± 30.6 m (95% CI)], the next closest was between males [mean =
289.9 ± 18.9 m (95% CI), and the furthest was between females [mean = 309.5 ± 24.9 m (95% CI)]. Just before the start of dispersal, family units seemed to dissolve, with a mean spacing between individuals of 613.4 ± 148.9 m.

PFAs showed two main significant effects. In fact, PFAs varied between years (with owlets having larger PFAs in 2004 [mean = 0.4 ± 0.10 Km2 (95% CI)] than 2005 [mean = 0.1 ± 0.04 Km2 (95% CI)]) and with time since fledging; owlets increased the areas prospected from 0.16 ± 0.05 Km2 when they left the nest to a the maximum of 0.94 ± 0.28 Km2 just before dispersal (F_{1,5} = 308.74, p < 0.0001; Fig. 1d). We did not detect any effects of owlet sex on PFAs.

**Scaling test for directed movement and fractal analysis**
Path tortuosity significantly decreased with time since fledging (r = -0.39, p < 0.05; Fig. 2a). Paths were more tortuous when owlets left the nest [mean=1.39 (95% CI: 1.12-1.27)] than at the end of the entire dependence period [mean=1.09 (95% CI: 1.06-1.11)]. At the same time as when the mobility of owlets reached the highest level (i.e., when they also travelled significantly farther distances), their movements described straighter paths.

The statistic CRW_{Det} was negative during the entire PFDP (Fig. 2b), indicating that the movement paths covered a shorter distance than a CRW would. The confidence intervals do not include zero, so the power of the test is sufficient to conclude that juvenile paths during the dependence period was unoriented.
Figure 1. Movement characteristics of fledgling eagle owls among the 6 blocks of 20 days-period during the postfledging dependence period. Values are means and error bars are ± 95% confidence intervals. (a) Mean distance between successive nightly locations, (b) distance from the nest, (c) distances among siblings, and (d) size of postfledging areas all increased with time throughout the postfledging dependence period.

Discussion
The analysis of the fledgling movements allowed us to detect several different behaviours during the PFDP. After leaving the nest, owlets moved with short steps, focusing their activities at or very close to the nest. Consequently, at this time, the PFAs prospected by young were limited to areas around the nest. After a few weeks, the movements of fledglings showed a marked change, with their movement trajectories longer than initially observed. Moreover, they were frequently located farther from their nests. Although we did not directly analyse the relationships between body condition and feather development and movements, this change in postfledging behaviour may be probably due to the increased flying ability of owlets, as reported for other species (e.g., Belthoff and Ritchison, 1989, Ferrer 1992, King and Belthoff 2001, Míguez et al. 2001). In fact, when the young leave the nest (approx. 40-45 days): (a) primary remiges and
rectrices (approx 8-9 cm of feather visible out of the sheath) are only 80% and 40% of their definitive length respectively; (b) secondaries are still encased in approx 7-8 cm sheathings; and (c) wing coverts are only starting to emerge (Penteriani et al. 2005c). Because at this stage they cannot fly but rather walk and jump among rocks and bushes, the movement patterns we observed mainly reflect this form of displacement, i.e. that of a “terrestrial bird” that cannot still use its wings.

Although most fledglings included the nest within their activity area throughout the entire PFDP, young eagle owls continued to expand their PFA size indefinitely until departing from the parent territories. Similar patterns reported by McClaren et al. (2005: goshawks Accipiter gentilis), Wood et al. (1998: bald eagles Haliaeetus leucocephalus), and Beltzoff and Ritchison (1989: eastern Screech-Owls Megascops asio) suggest that nests are still important throughout the postfledging period for raptors.

In the early PFDP, siblings tended to move together, with a constant distance between them during the first weeks. But, as independence neared, the distance increased progressively and family units seemed to partially dissolve. This is in accordance with Newton’s (1979) idea that fledgling of raptors tend to perch apart, as also observed by Bustamante and Hiraldo (1990), Ceballos and Dorázar (1990) and Bustamante (1994) (but see O’Toole et al. 1999). Increased sibling distance has been attributed to some conflict behaviours between juveniles as long as they grow or increased flight abilities.

Although sibling distances increased among the entire dependence period, juveniles of different sexes tended to stay close together, during the whole PFDP. Such a link among siblings during the whole PFDP does not necessarily break up after the start of dispersal (Delgado & Penteriani, unpublished results). In contrast to other raptor species like the black kite Milvus migrans (Bustamante & Hiraldo 1990) and the lesser kestrel Falco naumanni (Bustamante & Negro 1994), some eagle owls move together during the first steps of dispersal (Delgado & Penteriani, unpublished data).

Spatial and temporal movement patterns
Our fledgling eagle owls showed unoriented movement (CRWdm < 0; Nams 2006b). This is not surprising due to the fact that: (a) they are fed and protected by their parents. Consequently, they don’t need heading its movements towards shelters or foraging areas; (b) after leaving the nest, young are embedded in a new habitat that they have to learn, i.e. they move randomly during territory explorations; (c) their flight abilities and perceptual range are not yet completely developed, so unoriented walk represent the best strategy to cover larger areas at small scale (Garcia et al. 2005).
The fledglings also should increase their perceptual range during the PFDP. In early PFDP movement paths were more tortuous, and became progressively straighter as independence approached. Since the paths were unoriented then we suggest that this increase in straightness may indicate an increase in their perceptual range, as follows. The perceptual range, the maximum distances from which an animal can perceive the presence of a particular landscape element as such (Zollner 2000), represents the informational landscape window for the animals. When animals are moving with an unoriented search strategy, the behavioural mechanisms governing movement are working at small spatial scales (Nams 2006b), and those small scales are determined by the perceptual range. Increasing the perceptual range would increase the natural step length of their movement path, resulting in straighter paths.

An animal's perceptual range can be considered as a determinant of population dynamics (Pulliam et al. 1992, Lima and Zollner 1996, Zollner 2000). From early PFDP
Figure 2. This illustrates how animals can change the movement paths during the PFDP. (a) Scaling test applied to movement paths of young eagle owls during the postfledging dependence period. CRWDiff measures the distance travelled by the movement path as compared to a correlated random walk (CRW). The significantly negative CRWDiff values show an unoriented movement. (b) Path tortuosity (Fractal D (mean ± 95% confidence intervals) decreases with time throughout the postfledging period. Values are means and error bars are ± 95% confidence intervals. After owlets leave the nest movement paths become progressively straighter as independence drew near.
individuals are developing, day-to-day, the ability to perceive habitat at a distance like an important behavioural mechanism that may have influences in the whole of the biological life cycle. Perceptual range has important ecological implications since it may be determinant of an appropriate search strategy (Zollner and Lima 1999) and, consequently, influence both fledgling survival (i.e. their availability as future floaters of a population) and distribution patterns of (meta)populations.

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

To conclude, little is known about how animals make movement-related decisions during the PFDP, nor do we have a good understanding of how the different behavioural search strategy options facing for animals in this critical period might influence their fate. In fact,
Acknowledgements

For their help with logistics we are grateful to P. Barceló, X. Castells, R. Lourrigo and G. Penuelas. The first draft was improved by the criticisms of A. Banks. Funding for this study was provided by a research project No. CGL2004-02780/BOS of Spanish Ministry of Education and Science and LICOR43 (Diego Zamora S.A., www.babh-sld.com). During this work M. M. Delgado was supported by a doctoral grant of the Junta de Andalucía (Consejería de Educación y Ciencia). We manipulated and marked owls under the Junta de Andalucía — Consejería de Medio Ambiente permits No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02.
4
Behavioral States Help
Translate
Dispersal Movements
into Spatial Distribution
Patterns of Floaters

by

María del Mar Delgado & Vincenzo Penteriani
The need to study animal movements during dispersal to better understand population
dynamics has been recently considered to be one of the most crucial topics in spatial ecology.
Dispersal is a non-linear process in which different behavioral mechanisms could be
affecting movement patterns. When analyzing trajectories of organisms within patches, one
of the most common approaches is to describe movement features by random walk models.
Some models (e.g. the residence index) express in terms of random walk parameters the
individual movements within a specific area, trying to relate movement patterns to the
distributions of organisms in space. However, predicting the spatial spread of animal
populations by only taking into account movement trajectories of individuals could not fit
the complex distribution of individuals across heterogeneous environments. When testing
empirically such a prediction by the residence index, as an example of a random walk model
used to predict the spatial equilibrium distribution of individuals, we found the index
severely underestimated the spatial spread of dispersing individuals. The most important
failure of random walk theoretical models is that they only take into account the effects of
environmental conditions on individual movements, completely overlooking the crucial
influence of change in behaviors over time. Such a result warns us of the importance of
taking into account the possible change in an organism's behavior during its life when
predicting general rules of (meta)population abundance, distribution and dynamics from
patterns of animal movements.

KEYWORDS: Bubo bubo, dispersal, ecological diffusion, movement behavior,
movement models, path analysis, population dynamics, residence index
Patterns of animal movement provide a mechanism 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 (Morgen et al. 2004), the coexistence of competitors (Keeling and Grenfell 1997) and, more generally, population dynamics (Kareiva 1990, Turchin 1991, 1998, Hanski 1998). Animal movements vary along heterogeneous temporal and spatial scales (Johnson et al. 1992), and such variation can influence the complex patterns of population spatial structure (Turchin 1991, Johnson et al. 1992, Crist et al. 1992, Wiens et al. 1995, Turchin 1998, Armsworth and Roughgarden 2005).

The analysis of movement patterns is a relatively new topic in ecology and has been largely limited to a few organisms due to the difficulties in sampling animal locations and displacements over extended periods of time and space (Hancock and Mulner-Gulland 2006). This is particularly true in the case of vertebrates during natal dispersal (hereafter dispersal), i.e. the movements from where they were born to where they will breed. In the last decade, dispersal has been the subject of a number of theoretical and empirical studies (e.g. Clobert et al. 2001, Nathan 2001, Bullock et al. 2002), showing that it is a fundamental process underlying population dynamics (Turchin 1998, Skalski and Gilliam 2003). However, while empirical studies have been 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 theoretical models regarding the dispersal process lack a great deal of realism (Travis and French 2000, Godwin 2003, Gautestad and Mysterud 2005), and do not incorporate key behaviors affecting dispersal strategies (e.g. Hanski 1994, Hanski and Thomas 1994, Doebeli 1995, Travis and Dytham 1999). As a consequence, dispersal is a good example of the common problem in ecology of having some knowledge about patterns but poor knowledge about the process behind these patterns (Penteriani in press). In fact, dispersal is one of the most important, yet least understood, features of ecology, population biology, and evolution (Wiens 2001).

Dispersal has been frequently considered as a fixed species-specific strategy, despite it being a complex process involving the behavior of individuals. It can be subdivided into three sequential, but behaviourally distinct, phases (Andreassen et al. 2002, Clobert et al. 2004, Bowler and Benton 2005, Heinz and Strand 2006, Baguette and Van Dyck 2007): (1) start, an individual leaves its place of birth, (2) transfer or wandering, search movements by the floating individual (sensu Penteriani et al. 2006a) while exploring other areas for a variable time period before it definitively settles in a new area, and (3) stop, the individual settles in a more stable zone, i.e. the temporary settlement area occupied during the longest time period across the whole dispersal process or until it becomes an owner of a breeding territory (Penteriani et al. 2005a, b, 2006b).
Although these stages may display different condition dependencies (Bowler and Benton 2005), they were rarely taken into account in empirical studies. There is especially little information on animal movements during the wandering phase, and empirical data on behaviors is almost absent in the vertebrate literature (Andreaassen et al. 2002). In addition, few studies (e.g., Danchin and Cam 2002, Kokko and Ekman 2002, López-Sepulcre and Kokko 2003, Penteriani et al. 2005a, b, 2006a) have focused on the relationship between breeders and the non-breeding portion of a population or floaters (i.e., dispersing individuals able to enter the breeding population when a territory or a suitable mate becomes available; Penteriani et al. 2006a). Because of the strong link between floater dynamics within their settlement areas and breeding population equilibrium and persistence (Penteriani et al. 2005b, c, 2006), studies of population dynamics and analyses of population viability that ignore the dynamics of dispersers within settlement areas may fail to understand population patterns and trends. Selection of the settlement areas, dispersal distances, rate of dispersal success, as well as mortality rates during dispersal largely depend on the search strategy that individuals employ once they have left their original habitat patch (Conradt et al. 2003, Leon-Cortés et al. 2003, Doerr and Doerr 2004, Conradt and Roper 2005). Because dispersal movement behaviors have important consequences in population, community, and ecosystem composition and functioning (Wiens 1985, 1996), ecologists need to identify key behaviors affecting movements of animals as they float in search of stable settlement areas and breeding territories.

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 effectively predict the pattern of animal distribution on short time scales, they tend to fall when longer time periods are taken into consideration. One reason for this shortcoming may rest with problems associated with not considering the influences of both individual behaviors (Fride et al. 1998, Morales et al. 2004) and different habitat conditions (Jonsen and Taylor 2000, Filr et al. 2005) on movement patterns. Above all, the premises of ecological theory related to animal dispersal and, consequently, individual distribution and abundance, urgently need more realistic assumptions that satisfy and represent the real dynamics determining the processes we observe at either individual, population, or community levels (Gaulstad and Mysterud 2005).

In this paper, our immediate goal is to characterize behavior during the wandering (searching) phase through the analysis of movement characteristics. We examine movement length, duration and turning angles of radiotagged eagle owls (Bubo bubo, for more details on the species see Penteriani et al. 2005c, d). Although some studies of animal movements have been carried out to quantify movement paths (Turchin 1991, Wiens et al. 1995), few have been designed to understand behavioural patterns of animals moving long distances (Bascompte and Viá 1997,
We recorded the exact position of each bird weekly, typically when owls were at their diurnal roost.

Analysis of movement paths and the residence index
Because we were interested in describing behaviors during the wandering phase of dispersal, the first step of our analysis was to determine both the start and the stop of dispersal. To identify the start, we plotted both the beeline distance from their natal nest for each location and the average of beeline distances between the whole set of locations and the nest (i.e. the global mean distance) covered for each individual during the dispersal period. Initially, the distance from the nest for each successive location should fluctuate around a low value, as juveniles remain in the parental home range. Following Falomires et al. (2000), we considered dispersal to have started when the distance of each location from the nest became larger than the global mean distance traveled by each animal to its nest (Fig. 1A). That is, when the distance of each location from the nest started increasing progressively rather than fluctuating around a low value. The stop for each individual was determined by plotting the length of successive moves against the average of beeline distance they travelled through. We considered that owls reached the stop phase when the distances became smaller than the average distances of previous moves travelled by each dispersing owl (Fig. 1B); that is, the animal settled somewhere when the distance between successive moves stopped increasing. It is important to call attention to the fact that several stop phases can occur during the

Materials and methods

Radiotracking procedures
We radiotagged 33 owlets from 11 nest sites (2003: n = 6; 2004: n = 10; 2005: n = 17).
whole dispersal process (i.e. from the departure to the nest to the settlement within a breeding territory), and the real end of dispersal only occurs when a floater occupies a breeding territory. Any successive definitive movement from its breeding area represents breeding dispersal and not dispersal sensu strictu. For the scope of this work, and following Andreassen et al. (2002), the stop phase was the moment in which distances of movements travelled by a floating owl revealed that it settled in a stable settlement area.

Our second step was to identify different behaviors of the individuals in the wandering phase. We initially split the data set of the observed radio-locations of each floater into small sequential blocks comprised of a month time interval. Following Palomares et al. (2000), the choice of the temporal bracket was an arbitrary choice. Successively, we measured the total distance between the whole
Figure 1. (A) Analytical determination of the beginning of dispersal. The black line represents the distances (m) between successive moves. Reference line indicates the average distance covered by a dispersing individual to its nest. We considered that an individual started dispersal when all the recorded move distances were superior to the mean of the whole movements. (B) Analytical determination of the stop of dispersal movements (see text for more information). Dark grey blocks represent movement distances when owls are searching for a stable settlement area or a breeding territory; light grey blocks are the distances after the stop of dispersal movements. Reference line indicates the average distance of previous step covered by an individual. We designated that individuals found a stable settlement area or breeding territory when all the recorded move distances were below the mean of all previous movements.
set of locations in each of these blocks, and calculated both the net distance in each block and the net distance from each of these blocks to the natal nest. We separate all paths into two groups matching different behavioural state representing phase during the wandering period (Zollner and Lima 1999): (1) the intensive behavioural state, the observed total distance was higher than the observed net distance (that is, when individuals were moving within an established area; Fig. 2A); or (2) the extensive behavioural state, the observed total distance fluctuated around the observed net distance from locations in each block or was smaller than the net distance from the last location in each block to the nest (i.e., when owls were moving; Fig. 2A). For each movement path segment of each behavioural state we estimated the minimum convex polygon to find out the overlap between individuals along the different phases of the wandering period and calculated the mean distance between the centers of the areas described by the two behavioural states. Moreover, to make predictions on the relationships between the movements and behavioural states of individuals we calculated and used the distributions of some movement variables (mean lengths, durations and the mean cosine of turning angles between successive locations) for each movement path segment of each behavioural state. While an intensive behavioural state should be characterized by both small-scale movements of short lengths and many reversals and large turning angles, movements in an extensive behavioural state should be longer and characterized by a low rate of turns, with angles smaller than in the intensive behavioural state (Zollner and Lima 1999).

Figure 2. Analytical determination of the different behavioral states in a dispersing owl radiotracked during the wandering phase of dispersal. References lines indicate the total distance between all locations in each block of a month time interval (solid black line), the net distance in each block of a month time interval (grey line), and the net distance from each block to the nest (dotted black line). A floating owl is in an intensive behavioral state (a) when the observed total distance is higher than the observed net distances. When individuals are in an extensive behavioral state (b) the total distance fluctuate around the observed net distance from location in each block or is smaller than the net distance from each block to the nest.

Finally, we used the residence index to compare the predicted vs. real spatial distribution of dispersing owls. Because the paths describing the two above-cited states delimited two spatially segregated consecutive areas, we estimated for each one:

1. mean movement features, as the mean length \( \bar{L} = \frac{1}{n} \sum L_j \), the mean squared length \( \bar{L}^2 = \frac{1}{n} \sum L_j^2 \), the mean duration
\( \tau_j = \frac{1}{n_j} \sum_{i=1}^{n_j} \cos \theta_i \), and the mean cosine of turning angle \( \psi_j = \frac{1}{n_j} \sum_{i=1}^{n_j} \cos \theta_i \), \( n_j \) being the total number of moves recorded for all paths in group \( j \); (2) the quantities \( \gamma = M_1 / a^2 \) and \( \phi = \gamma + (2 - \gamma)w \), to obtain the mean values of \( \gamma \) and \( \phi \) necessary for index computation; and (3) the exponent \( \alpha = 2(\sqrt{\mu_2 - \mu_1})/(2 - \gamma)(\sqrt{\mu_2} - \sqrt{\mu_1}) \), necessary to obtain the Turchin's residence index (1991):

\[
P_j = \eta \psi_j \gamma^{(2 - 2\psi_j) - \psi_j}
\]

We computed the ratio between both residences index calculated in the two areas delimited by the different behavioural states to obtain the predicted ratio (that is, the distribution of organisms expected by the model). Then, we estimated the observed distribution of flocks in the spatially segregated consecutive areas delimited by the two behavioural states as the number of dispersing owls per unit area. We calculated the coefficient between the densities recorded in each area to obtain the observed ratio (that is, the distribution of organisms recorded). 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 characteristics of movements

Most juveniles started their dispersal at the end of August at a mean (± SD) age of 170 ± 20.51 days-old (range = 131 - 232 days-old). Although there was a high degree of individual variation, we found that 30% of eagle owls found a stable settlement area (i.e. shifted from the wandering to the stop phase of dispersal) in the middle of March at a mean (± SD) dispersal age of the stop phase of 395 ± 109.86 days-old (range = 161 - 640 days-old).

![Graph showing distribution of dispersing distances of eagle owls](image)

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 that we identified during dispersal. Black bars represent frequency of distances traveled in the intensive behavioral state, with short step lengths and mode close to zero. The extensive behavioral state (gray bars) is characterized by longer step lengths than the intensive behavioral state and non-zero model distribution.

During the wandering phase of dispersal the majority floating owls (n = 17; 52% of all tagged owls) showed biphase movement behavior, i.e. they switched from the intensive behavioral state typical of
the beginning of dispersal, to the extensive behavioural state (Fig. 2). The time spent in the intensive (mean ± SD = 2.9 ± 0.8 months; range = 2 - 4 months) vs. the extensive (mean ± SD = 9.1 ± 4.7 months; range = 1 - 19 months) behavioural state varied significantly (t = 8.9, df = 79, p < 0.001; t-test). 11 owls (33% of all tagged owls) showed the intensive behavioural state only, whereas 5 individuals (15%) were permanently in the extensive behavioural state.

During the intensive behavioural state the movement behaviour of dispersing owls was characterized by small-scale movements. Individuals tended to move in tortuous paths, with the majority of turning angles concentrated around 166.5 ± 12.5° (circular mean ± 95% CI, Fisher 1995; Rayleigh’s test of uniformity, p < 0.001; Fig. 3A), indicating a high tendency to reverse direction. In this behavioural state, the displacements were generally over short distances, showing zero modal movement lengths and a fat-tailed distribution (Fig. 4), indicating that most movements were close to zero. When floaters exhibited this behavior, their temporal settlement areas overlapped broadly (34% of the total area used during the intensive phase; Fig. 2B).

By contrast, during the extensive behavioural state owls followed straight pathways, with turning angles concentrated around 121.8 ± 31.6° (circular mean ± 95% CI, Rayleigh’s test of uniformity, p < 0.001; Fig. 3B). This state is described by a non-zero mode characteristic of a longer step length distribution than during the previous

behavioural state (Fig. 4). During this latter state the settlement areas of different dispersers did not overlap at all (15% of the total area used during the extensive phase; Fig. 2B). The distributions of turning angles during the intensive and extensive behavioural state were significantly different (Z = 23.77, p < 0.05; Watson’s Two-Sample Test with Ties, Zar 1999).

Comparison of predicted and observed distributions by the residence index
Because the settlement areas used during the two behavioural states were consecutively separated in space (mean distance ± SD = 4036 ± 2258 m, range = 1048 - 7589 m; Fig. 2B), we measured the observed and predicted spatial distribution of owls in each one. Because observed density shifted from 5 (intensive behavior states) to 1 (extensive behavior states) owls per 10 Km², the observed ratio between extensive vs. intensive phases was 0.2. The predicted ratio, calculated between the
residence indices for the two spatially segregated areas, was 0.003. That is, for the extensive behavioral state, the index underpredicted (error = -98%; Table 1) the density of the individuals sharing the same settlement areas.

Discussion
Dispersal is crucial for the persistence of any species and is a key determinant of the viability of spatially structured populations and metapopulations (Duruńing et al. 1995, Hanski 1998, 1999, Ciobert et al. 2001, Murrell et al. 2002). As pointed by Pulliam (1992) and Henein (1998), making predictions about the persistence of a mobile species requires considerations on multiple and contemporaneous factors that describe the demographics and behavior of species under determined landscape conditions.

Dispersal is mainly the result of movements associated with daily activities (i.e. routine movements) and direct movements designed for net displacement and settlement at some distance from the previous location (i.e. special movements). Furthermore, these groups of movements are clearly distinguishable (Van Dyck and Baguette 2005) and both may contribute to inter-population movements. As an end consequence, behavioral movement decisions during the wandering phase of dispersal (i.e. the movements within and between patches while searching for a suitable habitat for successful breeding) can strongly influence the dynamics of spatially divided (meta)populations. Thus, understanding how animals make
decisions regarding movement and incorporating the direct and ultimate effect of these behavioral decisions into population models is an important step for predicting the trajectories of population dynamics.

The analyses of the movement paths of juvenile eagle owls during the wandering phase of dispersal revealed different movement patterns, with important behavioral differences in relation to some proximate factors, like spatial scale of displacements, configuration of trajectories, individual responses to conspecifics and individual-specific types of movement (see also Van Dyck and Baguette 2005). Within the behavioral states we observed in our floating population, some individuals showed extreme movement behaviors, that are they showed only a single behavioral pattern of movement during the wandering phase: 93% of the tagged owls showed an intensive behavioral state only, whereas 15% of them were permanently in the extensive behavioral state. Within a possible range of behavioral choices, the extremes of personalities in vertebrates (Dingemanse et al. 2003, Sith et al. 2004, Boon et al. 2007) were explained by Baguette and Van Dyck (2007) by the “shyness-boldness” dichotomy. Bold individuals are the most aggressive ones, relatively insensitive to external stimuli and able to take rapid decisions. On the contrary, shy individuals act with more caution and are more sensitive or adjustable to external situation, adapting themselves to the environment. Additionally, two empirical studies have documented that bolder individuals disperse further than shy ones (Fraser et al. 2001, Dingemanse et al. 2003). In our scenario, the bold individuals should be those owls showing a permanently extensive behavioral state, with larger and straighter movement trajectories, whereas the shy individuals should be the owls exclusively showing the intensive behavioral state (i.e. short movements and turning angles frequently reversing directions).

As for the 52% of floaters showing a biphasic movement behavior (i.e. they switched between the two states): (a) during the intensive behavioral state, a large number of individuals shared the same settlement areas and conspecific overlap was highest; (b) when in the extensive behavioral state, owls were localized in more exclusive and segregated areas with a notable reduction in conspecific density. With a high level of conspecific density, as during the intensive behavioral state, the best option of a territorial species may be to locate its own patch as quickly as possible, which can best be achieved by a straight search (Zollner and Lima 1999). The movement patterns observed in the extensive behavioral state mainly allowed the achievement of more exclusive and segregated areas. From an adaptive perspective, it makes sense for individuals to adjust their movement behavior according to current conditions, and this can result in a behavioral shift from shy to bold syndromes if there is variance in external conditions. Because causes, consequences, costs and benefits of dispersal can vary not only among species (Bowler and Benton 2005) but also within individuals, a plastic dispersal strategy is expected to respond to this variation. Our
empirical approach clearly supported the idea stressed by Van Dyck and Baguette (2005) that, because there is no one strategy that performs best in all conditions, dispersal can be considered as a dimorphic trait, with some individuals more sedentary and restricting their movements to an intensive or routine type, and some others more dispersive and capable to perform extensive movements. On a more general view, our results are consistent with recent empirical and theoretical studies that have pointed out that dispersal cannot be collapsed into a single parameter, since it is composed of interdependent stages which may display different condition dependencies (Cloquet et al. 2004, Bowler and Benton 2005, Baguette and Van Dyck 2007). Due to simplistic assumptions of some classic spatial population models, dispersal has been often considered as a fixed process: field studies as the present one highlights once again how the dispersal process is both dynamic and complex (Gautestad and Mysterud 2005), with different phases that may be strictly dependent on behavioural decision making.

The residence index states that a population, whose redistribution obeys the Fokker-Planck equation, should: (a) equal the ratio of individual densities in different patches, independent of species; and (b) always match the environmental boundary conditions like the spatial distribution of resources (Turchin 1991, 1998). This means that, if the spatial distribution of individuals is the result of random walk movements, animal population distribution holds an IFD. However, when applying the residence index to a population of a vertebrate species, we found it severely underestimated the real distribution of individuals in space, although the final spatial distribution of individuals continues to fit an IFD. This is a crucial point, because 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 to a looser distribution with no apparent constraints limiting their spatial explorations, i.e. with a free mobility that will ideally distribute themselves at various areas to maximize their fitness. Following our results, we think important to underline that the same species, depending on the status of its individuals (floater vs. breeder), may show both a free and despotic distribution. During dispersal, owls are not territorial and may homogeneously distribute themselves in the space, the distribution of local resources being the only constraints to both displacements and settlements. But when individuals leave the wandering status of floaters to become territory owners within the breeding population, the distribution will be also constrained by territoriosity, 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 organisms spend in the unit area. The highest densities of floating owls were found in those areas in which they spend the shorter portion 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 no density-dependence or conspecific interference, although they are among the fundamental determinants of the spatial distribution of animals (Hancock and Milner-Gulland 2006, Cote and Clobert 2007). Due to high population densities increasing intraspecific competition for local resources, individual interactions can be greatly reduced by repulsive movements, typically biased in the direction of a decreasing population gradient (Turchin 1989, Rosenzweig 1991). Our results showed an active strategy for dispersal, with balanced exchanges of fliers 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 homogenize population sizes; a fundamental factor that may lead the spatial distribution of animal populations close to the IFD (Doncaster et al. 1997, Cote and Clobert 2007).

It is generally admitted that random walk models are based on many basic hypotheses that are easily to control when working in lab conditions, but not in real environments. For example, random walk can be appropriate to model intensive or routine movements within habitat patches (Schtickzelle et al. 2005) but not for interpatch movements during which individuals frequently execute directed movements. In fact, because individuals adopting slow and intensive types of movements are more likely to be located than individuals in a fast-moving linear mode, some field studies designed to estimate dispersal parameters have been likely biased towards intensive or routine movements, largely overlooking special long-distance movements (Van Dyck and Baguette 2005). As an end consequence, any directed or long-distance movement will violate the basic principles of random models.

Although the random walks model has been proved to be valid for a variety of small, passive organisms, it is debatable whether this approach is suitable to describe more complex situations or species, especially when dispersal behavior of individuals is taken into account. An important assumption for random walks models is to consider animals moving with continuous but constant parameters over time: in the residence index calculation, the movement parameter \( \gamma \) is approximately the same in different patches (Turchin 1991). However, we found that the movement parameter \( \gamma \) significantly varied between the two patches we considered, probably as a consequence of the changes in the individual movement behavior that we observed during the wandering phase. When \( \gamma \) varies, the model predictions underestimate the degree of aggregation in the patch with high residence index. Such a possible violation of the assumption of the residence index was already contemplated by Turchin (1991), who highlighted the need to extend the derivation of the formula of its index to cover cases where \( \gamma \) vary in space (e.g. when organisms change movement behavior over time). Nevertheless, whether
the effect of dispersal behavior on the viability of spatially structured populations can at all be described by a simple formula is an open question. When applied to our scenario, one of most important failures of the index and, in a more general way, of the random walks theoretical models, is that they only take into account the effects of environmental conditions on individual movements and, consequently, completely overlook the crucial influence of the change in behaviors (i.e. behavioral states) over time. If the assumptions of the random walks model break down at the individual level, it will also have consequences for population dynamic modelling approaches: including individual behaviors should increase the predictive value of models incorporating animal movements. Although animal behavior is strongly influenced by landscape structure (Wiens 1999, Crist et al. 1992, With 1994, Cresswell 1997), it may be also influenced by temporal scales and, as time passes, behaviors other than locomotion may play increasingly important roles for movement patterns. Consequently, movement behaviors at detailed temporal scales represent a key component in understanding how individuals respond to spatial composition (McIntyre and Wiens 1999, With et al. 1999, Chris et al. 2002, Morales and Eliner 2002, Nams 2003).

Most important, in our opinion, is the fact that the application of real, accurate information on floater dispersal, distribution and abundance to ecological modeling of complex processes based on simple assumptions (i.e. random walks and diffusion processes) fits the challenge proposed by Gautestad and Mysterud (2005) and move a step forward in their attempt to more realistic frameworks that better satisfies ecological realism. Gautestad and Mysterud (2005) highlighted that some aspects of the behavioural ecology of real animals defy the broad applicability of the classic random walks approximations. Their most novel contribution to ecological theory has been the identification that: (a) the establishment of a home range implies nonrandom, memory-dependent revisits to formerly visited areas, site fidelity, familiarity; and (b) such a consequent mix of tactical and strategic habitat use may lead to the emergence of complex, multiscaled individual behaviors affecting modeling approaches of (meta)population. Following their challenge to express population kinetics (regarding the dynamic description of the factors behind population dispersal and the consequential spatial distribution of individuals) in a multiscaled processing framework, our data on behavioural shifts in movement patterns add novel empirical support to contribute new theory. If we have to be aware of the importance of the spatial memory capacity of individuals, allowing for strategic displacements, we have now learned that more realistic models on animal spatial distribution and abundance cannot ignore the possible change in an organism's behavior during its life. To conclude, our results highlight the importance to understand how animals make decisions regarding
movements and of accounting for the effect of temporal variations in animal behavior as an important step toward increasing biological realism in modelling dispersal.

Table 1. Estimated correlated random walk parameters and comparison between the predicted and observed models, as calculated by the residence index (Turchin 1991). The observed ratio (as the coefficient between the numbers of dispersing owls recorded in the two spatially segregated areas delimited by the two behavioural states) represents the real spatial distribution of floaters. The predicted ratio (the distribution of floaters expected by the model) was calculated as the coefficient between both residence index estimated in the two spatially segregated areas. Error = 100% \((\text{predicted ratio-observed ratio})/\text{observed ratio}\). The units of \(\mu\) and \(\tau\) are meters and days, respectively.

<table>
<thead>
<tr>
<th>Behavioral State</th>
<th>(\mu^a)</th>
<th>(v^b)</th>
<th>(\gamma^c)</th>
<th>(\gamma^d)</th>
<th>Observed Ratio</th>
<th>Predicted Ratio</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intensive</td>
<td>980</td>
<td>10</td>
<td>-0.4</td>
<td>1.8</td>
<td>0.19</td>
<td>0.003</td>
<td>-98.4%</td>
</tr>
<tr>
<td>Extensive</td>
<td>1760</td>
<td>13.2</td>
<td>-0.2</td>
<td>3.0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Mean step length  
\(^b\) Mean duration  
\(^c\) Mean cosine of turning angles  
\(^d\) Coefficient between the mean squared length and the squared mean length
Key Factors Driving Animal Movements

by

María del Mar Delgado, Vincenzo Penteriani & Vilis O. Nams
Patterns of animal movements mirror how the interactions of external and internal constraints affect individual behaviors during their displacements. By a natural field experiment on the eagle owl (Bubo bubo), we were able to explore how animals move in the real world. Fractal analysis and correlation random walks were used to compare movement trajectories and mechanisms of owls when using or not the same physical environment. Owls that traveled in areas close together had movement paths with more similar tortuositities. Moreover, the same individual showed similar movement trajectories when moved in the same area but different when traveled among different environmental scenarios. Despite the physical condition of individuals undoubtedly have an effect on movement patterns, some movement path characteristics seem to be more dependent on the physical environment. Our natural experiment offers a strong empirical evidence of the decisive importance of the external factors on animal movements.

KEYWORDS: Animal movement; Bubo bubo; eagle owl; external factors; fractal analysis; internal state; movement ecology; movement mechanisms
n a heterogeneous and complex natural world, the way in which animals move in their environment affects the fate of individuals and, consequently, the spatial structure, demographics and gene flow of animal populations (Kareiva 1990, Turchin 1998). Therefore, movement is a crucial mechanism driving population dynamics, community structures, and biodiversity of ecosystems (e.g., Crist et al. 1992, Wiens et al. 1996, Turchin 1998, Goodwing and Farhig 2002).

In the last decade, ecologists have become increasingly aware of the importance of studying the factors that influence the movements of individuals (e.g., Crist et al. 1992, Zollner and Lima 1999, Jonsen and Taylor 2000, Gruber and Herle 2004). It is a well-known fact that animal movements may depend on non-spatial and spatial factors. However, the intractable complexity of quantitatively describing animal movement patterns has prompted early workers to remove many important ecological interactions of such factors. For example, the majority of empirical studies relating biotic factors to animal movements have been designed under laboratory conditions or without taking into account the environment. These studies have shown that several internal factors may play an important role at determining the movements of individuals, such as individual condition (Newman et al. 1994, Nunes et al. 1998, Pennisi 2000, Mech and Zollner 2002, Zollner and Lima 2005), life stage (With 1994), specific organism traits (e.g., cognitive abilities, Vuilleumier and Perrin 2005), the susceptibility to competition and predator, as well as the level of conspecifics attraction (Danielson 1992, Fraser et al. 2001, Greene and Stamps 2001). For example, several studies have highlighted that movement decisions should reflect trade-offs between various factors constraining fitness, such as hunger and energy reserves (Jung and Koong 1985, Kareiva and Odell 1987). However, the studies designed to find out the effect of perceptual range on animal movements have been made important progresses (sensu Zollner and Lima 1996, Zollner 2000). In fact, these studies have suggested that organisms are expected to alter their movements, as well as experience differential fitness benefits or costs, according to habitat structure and composition (Tischendorf and Fahrig 2000, Wiens 2001). For instance, Bélisle and St. Clair (2001) found that the perception and response of individuals to landscape structure will be influenced by their internal state and their motivation, which will dictate their needs and how much risk they are willing to take in order to satisfy those needs.

On another front, empirical studies carried out to analyse the effect of the local and global environmental features frequently have not considered the individual internal state, sex and age. These studies have shown how many external factors, such as habitat fragmentation, patch distribution and composition, matrix quality, resource abundance and distribution, landscape types and configuration, presence of barriers and landscape connectivity (e.g., With and Crist 1993, Zollner and Lima

But animal movement ability is the result of multiple interactions of external and internal factors acting at various spatial and temporal scales. Therefore, the movement performances in natural habitats should reflect a trade-off between a complex mix of behaviour and choices, individual fitness, as well as the physical properties of the surrounding environment (e.g., Goodwing and Fahrig 2002, Morales and Ellner 2002, Morales et al. 2005). To date, however, there has been little empirical exploration of the mechanistic effect of the complex interaction between both biotic and abiotic factors on animal movements under natural conditions.

In addition, it has recently been emphasised that variation in movement behaviour have important implication for several evolutionary and ecological processes (Dingemanse et al. 2003, Davis and Stamps 2004, Hansson et al. 2004, Haughland and Larsen 2004). In fact, because animals moving across natural systems may encounter and respond to a range of environmental features at different scales, they are expected to use a range of behavioural movement responses to changes in the environment (e.g., Revilla et al. 2004, Haynes and Cronin 2006). Nevertheless, although several studies have previously showed the influence of landscape feature on animal movement patterns (e.g. Rotberg and Mangel 1997, Fraser et al. 2001, Morales and Ellner 2002, Morales et al. 2005, Haynes and Croning 2006), behavioural movement mechanisms has received little attention thus far (but see Heinz et al. 2007). For instance, a recent study on the large herbivore North American elk (Morales et al. 2005) has well illustrated how distinct movement patterns emerged in various simulated landscapes. In particular, they found that animals moving in homogeneous landscapes travelled shorter distances. However, individuals in heterogeneous landscapes showed more variable and highly skewed distance moved. But, because the presence of a pattern necessarily implies the presence of specific mechanisms that cause the pattern (Grimm and Railsback 2005), we believe that a better understanding of movement mechanisms could give us additional insights into animal movements.

During a 4-year study on the dispersal of an avian predator, the eagle owl (Bubo bubo; for more details on the species see Penteriani et al. 2007), we found a unique scenario that allowed us to explore how the interactions of external and internal factors in natural systems affect animal behaviour during natal dispersal displacement.

During dispersal, owls travel in different settlement areas (i.e. the temporary settling zones used during dispersal by non-territorial individuals or floaters, Penteriani et al. 2006, Penteriani et al. 2006) until they enter the breeding population as territory owners. The settlement areas often overlapped among individuals. This dispersing system was a natural experiment that allowed us to compare both the movements of: (1)
different owls (i.e. individuals from the same or different natal sites, of both sexes, and similar or different in physical condition) while using the same surroundings, and (2) the same owl when using the same area and when displacing among different ones.

To explore how the interaction between the surrounding environment and features of individual animals affects animal movements, we tested the following two hypotheses. If movements are principally influenced by: (1) environmental conditions, then movement paths of owls using the same areas should be more similar than for owls using different areas; or (2) individual physical conditions, then movement paths of owls should be very distinct from each other, whether or not they use the same areas.

Materials and methods

DATA COLLECTION

The study system and field methods

From 2003 to 2006 we studied eagle owl dispersal in the Sierra Norte (Sierra Morena massif), 20 km north of Seville (south-western Spain; more details in Penteriani et al. 2007). We radiotagged 39 owlets (2003: n = 6; 2004: n = 11; 2005: n = 14; 2006: n = 8) from 12 nest sites when they were approximately 35 days old. Individuals were fitted with a teflon ribbon backpack harness that carried a 30 g radiotransmitter (Biohacker Ltd, Wareham BH20 5AJ, Dorset, UK), with a mercury posture sensor that allowed us to discriminate rhythms of activity by changes in the radio signal of the transmitters. The backpacks were attached to owl wings. Each transmitter backpack and harness weighed less than 3% of the total body mass, as recommended by the U. S. Geological Survey Bird Banding Laboratory. Because young were still growing, back packs were adjusted so that the teflon ribbon could expand. After 4 years of continuous radiotracking of 13 breeders and 7 dispersing owls, we never recorded a possible adverse effect that could be directly attributed to backpacks on birds (Delgado and Penteriani, unpublished data; see also Sunde 2006 and references therein). Owls were aged following Penteriani et al. (2005) and were sexed by molecular procedures using DNA extracted from blood (Griffiths et al. 1998).

Individual tracks

Owls were tracked individually in 163 continuous radiotracking sessions during 2003–2006, with a total time duration of 1840.25 hrs, from when the owls started to disperse until they either died or their battery transmitters failed. A continuous radiotracking session is the following of a focal individual during the whole night (i.e. from 1 h before sunset to 1 h after sunrise; mean time duration of a radiotracking session ± SD = 11.28 ± 2.13 hrs). We recorded a location (n = 2994) each time that we detected a change in either individual posture or position (mean number of locations per radiotracking session ± SD = 13 ± 4.62). Such changes were detected by a fixed antenna located on the roof of a car. Locations were done using triangulation with a 3-element handheld Yagi-antenna connected to ICOM (IC-R20) portable receivers (www.icom.co.jp).
We used ArcView v 3.2 geographic information system (GIS) software to obtain map representations (1:25,000) of the different move paths.

DATA ANALYSIS
Analysis of movement paths
To characterize movement paths, we first estimated the fractal dimension (D). Fractal D measures movement path tortuosity, where D = 1 indicates a perfectly straight line, and D = 2 indicates a line so tortuous as to completely cover a plane. D was computed using the Fractal Mean estimator with the program FractaL (Nams 1996; Nams 2006a). We calculated an overall estimate of fractal D for each path, using the same range of scales for all movement paths (from 20 to 150 m). The upper limit was less than half the lengths of the longest paths, and the minimum scale was related to the minimum distance between locations (Halley et al. 2004). The same range of scales allowed us to compare fractal D among paths even though D varied with scale (Turchin 1996). Fractal D was normalized by loge (D-1).

Secondly, we measured how similar the movement paths are to correlated random walks. This was done using the CRW_{D_2} statistic, which measures the deviation in squared net distance traversed between the observed and CRW expected paths (Nams 2006b). Thus, CRW_{D_2} is zero if the movement path is a CRW, positive if the movement path is longer than a CRW and negative if the movement path is longer than a CRW. Finally, we estimated the overall speed of nightly movement paths based on the gross displacements, CRW_{D_2} and speed were both normally distributed.

Relating movement patterns to the physical environment
We first estimated the central point of each animal's nightly movements by the mean location. Then, we calculated the distance between the central points of all possible pairs of owl nights. We also estimated the difference in each movement path characteristic for each combination between the two owls.

To compare the movement of different owls, we used an analogous procedure to correlograms, to test for the effects of location on movement characteristics, as follows. We sorted all possible pairs of owl nights (excluding those pairs with the same owl) according to distances between nightly movements, and then grouped them into 500 m distance categories. 500 m distance intervals were chosen because the settlement areas explored by dispersers generally had less than 1 km of diameter (Delgado & Penteriani, unpublished), and so owls with activity centres separated by less than 500 m were likely exploring overlapping areas. Within each distance category, we estimated the mean difference in each movement path characteristic (fractal D, CRW_{D_2} and overall speed) between the two owls. A lower difference for shorter distances would signify that owls closer together have more similar movement paths.

-92-
To compare movements of the same individual, we first grouped all pairs of nights of the same owl into two groups: (a) individuals travelling in the same area when the distance between the central points of nightly pairs was less than 1 km; and (b) individuals shifting among different environmental scenarios when the distance between the central points of nightly pairs was more than 1 km. For each group, we estimated the difference in each movement path characteristic for all possible combinations between two nights of the same owl. We used Generalized Linear Mixed Models (GLMM; McCullagh and Nelder 1989) to test (a) if movement patterns of the same owl in the same area were similar; and (b) if movement patterns of the same owl in different surroundings were different. GLMM allowed us to calculate the ratio of variation among owls divided by variation within owls. Thus, a significant value means that movement paths differ more among owls as compared to within owls. The statistical analysis were performed with SAS macro program GLMMIX (version 8.2, SAS Institute, 2001), which iterates procedure MIXED (PROC MIXED in SAS software). Mixed-effects models permit both the fixed and random effects to be fitted in one analysis. Fixed effects model the mean values of the response variable as a function of covariates, while random effects model any patterns in the residuals around these fixed effects generated by, for example, repeated observations on the same individual. Because we had repeated measures data of the same individuals and to avoid pseudoreplication problems, individuals were considered as a random effect and the within individual effects a fixed factor. The main problem with non-independent or repeated measures data is that variation within individuals is part of the error estimate. Therefore, if variation within individuals is significantly less than among individuals, the error estimates could be currently decreased. However, the error estimation in Mixed-effects models is only taken from among individuals, not within individuals.

The response variables (i.e. log(D) (fractal D), CRW_{DEH} and overall speed) showed a normal distribution. Therefore, they were modelled in all cases using identity link function as the best logistic regression model (Littell et al. 1996). Finally, statistical significance was considered to be $P \leq 0.05$.

**Relating movement patterns to individual quality and sex**

We did not detect any significant effect between siblings on log(D) (fractal D), CRW_{DEH} and overall speed (always $P>0.10$). Consequently, omitting one of the siblings did not affect the results obtained in the study (results not shown), and all individuals were used in the subsequent analysis. In addition, Julian calendar date and owl age were tested as covariates. However, because we never detect any significant effect ($P>0.10$) on the response variables, we removed them from the models and data were all together pooled.

We used Generalized Linear Models (GLM; McCullagh and Nelder 1989) to test for the effects of physical condition and sex on each of the 3 movement characteristics.
To determine individual physical condition, we measured morphological, biometrical, biochemical and blood parameters when owls were approximately 55 days old. Morphological and biometrical measurements were summarized into a body condition index (BCI) estimated by a reduced major axis (RMA) regression (Green 2001), using logarithm of both body mass (to the nearest 10 g, with 1 kg Pesola scales) and tarsus length (using a digital calliper, ± 0.1 mm). The principal aim of the BCI is to separate aspects of body mass related to structural size from aspects reflecting fats and other energy stores. Thus, BCI measures animal’s fitness, with higher values meaning higher fitness (Green 2001).

To obtain biochemical measurements, blood samples were collected and stored in tubes with heparin at 4°C until arrival at the laboratory, where they were centrifuged for 10 min at 4000 rpm and then the plasma was separated and stored at -78°C. From plasma samples, cholesterol, triglycerides, uric acid, urea, glycerol and total proteins concentrations were determined using a spectrophotometer (Screenpoint 2, COR 5RL, Cineastra Florentina, Italy), using commercial kits (BIOLABO). These biochemical parameters have been shown to be good indices of body condition in birds (e.g., Alonso-Alvarez et al. 2002).

Blood smears (fixed with the GIEMLSA method) were used to measure both the immunodefense and the levels of stress and health. Thus, and following Figuerola et al. (1999), we estimated: (a) the total leucocyte count, by scanning 20 fields at 40 x, and then extrapolating the total number of leucocytes counted to 100 fields. This number is assumed to be equivalent to the number of leucocytes per μl of blood; (b) the proportion of the different types of white blood cells (eosinophils, lymphocytes, monocytes and heterophil) by counting 100 of white blood cells in each smears by microscopy (x 100) and under oil immersion (Ortega and Espada 2007); and (3) the intensity of the parasite Leucocytozoon spp. The presence of the blood parasite Leucocytozoon spp. was ascertained during white blood cells counts.

Results

There were some significant effects of location on movement path characteristics. Fractal D of movement paths was more similar when owls were closer together in space (Fig. 1a; \( r = 0.90, P < 0.001 \)). However, neither CRW_{def} (Fig. 1b; \( r = 0.23, P = 0.27 \)) nor speed (Fig. 1c; \( r = 0.0, P = 0.80 \)) showed a significant relationship with distance. Thus, different owls that spent time in areas that were closer together had more similar path tortuosituts, but there was no effect on travelling speeds nor similarities to CRW. CRW_{def} values for all owl paths were significantly less than zero (mean CRW_{def} = -0.12 ±0.07, \( P < 0.01 \)).

Fractal D differed more within owls as compared to among owls (\( R^2 = 0.02, P = 0.99 \)) when the same individual travelled among different areas. Moreover, the same individual showed similar path tortuosities when moved in the same area (\( R^2 = 0.17, P < 0.0005 \)). CRW_{def} and speed
were more similar within than among individuals, both when the same owl shifted among different environmental surroundings (CRW_in: \( R^2 = 0.24, P < 0.0173 \); speed: \( R^2 = 0.44, P < 0.0001 \)) and when remained in the same area (CRW_in: \( R^2 = 0.13, P = 0.0066 \); speed: \( R^2 = 0.27, P < 0.0001 \)).

We did not detect any significant effects of either sex (males = 27; females = 12) or physiological condition measurements (i.e., BCI, biochemical and blood parameters; all \( P > 0.5 \)) on either fractal D or CRW_in. The overall speed was the only parameter that showed a significant effect, with an interaction between sex and the BCI (\( R^2 = 0.37, P < 0.005 \)). That is, individuals with higher values of the BCI (i.e., better individuals) moved slower, especially if they were females (females: \( x = 743 \pm 173 \) m/hr; males: \( x = 904 \pm 92 \) m/hr).

**Discussion**

We have demonstrated the importance of the physical environment as one of the key factors affecting movement patterns of eagle owls. Although previous works have highlighted the importance of landscape properties (e.g., patch composition, fragmentation) and physiological constrains on movement decisions (e.g., Turchin 1998, Goodwing and Fahrig 2002, Fraser et al. 2001, Morales et al. 2005, Haynes and Cronin 2006), our results indicate that movement paths mainly reflect the characteristics of the habitat as a whole in where individuals move. In fact, when path tortuosity is explicitly analysed as a function of the physical surroundings: (a) the same individual showed different movement trajectories when shifting among different areas, but similar when moving in the same surrounding; and (b) path tortuosity was more similar between different owls moving within the same

![Graphs showing differences in movement characteristics](image)

**Figure 1.** Correlograms showing the differences in animal movement characteristics along a gradient of distances of the areas explored by owls. Each distance interval represents 500 m. The similar pattern found for Fractal D (a) indicated that the tortuosity of paths was more similar when different owls used the same area than when individuals moved in distant ones. CRW_in (b) and the speed of movement (c) presented a constant and a fluctuating pattern among distance intervals, respectively. These results suggested that such parameters were not related with landscape structure (see the text for more details).
areas than those moving in different ones (see also Fig. 2). Consequently, animals moving in a real world mainly reflect the individual capability to deal with the different components of the physical environment. Despite numerous processes and factors may play an additional role in determining animal moves (the previously cited trade-off), the complexity and heterogeneity of landscapes seem to have more of an effect than individual parameters. Therefore, and as pointed out by previous theoretical works (e.g., Turner 1999, Béisle and St. Clair 2001), the landscape represent a major factor driving animal movements.

Our results support previous findings obtained by controlled experiments with insects, showing the importance of spatial heterogeneity as a key factor governing animal movement patterns. For example, Jonsen and Taylor (2000) showed that calopterygid damselflies move away from streams on completely and partially forested landscapes but not on unforested ones. With (1994) demonstrated that different species can be interacting with landscape structure in similar ways, although it is possible to detect significant differences in the movement patterns within a species reflecting, for example, different life stages. Roland, Keyghobadi and Fownes (2000) showed a strong negative effect of distance through on between-meadow movements of alpine butterfly Parnassius smintheus, probably due both to a resistance to enter forest and to reduced rates of movement through forest.

Indeed, by computer simulations and experimental designs, these and other previous studies (e.g., McIntyre and Wiens 1999, Morales and Ellner 2002, Morales et al. 2005) addressed how different types of habitat affected individual movement responses. However, although their experimental systems included some aspects of landscape heterogeneity, they were generally very simple and sufficiently different from the study of organisms in their natural system, where complex behavioural responses to habitat features might be expected. In fact, these approaches have been devoted to improve the understanding of the influence of some physical features of landscapes on animal movements, such as habitat fragmentation, patch distribution and composition, resources abundances and distribution, landscape types, presence of barriers and landscape connectivity. However, our study looked at the effects of similar areas, not similar types of areas. That is, we do not analyse the effect of single habitat factors, but how the result of its multiple interactions (i.e. the habitat as a whole) is influencing the movement of animals.

The three movement path statistics measure two different aspects of movement: the mechanism and the specific parameters of that mechanism. The CRW_{DF} statistic measures how similar owl movement paths are to correlated random walks (Nams 2006b), which have been widely considered as the null hypothesis for animal movement (Turchin 1996, 1998). Thus, the CRW_{DF} statistic considers movement mechanisms. Speed and fractal D are specific parameters of that mechanism. For example, if many
individuals travel according with 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_{D10} results showed two interesting features with respect to mechanisms. First, the CRW_{D10} were all significantly smaller than zero. This means that owls travelled shorter distances than expected with a correlated random walk (Nams 2006b). Although we do not specifically analyse what type of movement mechanism the owls used, if the CRW_{D10} was smaller than zero at all spatial scales then the owls would be travelling with an unoriented movement. Second, the similarities in CRW_{D10} between owls did not significantly change with distance between explored areas. This suggests that location did not affect the movement path mechanism. On the other hand, although location did not affect travelling speed, it had an evident effect on fractal $D$ - fractal $D$ was more similar the closer together the areas were. Therefore, our results support that movement mechanisms are not as plastic as fractal $D$ because they do not vary with the distance and they are more similar within than among individuals. These results are based on the natural relationship between ecological processes and patterns: processes describe what animals should do, whereas patterns provide details (i.e. the information) of how they should do something. It is reasonable to think that animals moving for a particular reason use the same specific mechanism, independently of the habitat where they are. However, while moving with a specific mechanism to achieve a particular objective, animals are interacting with the different landscapes and the result of such interactions is the origin of the different emerging movement patterns observed. Indeed, movement patterns that are defining characteristics of a system are likely to be indicator of essential underlying processes and structures. Therefore, animal movement patterns provide information on the essential properties of a system (Grimm and Railsback 2003). To summarize, these results suggest that the features of the surroundings in which animals move determine the specific parameters of their movement paths but not the movement path mechanisms.

![Figure 2. Owls using the same area present similar path tortuosity (FD) that those 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. However, when the owl A uses the same area with the owl B (black; on the right of the figure), their movement trajectories are more similar (as reflected by the values of FD).](image)

Neither the overall structure of movement paths nor the behavioural aspects related to search movement.
mechanisms seemed to be related to the physical conditions of the owls measured at the fledging stage. A small exception to this general pattern was that females with better physical conditions (i.e. higher values of the BCI) moved slower. The speed of movement can be a key factor in some behavioural processes such as prey detection (Knoppen and Reddingius 1985) and space use (Benhamou and Bovet 1989). In particular, eagle owl is a sit-and-wait predator and prey capture is greatly influenced by pausing behaviour (Sonerud 1992): lower rates of movements may be the best way to learn about the environment in which animals settle. In fact, intermittent movements are beneficial because individuals have time to gain information of the habitat surrounding, save energy and, consequently, they represent an optimal foraging strategy (Pennisi 2000). Therefore, owls with good physical conditions (and especially heavier females, showing this species reversed sexual dimorphism) do not need to move so rapidly as individuals in poorer body conditions, which should be obliged to increase their rate of displacement (e.g. compensatory foraging; Norrdahl and Korpimäki 1998; Murray 2002 and references therein; Wissing et al).

To conclude, our natural experiment represents a strong support for the importance of the characteristics of the surroundings in which animals move on the patterns and mechanisms of movements. Because the involvement of individual movements can have profound effects at different ecological levels, going up our knowledge on how animals move in the real world, and interact physically with their natural environments, is critical to understand many fundamental ecological and evolutionary processes.

Acknowledgements
For their help with logistics we are grateful to P. Barcelomu, L. Camponi, P. Laureano and G. Pentelour. We are very grateful to IAS-movement ecology group for its appreciated teamwork, especially to John Fryxell, Wayne Getz, Marcel Holyoak, Hanna Kokko, Ram Nathan, Eloy Revilla and David Salo for stimulating discussions on animal movements. Funding for this study was provided by a research project No. CGL2004-02780/BIOS of Spanish Ministry of Education and Science and LICOR43 (Diego Zamora S.A.). During this work M. M. Delgado was supported by a doctoral grant of the Junta de Andalucía (Consejería de Educación y Ciencia) and V. Pentelou by a contract of the program “Incorporación de Investigadores al Sistema Español de Ciencia y Tecnología” (CCAA de Andalucía). We manipulated and marked owls under the Junta de Andalucía — Consejería de Medio Ambiente permits No. SCFIS-AFR/GGG RA- 260/02 and SCFIS-AFR/GMM RA-1904/02.
6

ROUTES TOWARDS ANIMAL DISPERsal:
EXTENDING THE GRAPH-
THEORY APPROACH

by

María del Mar Delgado, Miguel A. Fortuna & Vincenzo Penteriani
Animal movement and dispersal are major drivers of spatiotemporal patterns in ecosystems, being the spatial connectivity of habitat patches a crucial factor for the success of the dispersing individuals. In this study, we applied graph theory using the empirical occupancy and movement data on juvenile eagle owls (Bubo bubo) to build a spatial network that characterizes the connectivity of patch occupancy described during the dispersal process. Dispersing owls showed a heterogeneous patch occupancy where few patches were highly visited by different individuals, whereas the majority of nodes were visited by just one individual. We compared the real routes of dispersal with optimized and randomized ones, and found that the routes following by dispersing owls are an intermediate solution between minimize the number of occupied patches and explore randomly the available area. Finally, by analyzing the direction of the predominant winds in the area when dispersal started, we found that the dispersal pattern of eagle owls was largely influenced by dominant winds. Our findings suggest a clear asymmetric dispersal pattern, where not only the number of nodes and edges but also their functions patches can largely determines metapopulation viability.

Keywords: animal movement; complex networks; eagle owl; passive dispersal; spatial networks
Functional connectivity (sensu Bélisle 2005) can be defined as the result of the multiple interactions between individual behaviours and the characteristics and spatial arrangements of the habitat patches that an organism crosses when moving. Connectivity is also one of the main concepts behind our perception of animal dispersal (e.g. van Langevelde 2000; Goodwin & Fahrig 2002; Brooks 2003; Heinz et al. 2005; Hastings & Botsford 2006; Stevens et al. 2006; Graves et al. 2007). Within the complexity of the dispersal process, the most widespread view depicts it as the mechanism by which wandering individuals (or floaters sensu Fenteriani et al. 2006) create a numerical and gene flow from their original population to a different territory, area or (meta)population (Clobert et al. 2001; Bullock et al. 2002; Hanski & Gaggiotti 2004). Although there is a large history of research and much has been written, questions about dispersal have been difficult to answer and still represent a gap in our understanding of animal ecology (Bennetts et al. 2001).

Despite the lack of empirical data, several approaches have been used in the analysis and modelling of animal movements during the search or wandering phase of dispersal. In particular, random walk models and their diffusion approximations (i.e. correlated, biased and multiscale random walk models: Kareiva & Shigesada 1983; Gautestad & Mysterud 1993; Turchin 1998) have been largely used to evaluate movement pathways. Although these models can effectively predict the pattern of animal distribution on short time scales, they tend to fail when longer time horizons are taken into consideration. In fact the random walk models do not consider (a) the occurrence of behavioural changes during the lifespan of an individual and their influences on movement patterns (Firle et al. 1998; Morales et al. 2004); and (b) movement patterns can change when different habitat conditions are encountered (Jensen & Taylor 2000; Fraix et al. 2005). Since the idea that the nature and the spatial configuration of the matrix are features that can potentially influence an animal’s ability to disperse, path direction and colonization (e.g., Turner 1989; Gustafson & Gardner 1996; Zollner & Lima 1999; Schooley & Wiens 2003; Baguette & Van Dyck 2007), the importance of spatial scale was greatly emphasized. In fact, movement among patches is not simply a function of an organism itself, but also depends on the landscape through which it must move (Wiens 2001). While several authors have been applied fractal methods and Lévy walks to assess organism response to spatial scale heterogeneity (Wiens et al. 1995, Bascompte & Vila 1997; Bartumeus et al. 2005; Nams 2005), numerous dispersal models with spatially explicit landscapes have been developed (e.g., grid-based models: Gardner and Gustafson 2004; vector-based models: Bihan 2003; and object-oriented dispersal modeling; Vuilleumier & Metzger 2006). Some of these simulation models enable the integration of the relationships between species and landscape and have been considered powerful or criticable depending on the authors (see Vuilleumier & Metzger 2006).
However, although the success of the dispersing individuals can largely depend on the distance travelled through the matrix and the time spent in their search for suitable sites (or settlement areas), the spatial connectivity intrinsic to the areas crossed during dispersal has been widely recognized as a fundamental piece of such a process, but seldom considered explicitly. Connectivity is an intrinsic property of one of the oldest lattice data structures, the graph. In fact, as a landscape of patches (set of nodes) interconnected by edges, a graph path (a sequence of nodes linked by edges) implies that there is some ecological flux between the nodes (e.g. via dispersal; Urban & Keitt 2001). Because the connectivity among focal locations is typical of both dispersal and graph theory, this latter has the potential to represent a widely applicable tool to understand several crucial aspects of the dispersal process, e.g. interpatch movement patterns, features of stepping-stone area networks, locations of vital nodes and corridors allowing the connection among (meta)populations. In fact, under a purely spatial perspective, computing the quickest route in a road network (e.g. from a given source to a specific target) is an important problem used in diverse applications. Dispersal can undoubtedly be considered as an optimization problem and the specific properties of the graph theory approach may provide novel and unintuitive informations.

Graph theory has been applied in many disciplines (especially to detect efficient flows or routing in networks, webs or circuits; see review in Urban & Keitt 2001 and Strogatz 2001 and references therein). However, despite the fact that a graph-theoretic perspective allows power applications concerned with ecological connectivity, metapopulations and conservation biology (Fahrig & Merriam 1988; Verboom & Lenkester 1991; Taylor et al. 1998; Schippers et al. 1996; van Langevelde et al. 1998; Pascual-Hortal & Saura 2006 and references therein), it is not still widely appreciated in ecology. Although several applications have been focused on species interacting networks such as food webs (e.g. Paine 1966; Cohen 1978), mutualistic networks (Bastompte et al. 2003; Flueter et al. 2007), individual interacting networks such as animal societies (Lusseau et al. 2006) and, more recently, on a spatial context characterising the physical template inhabited by species (Fortuna et al. 2006), animal dispersal has been rarely explored by a graph-theoretic approach (but see Urban & Keitt 2001 and Brooks 2006).

Here we show the strength and applicability of the graph theory to the study of animal dispersal. Our first step has been to analyse the movement patterns during wandering phase of dispersal (i.e., search movements by the floating individual while exploring other areas for a variable time period before the individual definitively settles in a new area) of an avian predator (the eagle owl Bubo bubs; for more details on the species see Penteriani et al. 2007) by a graph-theoretic approach. First, we have applied a box-counting procedure to the spatial locations of individuals. In this way we have simplified the observed complex pattern of movement, shifting from
specific spatial coordinates to a well-defined patch occupancy pattern. Secondly, we built the *dispersal spatial network*, in which the nodes represent the occupied habitat patches and the links correspond to the owl movements among patches. Within such a spatial scenario, we then have compared the real dispersal routes with optimized and randomized routes, in order to gain information on the movement strategies of juveniles.

As an additional step of our exploration, and by using information of the direction of the predominant winds in the area when dispersal started, we looked at a possible role of aerial flows on such a process and, consequently, on a counterintuitive effect of passive dispersal on the interpatch movements of a large bird vertebrate (or a large bird). Finally, we highlight and discuss the potentiality of our approach for the study of (meta)population connectivity and population conservation from the perspective of floaters and settlement areas, key elements of population stability and persistence (Penteriani et al. 2005a,b, 2006).

**Materials and methods**

*Sample and data collection*

We radiotagged 42 juvenile eagle owls from 11 nest sites (2003: n = 6; 2004: n = 9; 2005: n = 13; 2006: n = 14) in the Sierra Morena (Southwest of Spain; more details in Penteriani et al. 2005c). We followed each individual from the moment in which it leaves the natal territory to disperse to when it reaches a temporary settlement area (i.e. an area in which individual settles—for a time length mainly function of the population saturation and probability of encountering an empty territory—before to become owner of a breeding territory) or a breeding area (Fig. 1a). Individuals were fitted when they were approximately 35 days old with 90 g radio-transmitters (Biotrack Ltd backpacks). Each transmitter weighed less than 3% of the total body mass, as recommended by the U. S. Geological Survey Bird Banding Laboratory. We recorded the exact position of each owl weekly, typically when they were at their diurnal roost sites. Locations of radio-marked individuals were determined by triangulations using 3-element hand-held Yagi-antennas (Biotrack Ltd) with Stabo (XR-100) portable receivers (Osaka, Japan). We used only the weekly locations since owls started the dispersal until they either died or found a stable settlement area (see Fig. 1b as an example of an individual route towards dispersal). To determine the beginning of dispersal, for each individual we plotted both the baseline distance between its natal nest and each weekly location and the global mean distance covered during the dispersal period. We considered dispersal to have started when the distance of each weekly location from the nest become larger than the global mean distance. On the other hand, to determine the end of dispersal, for each juvenile we plotted the distance between successive weekly moves against the average distance they travelled through them. We considered that owls settled in a stable settlement area when the distances become smaller than the average distance of previous moves. That is, when the
distance between successive movements stopped increasing.

Count-boxing procedure
The first step before the network analysis was translating the individual weekly spatial locations into a well-defined patch occupancy pattern (see Fig. 2a). We used a box-counting procedure from fractal theory (see Nams 2003 for an application of fractal theory to animal movement) consisting on counting, for different grids of different box-side length, the number of boxes containing at least one record inside (i.e. one individual within the patch, at least). By plotting the box-side length against the number of occupied boxes in a logarithmic scale, we were able to analyse the patch occupancy pattern across scales (Schroeder 1991). The box-side length (patch size) with the highest variability in the number of inhabitant individuals was of 1 km². For smaller box-side length, a huge number of patches were occupied by just one individual, whereas for larger box-side length very few patches resulted to be occupied.

Network analysis
After we depicted the general pattern of owl movements, we proceed to build the spatial network of dispersal where: (1) the nodes represented the habitat patches occupied by owls; and (2) the links corresponded to their movements among successive patches. The first exploration of the resulting spatial dispersal network (Fig. 2a) was directed towards the assessment of how important was each occupied node as a dispersal stepping-stone. The first step was to define the degree of each node, i.e. the number of individuals that occupied it during their dispersal movements. All nodes, excluding the natal and the final settlement nodes, have the same number of incoming and outgoing links: that is, when an individual arrived to a node, always left it. Multiple visits of the same owl of a given node were not count as additional links. This procedure represented a conservative way to establish how important had been each node for individual dispersal routes.
Figure 1. (a) Spatial locations of the natal (black circles, n = 11) from which the juveniles were radiotagged and the settlement/breeding areas (white circles, n = 43) 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.
Figure 2. The structure of the studied spatial network, i.e., the spatial patterns described by dispersing eagle owls, in which are represented the real routes followed by owls from the natal site to the final settlement/breeding area are represented (a), as well as the optimized (b) and randomized (c) routes (see explanations in the text). Nodes represent the crossed habitat patches and their size is proportional to the number of different individuals that occupied them. In black are represented those nodes also containing the nests in which juveniles were radiocasted.
Secondly, we compared the real routes to dispersal with optimized (Fig. 2b) and randomized (Fig. 2c) ones. An optimized route is the route that, crossing the minimum number of nodes among the ones occupied by owls and following the direction of the interpatch movements, links the natal site to the settlement/breeding area.

A randomized route is similar to the optimized, but includes the number of nodes resulting when randomly following the direction of the interpatch movements. Specifically, we took 10 randomized routes for each owl in order to estimate the number of patches occupied by each one in the traced randomized routes. Note that we assumed, for both optimized and randomized routes, that owls can only occupy realized occupied patches and they can only move among patches following the realized interpatch movements that were recorded. Thus, the null model used to test whether juvenile owls move randomly or optimally during dispersal is very conservative.

Comparisons among real, optimized and randomized routes were done by measuring the number of occupied nodes: the less patches an individual occupied, the straighter was its route from the nest to the settlement/breeding area.

Finally, we analysed the direction of the interpatch movements as an indication of the homogeneity or not of the dispersal trajectories of the individuals of the same population. In order to explore the direction of movements during the dispersal: (1) we assigned the 42 recorded movements to one of the 8 angles of 45° by which we divided the 360° of possible directions (0°, 90°, 180°, and 270°, corresponding to North, East, South and West, respectively); and (2) we explored the possible association of dispersal distances to the direction of the predominant wind at the moment of the start of dispersal. To do this, we compared the orientation of the owl movement paths with the direction of the wind in the study area (from July to September, when dispersal starts, and for the years of study; data bank of the Spanish National Institute of Meteorology). χ²-tests were used to compare the direction of the owl dispersal routes with both random and wind directions.

Results

Juvenile eagle owls showed a heterogeneous pattern of patch (node) occupancy during dispersal: (a) only a fraction of the available landscape was used (see Fig. 2a); and (b) the degree distribution of the patches is heterogeneous (Fig. 3). 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 to find a patch visited each time by more individuals decays as an exponential function ($F_{xy} = 68.42291$, $R^2=0.988$, $P < 0.001$). The mean number of occupied nodes per owl was $7.0 ± 3.7$ for real routes, $3.5 ± 1.1$ for optimized routes and $10.6 ± 4.8$ for randomized routes; real routes differed.
Figure 3. Degree distribution of occupied patches by dispersing owls. Inset, the cumulative degree distribution showing the fitting to an exponential function (solid line). Dashed line represents the fit to a power-law function.

Figure 4. Number of nodes occupied by either dispersing owls, randomized and optimized routes. Mean values and confidence intervals for mean at 95% are showed.
significantly from randomized ones \(t = -4.98, n = 42, P < 0.001\); paired t-test). This means that owls do not move randomly among habitat patches during dispersal, using less habitat patches than expected by chance. However, the difference between real and optimized routes \(t = 6.83, n = 42, P < 0.001\); paired t-test) shows that owls used more habitat patches than expected by the optimization, i.e. dispersing owls do not necessarily follow optimal routes in terms of economization of displacements (see Fig. 4).

During dispersal, the directions of movements did not fit a random pattern \(\chi^2 = 35.33, P < 0.001\). More than 61% of the dispersal movements were orientated 45° upper and down from 247.5° (between 202.5° and 292.5°, i.e. along a W-S-W direction), indicating a marked directionality (Fig. 5a). The direction of the wind was significantly different from the one expected by chance \(\chi^2 = 297.94, P < 0.001\): during more than 71% of the days, the wind blew down from 202.5° (between 157.5° and 247.5°, i.e. along a well-defined S-W direction; Fig. 5a). But, still more intriguingly and unintuitively, the directions followed by dispersing eagle owls strongly fitted the direction of the wind \(\chi^2 = 35.965, P < 0.001\).

**Discussion**

In metapopulation ecology, connectivity is mainly centred on migration rates among habitat patches, e.g. the probability that an empty patch will be colonized during dispersal (Mollanen & Nieminen 2002). This means that not all patches are of equal connectivity. Our real scenario showed a clear anisotropic flow of individuals, i.e. owls showed a dispersal flow polarized along both a specific axis and direction (Gustafson & Gardner 1996; Ferreras 2001). Implicit to this directionally biased dispersal pattern is the fact that we are faced with an asymmetric dispersal scenario (see Vuilleumier & Possingham 2006 for a review on factors determining asymmetric dispersal). This is particularly important when we consider that, in the context of metapopulation and source-sink dynamics, we have no simple theory for asymmetric dispersal involving several habitat patches (Figueira & Crowder 2006; Vuilleumier and Possingham 2006).

Connectivity is also acknowledged as a potentially desirable quality of networks of protected areas (Wilcox & Murphy 1985; Noss 1987), the success of animal dispersal being strongly related to patch accessibility (Heinze et al. 2005; Reed & Levine 2003). Consequently, an urgent need exists to develop effective support tools that can help to evaluate the connectivity of network areas of potential interest (Briers 2002; Rothley & Rae 2005). Several techniques to measure landscape connectivity and the impact of fragmentation have been used to address the spatial aspects of reserve design (e.g. Burkey 1989; ReVelle et al. 2002; Rothley & Rae 2005), as well as data from empirical studies have been used to estimate the costs to organisms of moving through heterogeneous landscapes (e.g. Adriensen et al. 2003). Recently, graph models of landscapes structure have been used (Bunn et al. 2000; Urban & Keitt 2001), allowing to both incorporate information regarding the dispersal capabilities of focal species and highlight the importance of...
individual patches in a landscape (e.g., effects of patch losses due to habitat destruction or other types of disturbance). However, data available on real species are minimal compared to simulation models on theoretical scenarios.

Our field study offers a unique opportunity to depict a real scenario during dispersal and to highlight the importance of focal nodes and edges 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. Empirical information as the one of the present study should constitute the fundamental knowledge to explore by the help of simulations the importance of the different elements of the structure of the dispersal graph on the dynamics of (meta)populations. Strong empirical backgrounds are the best option we have to obtain real answers on the effects and species-specific thresholds of node and edge removal (i.e., which dispersal routes and habitat patches are most influential on metapopulation processes and how much habitats/corridors can be removed before affecting the extinction likelihood of a population).

For example, our empirical results fit the theoretical scenario depicted by Vuilleumier and Possingham (2006), which suggest that asymmetric connectivity increases the chance that metapopulations will not be viable. Because the number of connected patches largely determines metapopulation viability in an asymmetric system, we can expect a serious decline of our population if the most frequented nodes or links connecting breeding territories to settlement areas would disappear or will be affected by environmental stochasticity. Because only the knowledge of the exact location of the routes to dispersal can proportionate real tool for species conservation and landscape management, a broad-spectrum increase of connectivity (a well-known management recommendation for decreasing the negative effects of fragmentation) is unlikely to benefit populations
characterised by asymmetric dispersal. Again, as pointed out by Vuilleumier and Possingham (2006), not only the number of patches involved in the system is important, but also their function (i.e. donor vs. recipient patches). For asymmetric systems, as our study case, the fate of donor-only (most of the breeding territories) and recipient-only (the temporary settlement areas) patches may determine significant impacts on the population dynamics. As an end result, the present study represent a strong empirical support to the claims of Vuilleumier and Possingham (2006), which who theoretically showed that an a priori assumption that the dispersal process is symmetric may be false and, consequently, have dramatic consequences on our ability to predict and manage (meta)populations. The graph theory showed once more its importance in solving ecological problems.

As remarked by Béisle (2005), anisotropic dispersal may result from variations in the ease of moves along the different axes and directions of movement. In our scenario, one of the most striking information that we highlighted was the role of winds in determining the paths of dispersal. This is not the first time that active dispersers (supposed to be only affected by landscape characteristics or individuals traits) show a mixed dispersal strategy, their patterns of dispersal being largely influenced by dominant winds (Fenner 1993; Walls et al. 2005). Such evidence is crucial in our understanding of how dispersal determines the fates of (meta)populations or, under a more wide perspective, the animal distribution in space. Especially when considering that dispersal, depending on its characteristics, has been proved to be a powerful mechanism behind synchronous or asynchronous fluctuations in population size (Kendal et al. 2000; Ranta et al. 2008). Depending on: (1) the species-specific importance of the wind direction in shaping dispersal routes; (2) the directionality of local winds at the start of dispersal (a character strictly dependent on the life-histories of the different species); and (3) the structure (e.g. connectivity among nodes) and characteristics (e.g. mortality risks) of the spatial network on which organisms are heading for because of winds, we can probably find the answers to several ecological puzzles concerning species distributions, colonisations and persistence.

Finally, and as evidenced by Walls & Kenward (1998), for species needing recovery plans, an accurate knowledge of dispersal behaviour can be a key factor of conservation success, since efficient reintroduction/restocking requires accurate knowledge of the animals’ movement patterns. Ignoring the importance of local winds at given moments of the species biological cycle can decrease the effectiveness of conservation plans and action, mainly if aerial flows oblige released individuals in not suitable but previously unpredictable directions and/or locations. Population studies, analyses of population viability and extinction risk assessments that ignore the potential complexity of the dispersal process may fail to understand how and why animal populations decrease.
Acknowledgements

We thank Jordi Bescamps for his excellent suggestions that greatly improved the clarity and accuracy of the paper. During this work M.A.F. was funded by the Spanish Ministry of Education and Science (Fellowship BES-2004-6682), and M.M.D by a doctoral grant of the Junta de Andalucía (Consejería de Educación y Ciencia). We manipulated and marked owls under the Junta de Andalucía – Consejería de Medio Ambiente permits No. SCFFS-APR/GCG RS-260/02 and SCFFS-APR/CMM RS-1904/02.
7

HOW BEHAVIOURAL TACTICS, PHYSIOLOGICAL AND ENVIRONMENTAL FACTORS CONTRIBUTE TO DISPERsal SETTLEMENT PATTERNS

by

María del Mar Delgado, Vincenzo Penteriani & Vilis O. Nams
Dispersal is a complex behavioural process in which search and settlement patterns largely depend on a wide range of factors. Given that the success of the dispersing individuals can largely be affected by the distance travelled through the matrix and the time spent in the search for suitable sites (or settlement areas), we explored the interactions among behavioural movement rules, physiological and environmental factors, and habitat preferences of dispersing eagle owls (Bubo bubo). Individual variations in movement behaviour at different temporal scales (nightly and overall) can lead to variation in settlement patterns (Movement direction hypothesis): individuals showing straighter movement trajectories at a larger scale travelled longer dispersal distances and reached the temporary settlement areas later than individuals showing tortuous paths. At small scales there were two strategies: owls could minimize distance travelled by travelling more tortuously at a small scale, or minimize time by travelling in straighter paths. Animal interpatch movements and, as an end consequence, the final spatial distribution of individuals, were influenced by both the physical environment and physiological factors (Movement abilities hypothesis). Such information showed how animals are successful to adopt different search tactics under different circumstances. Dispersing owls tended to select the same types of habitats for settlement areas as they experienced while wandering, but not the same as their nest site (Natal experience hypothesis).

KEYWORDS: Bubo bubo, behavioural trait syndromes, costs of dispersal, dispersal behaviour, Eagle owls, fragmented landscapes, habitat exploration, habitat selection.
Animal populations are a mix of breeders and dispersing individuals, with natal dispersal being a key process in shaping dynamics, spatio-temporal distributions, stability and the likelihood of extinction of (meta)populations (Turchin 1998; Hanski 1998, 1999; Clobert et al. 2001; Skalski & Gilliam 2003; Clobert et al. 2004). Dispersal is a three-stage process (Clobert et al. 2004; Bowler & Benton 2005; Van Dyck & Baguette 2005; Baguette & Van Dyck 2007). After starting dispersal (stage 1), floaters (sensu Penteriani et al. 2006a) travel through a more or less hostile landscape (stage 2, the wandering phase). During this time they explore different areas until they find a settlement area (stage 3). Settlement areas (see Penteriani et al. 2005a,b, 2006b; for more details) are those areas occupied during the longest time period of the whole dispersal, sometimes until floaters become territory owners and start breeding.

These settlement areas are very important. The decision to settle and the selection of the settlement areas may affect:

(a) individual fitness (Greene & Stamps 2001; Baker & Rao 2004); (b) the social and spatial behaviour of populations (Stamps & Krishnan 1999; Stamps et al. 2003; Selonen & Hanski 2006); and (c) competition for breeding places. In addition, some consequences of dispersal on the individual can only be detected after settling (i.e. deferred costs: health condition and timing of breeding; Stamps et al. 2005). However, despite their importance, settling zones are usually unknown or difficult to detect for most species. Furthermore, floater dynamics, dispersal movement within settlement areas and their locations, have been considered as less important, if not completely ignored, in most of the analyses aimed to determine population viability and persistence (Penteriani et al. 2005a,b, 2006a,b).

Not only are settlement areas important, but so are the search paths that lead to them. Because costs and benefits of dispersal can vary not only among species but also within individuals (Dingemanse et al. 2008; Drent et al. 2005; Van Dyck & Baguette 2005; Bowler & Benton 2005; Selonen & Hanski 2006), a plastic individual dispersal strategy is expected. For instance, Zollner & Lima (1999) found that for all simulated landscape configuration, an effective dispersal search rule would involve straighter movements. Specifically, they highlighted that nearly straight searcher could entail better dispersal success than both perfectly straight and less straight ones because (1) animals moving with strictly straight search rule could go right and miss all favourable patches; and (2) individuals travelling with more convoluted search paths are more likely to have redundant searches. These movement strategies can vary according to different factors such as current conditions (e.g., the risk of mortality), individual fitness, variations in the perceptual range, and the distribution and density of patches (Zollner & Lima 1999). In fact, the matrix which the animal travels is very variable (Wiens 2001) and can affect an animal’s skill to disperse, various characteristics of the movement
path and colonization (e.g., Turner 1989; Custafson & Gardner 1996; Schooley & Wiens 2003; Baguette & Van Dyck 2007). Such behavioural responses can largely influence habitat selection by dispersers (Conradt et al. 2003; Leon-Cortes et al. 2003; Doerr & Doerr 2004; Conradt & Roper 2006). Therefore, the individual routes become important.

Recent insights from habitat selection theories have tried to highlight the proximate cues guiding floaters searching for new habitats in their habitat choice (Schlaepfer et al. 2002). Many behavioural mechanisms may influence habitat selection. Although animals searching for new habitats should be mainly guided by those factors that are expected to enhance individuals’ fitness after they settle in a specific habitat (Stamps 2001; Thompson et al. 2003; Stamps et al. 2005; Fletcher 2006), some studies have showed how animals can also be attracted by another type of cues produced by factors that otherwise can reduce individuals’ fitness (e.g., ecological traps: Kokko & Sutherland 2001; Schlaepfer et al. 2002; Bettin 2004).

Here, our main objective was to explore: (1) when, where and how individuals search for settlement areas; (2) how spatial and temporal search strategies are influenced by costs of dispersal and landscape structure; (3) how and when individuals decide to stop their wandering life (e.g. searching for a settlement or a breeding area); and (4) where individuals settle when moving in a new environment.

To look at these different aspects of animal dispersal, we carried out a four-year radiotracking study on the juveniles of an avian predator, the eagle owl (Bubo bubo; for more details on the species see Penteriani et al. 2007a), from the beginning of dispersal to the reaching of a settlement area (or a breeding site), including the whole wandering phase. Three main predictions were tested across the present study:

1. **Movement configuration hypothesis:** following one of the predictions of Zollner & Lima (1999), animals travelling over longer distances should involve straighter movements. In particular, the previous cited nearly straight movements should allow individuals to search more rapidly and over larger distances than less straight movement path, limiting travelling time across the landscape matrix and, consequently, maximizing their probability to rapidly end up in a favourable habitat.

2. **Movement abilities hypothesis:** individual differences in movement patterns should depend on physiological factors and physical characteristics of the landscape. As longer distances or longer times spent before settling could be costly (Baker & Rao 2004), we expect that more efficient/healthy individuals avoid prolonged wandering phases by employing straighter and faster trajectories. Moreover, because an inhospitable matrix may imply significant problems while searching for a new habitat, straighter movements should occur more frequently in hostile
landscapes. If hypothesis 1 is true, and best individuals employ straighter movements, individual features and movement behaviours could act together in determining dispersal success (e.g., Fraser et al. 2001; Schickzelle et al. 2006; Baguette & Van Dyck 2007).

3. Natal experience hypothesis: when dispersing across unknown landscapes, individuals will select habitats similar to those surrounding the nest (e.g., Stamps 2001; Stamps et al. 2003). Thus, the areas frequented during the wandering phase, as well as the settlement areas, should show landscape characteristics (e.g. topography, patch composition and distribution, types of vegetation) similar to the natal areas.


data analysis

Dispersal movement patterns

First, we analysed behavioural movement properties independently of the underlying matrix for the two spatiotemporal scales (nightly and overall). We consider the following movement parameters. First was 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. We calculated an overall estimate of fractal D for each path, using the same range of scales for all movement paths (from 20 to 160 m). The upper limit was less than half the lengths of the longest paths, and the minimum scale was related to the minimum distance between locations (Halley et al. 2004). The same range of scales allowed us to compare
fractal $D$ among paths even though $D$ varied with scale (Turcich 1996). $D$ was computed using the Fractal Mean estimator with the program Fractal (Nams 1996; Nams 2006a), and was normalized by log ($D$-1). "Nightly" tortuosity means tortuosity of paths throughout one night, and "overall" tortuosity means tortuosity of the overall paths, with locations taken once per week. The third parameter was the overall travelling speed based on the gross displacements. Speed was normally distributed.

**Individual quality and sex**

Owls were aged following Penteriani et al. (2005a) and were sexed by molecular procedures using DNA extracted from blood (Griffiths et al. 1998). To determine individual physical condition, we measured morphological, biometrical, biochemical and blood parameters when owls were approximately 35 days old. Morphological and biometrical measurements were summarized into a body condition index (BCI) estimated by a reduced major axis (RMA) regression (Green 2001), using logarithm of both body mass (to the nearest 10 g, with 1 kg Pesola scales) and tarsus length (using a digital calliper, $\pm$ 0.1 mm). The principal aim of the BCI is to separate aspects of body mass related to structural size from aspects reflecting fats and other energy stores. Thus, BCI measures animal’s fitness, with higher values meaning higher fitness (Green 2001).

To obtain biochemical measurements, from plasma samples we determined cholesterol, triglycerides, uric acid, urea, glycerol and total proteins concentrations (for more details see Penteriani et al. 2007b), that have been recognised as good indices of body condition in birds (e.g., Alonso-Alvarez et al. 2002). Blood smears (fixed with the Giemsa method) were used to measure both the immunodefense and the levels of stress and health estimating the proportion of the different types of white blood cells (eosinophils, lymphocytes, monocytes, basophiles and heterophiles) by counting 100 of white blood cells in each smear by microscopy ($\times$ 100) and under 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 conditions (Figuerola et al. 1999).

**Landscapes**

We analysed landscape structure and composition to test (1) the effects of matrix heterogeneity on individual movement behaviour during the wandering phase of dispersal, and (2) habitat selection by dispersers. For each individual, we estimated natal, wandering, and settlement areas, using 95% minimum convex polygons (MCP; Hayne 1949) with locations from those life stages (Delgado & Penteriani, submitted). We evaluated both landscape structure and composition of the individual natal, wandering and settlement areas using ArcMap of ARCGIS version 9.0 (ESRI) based on a 1999 land cover map of the study area (Sistema de
Información Ambiental de Andalucía; Moreira & Fernández-Palacios 1995). At the spatial resolution and for the habitat types that we considered, the landscape did not change significantly during the period of study. We reclassified the map into 10 simpler, landcover elements defined by both the density of vegetation cover and the nature of vegetation. These are: urban areas, water bodies, forest, scrublands with trees, sparse vegetation with trees, scrublands, low vegetation, woody crops, and herbaceous. The resulting landscape elements represent more the structure of the vegetation than the dominant tree or herbaceous species. For each individual wandering area we calculated the proportion of the different habitat types.

Each land cover area in raster format (ESRI GRID; projection, UTM; datum, European 1950; and cell size, 0.5x0.5 Km) was used as a basic input data layer for measuring landscape metrics. We used the raster version of the FRAGSTATS 3.3 (McGarigal & Marks 1995) to calculate some of the most commonly used landscape-level metrics, that is: (1) total landscape area; (2) density and (3) number of patches; (4) mean patch size; (5) total amount of edge and (6) edge density; (7) mean patch fractal dimension; (8) patch density; (9) relative patch richness; (10) Shannon’s diversity and (11) aggregation index. Although FRAGSTATS can calculate more than 40 landscape metrics, many of them are highly correlated (Ritter et al., 1995). We excluded those indices which were highly correlated (r > 0.8) from the analysis. A full explanation and mathematical formulas of each landscape measurement are provided by the FRAGSTATS user’s guide (McGarigal & Marks 1995).

STATISTICAL ANALYSIS

We used a stepwise multiple regression analysis (Sokal & Rohlf 1995) to analyse the effects of search movement strategies and individual physiological factors on both distance and timing to settle.

In most movement models path variables are intricately related - e.g. paths that are longer tend travel for longer periods of time. In order to separate these, we first carried out a principal components analysis on dispersal time, net distance, and overall 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. Then in order to see the effects on 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. distance from nest and path length. This gave us the effects on time by itself, not a by-product of an effect on distance or total path length.

In order to explore how matrix heterogeneity and individual physiological parameters affect individual movement behaviour while searching for a settlement
area, we used Generalized Linear Models (GLM, McCullagh & Nelder 1989). To avoid possible autocorrelation problems due to data from siblings and from several years, we first tested the possible effect of nest and year. But neither of them were significant (always \( p > 0.10 \)). Thus, all individuals were used in the analyses. Because the probability distributions of the response variables (fractal D, speed and total path length) were normal, they were modeled using the identity link function. Each explanatory variable and their interactions were fitted to the observed data using the GENMOD procedure of the SAS package (SAS Institute 2001). The statistical significance of each variable was tested in turn in the model (forward stepwise procedure), retaining those that contributed to the largest significant change in deviance.

Finally, to test whether habitat selection of the settlement areas differs from habitat use within the natal home range or from habitat use of floaters during the wandering phase of dispersal, we used two stepwise logistic regressions between (i) natal vs. settlement area; and (ii) wandering vs. settlement area. We entered into the stepwise logistic models as explanatory variables the indices calculated to describe landscape structure and composition. For all analyses, means are given ± SD, and statistical significance was set at \( p < 0.05 \).

Results

The mean distance between the settlement area and the natal territory moved by dispersing owls was 6900.6 ± 6726.3 m (range = 1039.5 - 34733.2 m) and the mean dispersal age was 300 ± 96.9 days (range = 164 - 640 days).

Movement configuration hypothesis. The first principal component explained 66% of the variation in movement paths, and this component was almost composed equally of effects from time, distance and path length. 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. Only fractal D\(_\text{mean}\) significantly affected this principal component (\( R^2 = 0.26 \); \( B = -2.84, p < 0.029 \)). The negative component slope (B-value) means that when owls travel quite tortuously at a large scale (i.e. not perfectly straight), they find settlement areas sooner, and at a shorter distance from the starting point. Because this search strategy seems to correspond with the so-called nearly straighter search by Zollner & Lima (1999), which allows animals to locate a new patch sooner without redundant searches, such a result agrees with the first hypothesis.

After removing the effects of the other variables, by regressing residuals, dispersal distance was significantly affected by fractal D\(_\text{nightly}\) (\( B = -19900, p < 0.022 \)) and fractal D\(_\text{overall}\) (\( B = -12700, p < 0.009 \)). The negative components mean that owls
travelling with more tortuous paths at both small and large scales find settlement areas at shorter distances from nests, independently of time travelled. Time to settle was significantly affected only by fractal Drightly ($B = 0.222$, $p < 0.03$). The positive component means that owls travelling with more tortuous paths at small scales took longer to find settlement areas, independently of distance travelled.

Movement abilities hypothesis. Landscape significantly affected movement path characteristics. In particular: (1) overall movements (fractal Doverall and path length) were positively affected by the total number of edges and inversely related with patch density (Table 1). Owls showed the straightest and longest paths when travelling across habitats characterised by high numbers of edges, but with low density of patches. Owls also showed the longest paths when travelling through open habitats (i.e. sparse vegetation and herbaceous patches); (2) fractal Drightly was affected by the interaction between the total number of edge and the mean patch size (Table 1). That is, at smaller temporal scales, dispersal movements were clearly patch-area dependent, with individuals showing the straightest trajectories when crossing the largest patches.

Some individual health aspects significantly affected movement path characteristics. Neither distance, timing to settle, fractal Drightly, nor total path length were affected by any sex or physiological condition measurements (i.e. BCI, biochemical and blood parameters; all $P > 0.5$). On the other hand, the overall speed nightly was affected by the interaction between sex and BCI. That is, individuals with higher values of the BCI (i.e. better physical conditions), especially if they were females, moved slower during nightly movements. Also fractal Doverall was affected by the number of lymphocytes. That is, owls with lower values of lymphocytes (i.e. better individuals) moved straighter overall (Table 1). These concur with the second hypothesis.

Natal experience hypothesis. Wandering and settlement areas were very different from natal territories (Table 2); but wandering and settlement areas were quite similar to each other (Table 2), the only difference between them being the presence of urban zones in the areas crossed during the wandering phase. Therefore, our data do not support the hypothesis that dispersing individuals will select habitat similar to the landscape surrounding the nest.

Discussion
Dispersing owls showed different movement patterns at different spatial scales. At a larger scale, owls travelling with the straightest movement trajectories travelled over longer distances from the nest. On the contrary, individuals dispersing with nearly straighter movements find settlement areas sooner. These results concurred with the predictions postulated by Zollner & Lima (1999) as regards to (1) animals optimally...
searching over longer distances should involve straighter movements; and (2) nearly straight movements always produced better dispersal success. The results of many studies analysing inter-patch movements on various taxa are consistent with our findings that nearly straighter search at large scale should produce better dispersal successful (see Zoller & Lima 1999 and references therein). On the other hand, at smaller scales, owls showed two different strategies. The two types of dispersers can be related to the bold and shy dichotomy (e.g. Skalski & Gilliam 2000; Fraser et al. 2001; Dingemanse et al. 2003; Si et al. 2004; Boon et al. 2007; Baguette & Van Dyck 2007): (1) shy individuals, limiting their dispersal distance (that is, not venturing as far into the hostile matrix) but searching for longer time periods before settling; and (2) bold individuals, searching straighter and for longer distances, but exploring more unfamiliar spaces and thus finding desirable area more rapidly. Thus, owls really did not change how far they venture in the overall matrix but how intensively they search the areas at smaller scale.

Understanding the scale at which animals change their movement behaviour is crucial to understand ecological processes involved at larger scales. A central issue in ecology is to what extent the patterns at fine scale can be explicitly extrapolated over larger extent and generally at coarser resolution. There have been several studies of scaling with models (see Urban 2005 and references therein). For instance, Morales & Elner (2002) used an experimental model system with Tribolium confusum beetles (Coleoptera, Tenebrionidae) to examine how realistic movements at small scale can predict the rate of spatio-temporal spread of organisms. This and others studies (e.g. With & Crist 1996; Jonsen & Taylor 2000) have found how difficult it is to extrapolate fine-scale information across scales mainly because individual behaviour change under different habitat condition or when different activities are undertaken (Frait et al. 2005). This is why we chose to study a priori dispersal patterns at two different scales (nightly vs. overall movement patterns). As an end consequence, our results offer now a clear example of the crucial importance of the scale in our interpretation and understanding of ecological phenomena.

Our findings suggest that dispersing owls altered their movement patterns in response to spatial and temporal scales. Our results are in accord with some previously studies that have demonstrated how animals can alter their behaviour from routine movements within patches to more direct displacements between patches (e.g. Johnson et al. 2002; Baguette 2003; Frait et al. 2005 and references therein; Baguette & Van Dyck 2007; Schickzelle et al. 2007).

The matrix heterogeneity strongly affected several movement parameters, with individuals travelling over different distances and for different times depending on which environment they encountered. Straighter movement behaviour was more frequent in landscapes rich in patch boundaries and low patch density where longer and straighter movement trajectories may
allow animals to search more rapidly and over larger distances (Zollner & Lima 1999; Van Dyck & Baguette 2005; Schtickzelle et al. 2006) and increase the probability of finding a valuable habitat compared to a more tortuous movement.

In our study area, large patches are cultivated areas such as cropland or pastureland - an inhospitable matrix for owls. We found that owls cross such large patches by moving straighter and, if necessary, longer paths than when they were embedded in a more forested habitat, as a dehesa. These results have previously been documented by Revilla et al. (2004), that found that Iberian lynx (Lynx pardinus) avoided to move in open areas if the matrix was fragmented, generally not staying in such kind of habitat for more than one period of activity.

These differences in behaviour may be explained in terms of dispersal costs and benefits, related to both the quality of and the physical structure of the environment (Dittendorfer et al. 1999; Boughton 2000). Previous studies have shown that habitat fragmentation causes higher dispersal costs, and that longer travels increase the hazard of mortality (e.g., Mennechez et al. 2006; Hansson et al. 2004, but see Haughland & Larsen 2004 and references therein). For instance, ruffed grouse (Bonasa umbellus) experience higher predation risk in unfamiliar areas and compensate for it by changing their movement rates (Yoder et al. 2004). Similarly, three species of Elodes beetles (Coleoptera: Tenebrionidae) varied significantly in net squared displacement of among various microlandscape mosaics that differed in both the coverage and the spatial pattern of patches (Wiens & Milne 1989). These different behavioural responses related to the environment may reflect animal effectiveness of learning to adapt to different circumstances. Because mortality risks are greater with more time spent and distance travelled in the matrix (Zollner & Lima 1999; Baker & Rao 2004), it is advantageous to reduce these.

Although neither the dispersal distances nor the timing to settle seemed to be directly related to the physical conditions of the owls, there was a weak and indirect influence between owls' physical conditions and search movement patterns. Those individuals with lower values of lymphocytes (i.e., better individuals) were more risky and exploratory, describing straighter trajectories (fractal Doverall) and, therefore, travelled longer distances but for shorter times before settling. Furthermore, females in better physical condition (i.e., higher values of BCI) moved slower during nightly activity periods. Lower rates of movements could be beneficial because they allow individuals to gain information of the environment and save energy (Zollner & Lima 2005). Owls with good physical may not need to move rapidly (they do not need increase their rate of habitat prospecting and, consequently, prey encounters) and are more free with their time than individuals in poorer body conditions (e.g., compensatory foraging; Norrda hl & Korpiński 1998; Murray 2002 and references therein; Wirssing et al. 2002).
In the context of habitat selection, an extensive body of studies has been focused on the proximate mechanisms and multiples causes that may be involved in habitat selection by dispersers. For example, familiarity with the cues that floaters experience in its natal habitat provides information that might increase its level of preference for a different type of postdispersal habitat that shares cues with the natal habitat (Davis & Stamps 2004; Stamps & Blozis 2006; Stamps 2006; Stamps & Swaisgood 2007). Other studies have demonstrated how different factors can influence dispersers’ decision to settle, as local demographic or environmental cues (Lima & Zollner 1996), or despotic exclusion from contrasting habitat (Freiwell & Lucas 1970). For instance, Haugland & Larsen (2004) demonstrated that settlement patterns of North American red squirrels (Tamiasciurus hudsonicus) better correlated with explorative movements and habitat availability in relation to the natal territory. 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. This highlights the importance of the familiarity with the immediate environment. As claimed by Stamps (2001), individuals may prefer to settle in post-dispersal habitats similar to their pre-dispersal habitats, because (1) this behaviour reduces the costs of assessing suitable habitats (habitat cueing), or (2) experience in pre-dispersal habitat improves performance if an animal settles in the same type of habitat after dispersing (habitat training).

To conclude, our results support the idea that movements vary not only among species and individuals but also among landscapes (Wiens 2001; Revilla et al. 2004; Merckx et al. 2003; Schlickzelle et al. 2007), and the final settlement pattern is therefore affected by a combination of behaviour, physiological parameters and the spatial configuration of the matrix. Therefore, understanding how individuals move through fragmented landscapes (i.e. both the likelihood to undertake dispersal and the ways in which they move) becomes important to improve our understanding on the dispersal process and for predicting the effects of landscapes on population dynamics and the spatial distribution of organisms.
Table 1. GLMs testing Movement abilities and Movement configuration hypothesis: movement path characteristics were significantly affected by both matrix heterogeneity and individual physiological parameters.

<table>
<thead>
<tr>
<th>Movement path characteristics</th>
<th>Parameter estimate ± SE</th>
<th>$r^2$</th>
<th>$P$</th>
<th>% variance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. Fractal D (overall)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total number of edge</td>
<td>-0.002 ± 0.001</td>
<td>3.64</td>
<td>0.056</td>
<td></td>
</tr>
<tr>
<td>Patch density</td>
<td>0.041 ± 0.055</td>
<td>4.12</td>
<td>0.042</td>
<td></td>
</tr>
<tr>
<td>% lymphocytes</td>
<td>0.005 ± 0.002</td>
<td>4.92</td>
<td>0.026</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.82 ± 0.14</td>
<td>-</td>
<td>-</td>
<td>52</td>
</tr>
<tr>
<td>b. Total path length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total number of edge</td>
<td>0.058 ± 0.032</td>
<td>6.50</td>
<td>0.006</td>
<td></td>
</tr>
<tr>
<td>Patch density</td>
<td>-7528 ± 2306</td>
<td>7.50</td>
<td>0.006</td>
<td></td>
</tr>
<tr>
<td>Sparse vegetation with trees</td>
<td>19397 ± 13225</td>
<td>8.00</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>Herbaceous</td>
<td>21629 ± 11496</td>
<td>3.39</td>
<td>0.050</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>11042 ± 11057</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>c. Fractal D (ugly)</td>
<td></td>
<td></td>
<td></td>
<td>99</td>
</tr>
<tr>
<td>Mean patch size × of edges</td>
<td>-0.004 ± 0.001</td>
<td>4.80</td>
<td>0.028</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-1.220 ± 0.038</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>d. Speed (ugly)</td>
<td></td>
<td></td>
<td></td>
<td>68</td>
</tr>
<tr>
<td>Body condition index × sex</td>
<td>-4046 ± 1613</td>
<td>5.74</td>
<td>0.016</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-891 ± 49</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Results of stepwise logistic regressions exploring the Natal experience hypothesis. The regressions relate various landscape indices between settlement and a) wandering areas and b) natal areas. These show that settlement areas selected by dispersers were more similar to their wandering areas than their natal territories, with the presence of urban areas during the wandering phase the only parameter making those areas different. However, several parameter related to landscape composition significantly explained how much different were both settlement and natal areas.

<table>
<thead>
<tr>
<th>Landscape structure and composition</th>
<th>Parameter estimate</th>
<th>$\chi^2$</th>
<th>P</th>
<th>% variance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. Wandering area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urban areas</td>
<td>-1.24 ± 0.68</td>
<td>6.87</td>
<td>0.009</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1.89 ± 0.80</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>b. Natal area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water bodies</td>
<td>-6.5 ± 3.26</td>
<td>5.41</td>
<td>0.023</td>
<td></td>
</tr>
<tr>
<td>Scrubland with trees</td>
<td>-6.00 ± 7.12</td>
<td>4.03</td>
<td>0.050</td>
<td></td>
</tr>
<tr>
<td>Woody crops</td>
<td>22.5 ± 10.8</td>
<td>5.21</td>
<td>0.022</td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-0.22 ± 0.27</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Acknowledgements

For their help in the field we are grateful to P. Bortolozzi, L. Campioni, R. Lourenço & G. Fontanari. We thank M. Perera for her invaluable advice and support. Funding for this study was provided by a research project No. CGL2004-02780/ROS of Spanish Ministry of Education and Science and LICOR43 (Diego Zamaora S.A.). During this work M.M. Delgado was supported by a doctoral grant of the Junta de Andalucía (Consejería de Educación y Ciencia). We manipulated and marked owls under the Junta de Andalucía - Consejería de Medio Ambiente permits No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02.
8

LEVELS OF FAMILIARITY THROUGH NATAL DISPERSSAL

by

María del Mar Delgado, Vincenzo Penteriani & Vilis O. Nams
Information plays a crucial role in several animal decision-making processes like movement decisions. Finding out how individual knowledge on the location, type or quality of local resources (i.e., familiarity) influences animal movements can improve our understanding of many behavioral choices and ecological processes and patterns. The effects of familiarity on animal movement decisions are revealed when comparing the what, where and how learning between individuals that are still acquiring information vs. individuals with a more complete knowledge of their surrounding. We analyzed movement patterns of the two classes of eagle owls (Bubo bubo): floaters (dispersing individuals wandering across unknown environments or already settled in temporary settlement areas) and breeders (territory owners with a fixed home range). We found that: (1) at the beginning of dispersal, individuals tend to move faster than when established in a temporary settlement area, traveling large and straight paths with long move steps; (2) floaters in a permanent settlement area show quite fixed home ranges (i.e., they are not still wandering individuals moving randomly across unknown environments) and movement behavior similar to territory owners. That is, movement patterns experienced an evident transition from exploratory strategies (when animals have incomplete information of the environment) to a more familiar way to exploit their home range as better they get to know the environment.

KEYWORDS: Bubo bubo; dispersal; familiarity; home range; experience; learning; fractal analysis; movement behavior; movement search strategies
Cognition abilities and learning affect behaviors and choices related to habitat selection, mate choice, foraging, social interactions and space use (Dukas 2004, Dall et al. 2005). Until now, most of models that have been used to explore some aspects of spatial learning have assumed that individuals are "omniscient", i.e. that they have complete information on the quality of all patches in the habitat. However, it is unlikely that individuals could have an a priori information on the surrounding (e.g. Vos et al. 1998 and references therein, Stamps and Krishnan 1999): individuals needs time to acquire knowledge on the surroundings in which they move and, consequently, adopt some site-specific mechanisms or rules which allow them to exploit habitat patches optimally (Stamps 1995, Thiedt and Hoffmeister 2004, Dall et al. 2005).

Animal movement is an essential mechanism underlying many ecological processes at individual (e.g. home ranging, site fidelity, foraging), population (e.g. metapopulation connection and persistence, invasion spreading), community (e.g. assemblages, species coexistence), and ecosystem (e.g. ecosystem rate limitations) levels. The implications of movement behavior on several evolutionary and ecological processes have been recently emphasized (Dingemanse et al. 2003, Davis and Stamps 2004, Hansson et al. 2004, Haugland and Larsen 2004). In particular, spatial memory and learning allow animals to move through their landscape as efficiently as possible (Saarenmaa et al. 1988, Vuilleumier and Perrin 2006). However, there is still a lack of knowledge on the characteristics of the process by which individuals learn and acquire experience to move within and through environments (e.g. Dukas 2004).

Three central types of territorial learning have been suggested by Stamps and Krishnan (1999), and these can be generalized to spatial learning in general. These are: (1) the what, refers to the assessment of major habitat features as roost sites, cover, hunting perches and foraging areas; (2) the where, referred to the learning of the location of these habitat features; and (3) the how, related to the acquisition of motor skills that facilitate the most efficient use of the habitat (see also Stamps 1995), i.e. the best exploitation of the elements that they have discovered by the two previous types of learning. This process of information acquisition does not occur instantaneously (Stamps and Krishnan 1999), and the increase of the value of familiar space is a function of the time individuals that settle in an area (Stamps 1995). In addition, what and where may represent two consecutive moments of the same learn process: when an individual achieves to locate a specific resource (the what), it also learns its spatial location (the where).

Because the increase in the value of familiar space as a consequence of learning is one of the key factors determining animal movement patterns (Stamps and Krishnan 1999), we can hypothesize that individuals actively sampling novel and temporary patches should show a different
movement behavior than when they settle in a stable area (when they are expected to have enough time to efficiently combine the what, where and how learning). Dispersal represents a unique scenario to test this hypothesis because of the specific stages that individuals go through (Stamps 2001, Andreassen et al. 2002, Clobert et al. 2004, Bowler and Benton 2005, Heinz and Strand 2006, Baguette and Van Dyck 2007).

The eagle owl (Bubo bubo; for more details see Penteriani et al. 2007) has a multiphase dispersal process (Delgado and Penteriani submitted), where after starting dispersal (start phase), floating owls (sensu Penteriani et al. 2006a) are suddenly embedded in an unknown environment. At the beginning, during the wandering phase (i.e. searching), they explore different areas for a variable time period. Once they find a suitable temporary settlement area they enter the stop phase of dispersal (Penteriani et al. 2006a,b, 2006b). Such settlement areas represent those zones occupied during the longest time period of the whole dispersal, sometimes until floaters become territory owners and start breeding. At this stage, due to the amount of time they spend in the settlement area, individuals become more familiar with their environment and learn what significant habitat features are in the area, where these are and how to move to exploit them. Therefore, the comparison of movement behaviors of both floaters throughout the dispersal process and territory owners represents a unique opportunity to evaluate the effects of local familiarity on animal movement decisions.

By using the data of a 4-year radiotracking study on the movement behaviors of eagle owls, we tested the following hypotheses on the effects of local familiarity on animal movement patterns: (1) as a consequence of the increase in the value of familiar space, the what, where and how learning caused a radical change in the movement patterns of individuals and (2) owls in the stop phase should show movement patterns more similar to territory owners than wandering floaters at the beginning of dispersal.

Materials and methods
To test the two hypotheses we used data from 40 juveniles (from 12 nest sites) and 9 territory owners radiotagged in 2003-2006.

We followed both territory owners and juveniles individually in continuous radiotracking sessions (n = 288 entire nights) during a total time of 1214.27 and 1840.25 hrs, respectively. A continuous radiotracking session means following a focal individual during the whole night (i.e. from one hour before sunset to one hour after sunrise; mean duration of a radiotracking session ± SD = 10.56 ± 0.08 hrs), recording a new location (n = 4758) each time that we detected a change in either individual posture or position (mean number of locations per radiotracking session ± SD = 18 ± 4).

DATA ANALYSIS
Defining dispersal phases
To determine the different phases (i.e., start, wandering and stop phase) of dispersal, we recorded the exact position of each juvenile weekly, typically when owls were at their
Learning the what
To detect if individuals were acquiring, retaining and using information on two significant habitat features, the roost sites and foraging area, we proceeded as follows.

Roost sites: we calculated the distance between the first and the last owl location recorded on the same night (that is, before the start and after the end of the nightly activities). Animals with a preferred (i.e. learned) diurnal roost site are expected to frequently return to it after their nightly activity period. Therefore, we hypothesized a shorter distance between the first and the last location recorded in the same night once owls have settled in an area (i.e. floaters within settlement areas or territory owners).

Foraging areas: firstly, we calculated the individual home ranges by identifying 50, 75 and 95% core areas (Adaptive Kernel Contouring method, Worton 1989) using ‘Home Range’ extension (Rodgers and Carr 2002). We used least-squared cross validation (LSCV) to select the smoothing width because it minimizes the estimated error for a given sample (Silverman 1986). Secondly, this information was used to: (a) identify foraging areas; and (b) calculate their extensions relating to the total area of the home ranges. We predicted that because wandering individuals are exploring novel areas and, consequently, continuously sampling different patches, they do not show movements within well defined foraging areas. However once owls have settled in an area they tend to concentrate their foraging efforts in specific restricted areas, because they have learned
the spatial distribution of resources within their home range.

Learning the where
Dispersing through new habitats vs. crossing its own home range are very different scenarios involving different spatial domains, and thus we might expect that the structure of an animal’s movement path qualitatively change. We tested this measuring path structure as a function of spatial scale, by the following three procedures as described in Nams (2005):

(1) We measured path tortuosity of each nightly movement path as a function of spatial scale (from 20 to 1000 m), using the Vfractal estimator with Fractal 4.0 software (Nams 2005). Fractal D near 1 indicates a perfectly linear movement, whereas D near 2 suggests approximately Brownian (plane-filling) movement. A discontinuity in Fractal D vs. scale relationship indicates a change in path structure from one spatial domain to another.

(2) We also measured the variation in path tortuosity as a function of spatial scale. A sharp drop in the variance of tortuosity also indicates a change in path structure from one domain to another.

(3) Finally, we measured the correlation in tortuosity between pairs of adjacent path segments, as a function of segment length. If the segments are much smaller than patch sizes, their correlation would be positive because both path segments would be either inside or outside of a patch. For segments that are the size of patches, one would be in a patch (and therefore tortuous) while the adjacent would be outside (and therefore straight), and thus, their correlation would be negative. Finally, when segments are large enough to cover several patches, then their correlation would be zero. Thus, when there is a zero correlation at all scales this means no patch use, while a positive correlation of tortuosities dropping to a negative correlation indicated a path use. In such a case, patch size may be estimated as the spatial scale at which the correlation declines below zero (Nams 2005).

Learning the how
In order to characterize owls’ motor skills (i.e. how individuals exploit the elements inside the space in which they move), we estimated various movement path statistics. First we estimated path tortuosity, by the overall fractal dimension (D). This was done using the same range of spatial scales for all individuals (from 20 to 160 m), with the upper limit set at less than half the lengths of the longest path, and the lower limit the minimum distance between locations (Halley et al. 2004). Using the same range of scales allowed us to compare Fractal D among paths even though D varied with scale (Turchin 1996). D was computed using the Fractal Mean estimator with the program Fractal (Nams 1996, Nams 2006), and Fractal D was normalized by log (D-1). Because dispersal costs are many and floaters’ only hope is to locate a patch as quickly as possible, we expected that wandering dispersing owls traveling through unknown matrix should follow straighter paths than animals moving in a familiar habitat (Zollner and Lima 2005). Finally, we estimated the overall traveling speed, mean step lengths
and the total length of nightly movement paths. Both the overall speed and the total path length were based on the gross distance traveled.

We predicted that wandering owls who are in unfamiliar areas, but are searching for patches to successfully settle in a quite stable settlement area, should travel faster and straighter than individuals who know that area.

**STATISTICAL ANALYSES**

Because repeated measures were made for each owlet, we considered individuals as sampling units (SUBJECT Statement in PROC MIXED), and used a repeated measurements mixed model (PROC MIXED in SAS software; SAS Institute 2001). Because we radiotagged many owls per nest, we tested the possible effect of nest as an additional random effect (Littell et al. 1996). But the effect of the nest was never significant (always p>0.10) and was therefore removed from the model. We used a restricted maximum likelihood method (REML) to estimate all the unknown variance-covariance parameters (Jenrich and Schluchter 1986) and selected autoregressive (AR1) as the covariance structure that best fitted Akaike Information Criterion (AIC). The variance structure with the lowest AIC value is deemed the best one. Finally, statistical significance was considered to be p<0.05.

**Results**

Most juveniles started their dispersal at the end of August (mean age at the beginning of dispersal (± SD) = 170 ± 20.51 days-old; range = 151 - 232 days-old). Although there was a high degree of individual variation, 50% of eagle owls found a stable settlement area (i.e. shifted from the wandering to the stop phase of dispersal) in the middle of March (mean dispersal age of the stop phase (± SD) = 395 ± 109.86 days-old, range = 181 - 640 days-old).

**Learning the what**

Floaters during the wandering phase showed significantly larger distances between the first and the last location recorded in the same night than both floaters during the stop phase and territory owners (F_{23} = 14.99, P < 0.0001; Table 1). As expected, individuals already established in a stable settlement area (or owner of a territory) come back to a given roost site or area more frequently (i.e. they showed shorter distances between the first and the last location recorded in the same night) than do owls during the wandering phase. On the contrary to what was hypothesized for foraging areas, we did not detect any significant differences in the relative size of the foraging areas (F_{23} = 2.06, P = 0.13) among the different life stages. However, the relative size of foraging areas gradually decreased (Table 1) from territory owners to the wandering phase of dispersal. The floaters in the stop phase showed an intermediate behavior between the wandering and territorial owls.

**Learning the where**

There was a gradual change in response to spatial scale across the two phases of dispersal (Fig. 1). During the wandering phase of dispersal, owls moved with homogeneous movement paths. This was shown by the continuous change in Fractal D and variance with spatial scale, and the
non-positive values of correlation (Fig. 1). On the contrary, territory owners showed the most heterogeneous paths, with strong responses at different spatial scales (Fig. 1). This was shown by the drop in Fractal D and variance at ~350 m, and the crossing of the y-axis from positive to negative values by the correlation at ~300 m. These indicate two potential domains of scale for territory owners, suggesting that their movement paths differed qualitatively at scales of below 300 m and above 350 m. The owls in the stop phase showed intermediate responses to the wandering and territorial owls.

Learning the how
The repeated measurements mixed models show that almost all variables describing motor skills experienced a gradual but significant transition from the beginning of dispersal to the acquisition of a territory. Wandering individuals with an incomplete information of the environment traveled faster ($F_{23} = 5.73, P = 0.0048$; Table 1) with longer step lengths ($F_{23} = 7.30, P = 0.0035$; Table 1), and had the longest ($F_{23} = 12.09, P < 0.0001$; Table 1) and straightest trajectories ($F_{23} = 6.51, P < 0.0021$; Table 1). On the contrary, territory owners moved slower, with shorter and more tortuous movement paths. Floater in the stop phase clearly represented a transition stage between owls at the beginning of the dispersal and territory owners, characterized by high traveling speed but quite shorter and more tortuous movement trajectories than floaters during the transition phase (Table 1).

Discussion
Animals living in a changing world have to continuously reduce uncertainty by gathering information (Dall and Johnstone 2002). Our findings suggest that movement behaviors experienced a transition from wandering exploratory strategies to a more specific use of spatial resources when the individual increases the value of familiar space. At the beginning of dispersal, when individuals frequently travel across unfamiliar (and sometime unfavorable) areas, they have less time to become familiar with their surroundings. Uncertainty regarding location of conspecifics, predators and resources may pose significant problems (Stamps 1993, Stamps and Krishnan 1999, Dall et al. 2005). But the costs of uncertainty during dispersal may be reduced by becoming familiar with the spatial and social environment - e.g. searching actively for temporary, stable settlement areas. This phenomenon is mirrored by the observed changes in movement patterns showed by dispersing owls when they reach a settlement area. At that moment, although floaters never show territorial displays (Delgado and Penteriani, unpublished results) they do have a well-defined home range, as is common to the floaters of many bird species (e.g. Smith 1978, Arcese 1989, Zack and Stutchbury 1992). Floaters’ home ranges represent a well-known and described phenomenon, but this is the first time, to our knowledge, that it has been possible to describe detailed aspects of the movement behavior when floaters remained in a defined area. Moreover, our study also highlights that the home range of floating birds is not a characteristics of the floating population from their
beginning (i.e. when individuals start dispersal), but a consequence of the time they have spent as dispersing individuals.

The benefits of local familiarity have been generally linked with the increase in foraging efficiency, breeding performance and survival (Pärt 1995). By learning the physical and social structure of their environment floaters can remember the location and qualities of the resources they learn about, attend to conflicting needs and sensory inputs, engage in social interaction, and balance all of these considerations.

Despite we did not detect any significant differences in the relative size of the foraging areas among the different life stages, the fact that preferred foraging areas within the home ranges used by floaters during both the wandering and the stop phase of dispersal seemed to be less restricted than for territory owners could be the result of individual adjustment responses of foraging behavior to local habitat structure (Fortin 2002). Because the home ranges of floating owls are not defended, the higher mobility of nonbreeders allows them to displace among different hunting areas more easily than breeders. Constrictions as complex social organization and territoriality among neighbors could oblige territory owners to respect the limit of their home range to avoid the high cost of intrusions in neighboring territories.

The concepts of territory and home range involve pivotal differences. Home ranges refer to areas: (a) over which an animal travels in its day-to-day activities to join the most focal elements for their survival; (b) which, due to the scattered distribution of resources, also include large portions of landscape that individuals are just passing through; and, consequently, (c) that are too large to be efficiently protected from intrusions (e.g. eagle owls are territorial only in a restricted portion of the home range; Delgado and Penteriani 2007). On the other hand, territories refers to an exclusive portion of the home range that is defended to exclude other conspecifics (Maher and Lott 1995) and, consequently, does not overlap with the home range of neighboring residents. These differences between home ranges and territories explain some of the different behaviors we observed. To improve the efficacy of territory acquisition and defense, territory owners exhibit a complex array of behavioral patterns, such as site-specific aggressiveness, the ability to discriminate neighbors from intruders, and contests involving complicated exchanges of communication signals (for more information see also Penteriani et al. 2007). Floaters, who do not show such behavioral displays because they do not actively defend an exclusive area, can benefit from living in a restricted area through gaining knowledge of the habitat and establishing dominance relations with other floaters and territory owners (Smith 1978, Stutchbury 1991, Bruinzeel and van de Pol 2004). The needs for territorial tasks (as well as reproductive ones) of territory owners could also contribute to the faster movements of floaters during dispersal in comparison to territory owners.
Figure 1. Analysis of movement patterns of juvenile owls, during the wandering and the stop phase of dispersal, and territory owners. The following statistical were estimated at different spatial scales: Fractal D measures path tortuosity, variance measures variance in tortuosity among path segments, and correlation measures correlation in Fractal D between adjacent path segments. Dispersing owls showed homogeneous movement paths (i.e. defining a unique domain of scale), while territory owners showed two domains of scale (i.e. they were traveling with heterogeneous paths): below 300m and above 350m. Dotted lines represent 95% confidence intervals.
For example, territory owners spend large amounts of time calling on posts located close to the core areas of their home range, both for territorial demarcation and mate-mate communication (Delgado and Penteriani 2007). This means long pauses of territory owners on strategic posts, which are not included in the time budget of floaters that mainly roost, hunt and survey new areas (Delgado and Penteriani, unpublished data). Differences in the speed of movement may also have generated the detected differences in landscape interaction between dispersers and territory owners, which in turn may also be reflecting differences in individual perceptive resolutions (With 1994). Animal perceptive resolution, which may integrate sensory perceptive abilities, physical constraints and behavioral preference, is inversely related with the rate of movement. The ability of animals to perceive habitat heterogeneity at small scales decreases as speed increase, whereas the spatial extent at which they operate increases (Kolasa and Rollo 1991). Because floaters moved faster than territory owners, floaters perceive environmental patterns at a larger spatial scale and, as consequence, dispersing owls show a large and unique domain of scale. On the other hand, territory owners can operate at different and well-defined domains of scale, each one reflecting different aspects of their biology (e.g., foraging behavior, crossing home range and reproduction).

Animal movement behavior can be classified in random and systematic strategies (Fortin 2002). In systematic movement strategies, which only work when some a priori relevant information is available, the rules to optimally cover a given area are based on quite fixed and controlled plans. By contrary, in a random strategy, animals must attempt to move in order to optimize their chances of locating resources (i.e. food, mates, shelter, breeding habitats), relaying the search rules on stochastic processes. Although it is not possible to completely neglect the existence of chance in nature, sensorial or cognitive improvements could override the need of random search in nature by, e.g. creating more and better sensory cues, improving high-level environmental information-processing mechanisms and synchronizing spatial variations of the abundances of resources.

Dispersal costs are many and might include the risk of starvation and other sorts of mortality. In general, animals dispersing through an inhospitable and unknown habitat should follow straighter paths, to better avoid redundant searches, and to locate a patch as quickly as possible (Zollner and Lima 1999). Wiens et al. (1997) found that darkling beetles (Eledos obsoleta) move in straighter paths through high-risk areas than they do through low-risk ones. A variety of other organisms (Crist and MacMahon 1991, Madison 1997) follow straighter paths when displacing long distances through
unknown habitats. When habitat features are known, as is the case for floaters during the stop phase and territory owners, individuals should be able to efficiently regulate its movements (Klaassen et al. 2006). This was supported by the observation that already fixed owls in the stop phase of dispersal can adjust the length and the tortuosity of their movements, showing movement patterns more similar to territory owners than wandering floaters.

Finally, while spatial familiarity is one of the multiple key factors in determining movement patterns, the patterns we recorded could also result from owls in the wandering phase needing to prospect more areas than already fixed individuals (i.e. floaters in their settlement areas and territory owners). Active search generates the patterns of movements that we observed - mainly locations of roost sites, pattern of path tortuosity and domains in movement paths, as well as paths and step lengths. That is, two non-mutually exclusive elements should be taken into account when explaining movement behaviors: the different needs due to dissimilar social status (e.g. wandering floaters vs. breeders) and the progressive learning of the spatial environment individuals move across.

Acknowledgements

For their help in the field work we are grateful to P. Bartolozzi, L. Campana, R. Laurenga and G. Penteriani. The first draft was improved by the criticisms of Reut Arni. Funding for this study was provided by a research project No. CGL2004-02780/BOS of Spanish Ministry of Education and Science and LICOR43 (Diego Zamora S.A.). During this work M. M. Delgado was supported by a doctoral grant of the Junta de Andalucía (Consejería de Educación y Ciencia). We manipulated and marked owls under the Junta de Andalucía – Consejería de Medio Ambiente permits No. SCFFS-AFR/CGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02.
Conclusions
During the last 30 years, the study of animal populations has shifted from a less complex science, mainly based on the breeding portion of single units or populations, to a more refined discipline which explicitly recognizes that populations are composed of multiple fractions (the metapopulations), whose complex dynamics and individual behaviours determine their characteristics and fates.

At the beginning, the most crucial mechanisms regulating animal populations were intrinsic properties of breeders only. On the one hand, we were exclusively focusing on the ecology of those individuals that reproduce and, on the other, when immigration by natal dispersal was considered, nonbreeding individuals were purely considered as a numeric entity without identity, whose main interest was their immigration rates. The nineties represent a very fertile decade of explorations on animal populations, revealing to us part of the previously undetected ecological complexity of populations. The *Metapopulation Ecology* by Hanski (1999) offers an example of the complexity of animal populations by analysing them as a complex unit composed of different pieces, the metapopulations. Coupled with the fractioning of the original concept of a population as a single unit, nonbreeders started then to acquire their legitimate, important role in the equilibrium of (meta)populations. Through simply moving from one location to another, the process of natal dispersal (i.e. the movements between the natal area and the area where breeding first takes place; Clobert et al. 2001) and dispersing individuals have become crucial elements regulating population dynamics, trajectories, spatiotemporal distributions and stability, as well as their likelihood of extinction.

However, despite its importance, the dispersal process still represents a significant gap in our understanding of animal ecology (Doerr and Doerr 2005). This is very surprising, given the amazing number of studies on this topic and the huge amount of literature that has been written on the subject. For example, by simply introducing the term dispersal in one of the most important and complete tables of bibliographic information from the scientific world’s (the Current Contents Connect) we can find more than 20000 studies on such topic. So, where is the origin of the dispersal “black hole”, i.e. why do we still
have an incomplete understanding of dispersal? As remarked by several authors, the combination of the lack of empirical data (especially on vertebrate species) with the difficulties of considering dispersal as a complex, dynamic process, could be one of the main reasons for this setback. Moreover, during the last decades, dispersal studies have mainly focused on the cues used in the first steps (i.e. when individuals take the decision to leave their natal site) and the last stages (i.e. when dispersing select a stable settlement area), while little is still unknown about the intermediate, wandering phase.

In spite of these constraints, a greater understanding of the dispersal process has been achieved by approaching it under the perspective of the animal movement patterns. In fact, several novel facts were highlighted on the: (a) causes and consequences of dispersal (Clibert et al. 2001); (b) variation in time and in space of its costs and benefits (Deno et al. 1989, Waser et al. 1994); (c) beneficial and detrimental effects of dispersal patterns on the persistence of spatially structured systems (Hanski 1999, Heino 1997, Penteriani 2006); as well as (d) on the behavioural basis underlying individual decisions during such process (Bowler & Benton 2005, Delgado & Penteriani, in revision). Several approaches have been used in the analysis and modelling of animal displacement in space. Initially, diffusion theory (Okubo 1980, Kacser 1983, Andow 1990) was useful in describing animal movement patterns, providing a natural spatial extension of Lotka-Volterra models. Ordinary (i.e. Fickian) diffusion models assume that particles (e.g. biological organisms) move independently and execute a simple random walk. A theoretical diffusion models largely used to evaluate movement pathways have been the correlated and biased random walk, which assume independent distributions of move lengths and move angles having a net directional bias (Kareiva and Shigesada 1983, Boquet and Benhamou 1988, McCulloch and Cain 1989, Bergman et al. 2000, Bartumeus et al. 2005). Although random walk models (and their diffusion approximations) have been particularly useful in situations where movement behaviours were difficult to observe and can effectively predict the pattern of animal distribution on short time scales (Turchin 1998), they also showed important limitations (Patlak 1953, Turchin 1989, 1991, Johnson et al. 1992, Holmes 1993). For example, random walk models tend to fail when longer time horizons are taken
into consideration, mainly due to not considering the occurrence of behavioural changes during the life-span of an individual and their influences on movement patterns (Firle et al. 1998, Morales et al. 2004), as well as the possible changes of movement patterns when different habitat conditions are encountered (Jonsen and Taylor 2000, Frair et al. 2005). To solve some of the problems of diffusion models (mainly directional biases during movement), more recent diffusion models have incorporated directed movements, i.e. patterns of moves characterized by persistence of direction and variations in the medium that the animal is travelling in (e.g. net bias, Okubo 1980; prey taxis, Banks et al. 1987; or advection terms, Turchin 1989). Lately, because movement pathways are strongly influenced by environmental structures, the importance of spatial scale has been emphasized by these studies. Therefore, models on animal movements have been extended to heterogeneous landscapes by simulating movements in percolation networks (i.e. the probabilities of movements is a direct function of landscape patterns, Gardner et al. 1989, Johnson et al. 1992). More recently, several authors have applied fractal methods (Wiens et al. 1995, Nams 1996, Bascompte and Vílal 1997, Nams and Bourgeois 2004, Doerr and Doerr 2004) and Lévy walks (Bartumeus et al. et al. 2005) to assess organism responses to spatial heterogeneity.

Although several empirical supports exist for some of these models, they generally come from experimental studies or data on short-term movements of invertebrates, which may be expected to show less complexity and variability than dispersal in vertebrates moving through a heterogeneous and complex natural world. When considering an animal searching for suitable habitat patches while dispersing through a matrix landscape, we have to take into account that, during the travel from the natal to the breeding patch, the movements will be influenced by, for example, matrix habitat variability, density, competition, predation and food availability. All these factors may generate different movement behaviours and search strategies. Moreover, these factors cannot be considered independently of the potential effect of animal cognitive abilities (With & Crist 1995, With et al. 1997, 1999) and learning capabilities (Stamps & Krishnan 1999). Animals can use significant powers of spatial memory and learning to move through their landscape as efficiently as possible (Saarenmaa et al. 1988, Vuilleumier &
Ferrin 2006). That is, animal movement ability and therefore, the dispersal process, is the result of multiple complex interactions of external and internal factors acting at various spatial and temporal scales.

On the one hand, my personal curiosities towards the complex ‘world’ of animal dispersal and the different behavioural strategies have guided my scientific interest towards such a process. On the other, I had been always fascinated by those species and systems that are less commonly studied and that, consequently, may also offer new and unexpected insights into ecological questions, giving us the possibility to find novel results. As an ending result, in the course of this thesis my co-authors and I have investigated the effects of the landscape’s characteristics, individual fitness and the organism’s cognitive and learning abilities on the dispersal movement behaviours of a long-lived species, the eagle owl (Bubo bubo). I have started my personal voyage across dispersal and the main component of this process, the floaters, with a detailed revision in which I resumed and discussed the different effects that floaters can have on the structure, dynamics and persistence of bird populations (Introduction 1.2). Because the potential influence that the postfledging dependence period, an intensive phase of experience and learning, may have on individuals’ behavioural strategies during the later crucial dispersal period, I have devoted the first episode (chapter 3) to describing and analysing the patterns of movement during this phase. Subsequently, I became wrapped up in the dispersal process. First of all, I characterised the behaviour during the wandering (searching) phase of dispersal through the analysis of movement characteristics. Keeping in mind the complexity of behavioural dispersal strategies, I compared the accuracy and realism of the predictions of random walk models on the spatial spread of animal populations (chapter 4). The following chapter has been especially focused on the effect of the interaction between the surrounding environment and features of individual animals (chapter 5). As a natural consequence of such a direction in my research, I was especially intrigued by the dispersal spatial network. I analysed it by comparing the real dispersal routes with optimized and randomized routes in order to gain information on the movement dispersal strategies of juveniles and the importance of connectivity on the dispersal process (Chapter 6). Because the individual variations in movement behaviour, the costs of dispersal and landscape structure can lead to variation in settlement patterns, I also explored (chapter 7) when, where and
how individuals search for settlement areas. Finally, I investigated how the learning abilities and the increase of the level of familiarity with the surroundings can cause a radical change in the movement patterns of dispersing individuals (chapter 8).

This thesis is based on 7 original manuscripts, all of them currently under review (first and second revisions) in SCI journals. I have contributed to the conception and planning of the studies, the acquisition, analyses and interpretation of data, and writing of all the articles.
RESÚMENES DE LOS CAPÍTULOS
Introducción

1.1

La dinámica del proceso de dispersión y los movimientos de los animales

Durante los últimos 30 años, el estudio de las poblaciones animales ha experimentado un abrupto cambio desde una ciencia poco compleja, centrada principalmente en la porción reproductora de las poblaciones, a una disciplina más refinada que explícitamente reconoce que las poblaciones es el resultado de la unión de múltiples fracciones (las metapoblaciones), en las que su compleja dinámica y el comportamiento de los individuos determina tanto sus características como su destino.

Al principio se consideraba que los mecanismos esenciales que regulaban las poblaciones animales eran sólo las propiedades intrínsecas de los reproductores. Es decir, estábamos exclusivamente centrados en la ecología de aquellos individuos que se reproducían. Y, cuando era considerada la dispersión natal, los dispersantes eran sólo considerados como unidades numéricas sin ninguna identidad, siendo casi el único motivo de interés su tasa de inmigración. Los 90 fue una década en la que se produjeron importantes cambios en la ecología de las poblaciones, evidenciándose la gran complejidad, hasta entonces desapercibida, de las poblaciones. El libro *Metapopulation Ecology* de Hanski (1999) es uno de los mejores ejemplos que refleja esa complejidad, en el que por primera vez se analizan las poblaciones como el resultado de diferentes piezas, las denominadas metapoblaciones. Al mismo tiempo que se reconoció la existencia de las metapoblaciones, los individuos no reproductores comenzaron a tener una mayor importancia, sobre todo en el papel que desempeñaban en el equilibrio de las (meta)poblaciones. A través del simple movimiento, de una localización a otra, los dispersantes y, por tanto, el proceso de la dispersión, fueron reconocidos como elementos cruciales en la regulación de la dinámica, la trayectoria, la distribución espacio-temporal y la estabilidad de las poblaciones. Sin embargo, a pesar de su importancia, el proceso de la dispersión todavía representa un “hueco” en nuestro conocimiento de la
ecología animal, hecho que es realmente sorprendente dado el gran número de estudios y cuanto se ha escrito acerca de este proceso. Sólo introduciendo el término dispersal en uno de los buscadores más conocidos y utilizados en el ámbito científico, nos encontramos más de 20000 trabajos centrados en la dispersión. ¿Por qué no hemos llegado a comprender el proceso de la dispersión? Entre otros muchos motivos, podríamos pensar que uno de los principales motivos ha sido la combinación de una falta de datos empíricos (sobre todo en vertebrados) con la dificultad de enfrentarse a la complejidad de este proceso.

A pesar de los factores limitantes que ha tenido el estudio de la dispersión, los análisis de los patrones de movimientos de los dispersantes han supuesto un gran aporte en nuestro conocimiento acerca de, por ejemplo, las causas y consecuencias de este proceso, sus costes y beneficios, los beneficios y prejuicios para las poblaciones y el comportamiento responsable de las decisiones que los animales tienen que tomar durante esta fase de su ciclo de vida. Aunque numerosas aproximaciones (modelos de difusión, de movimientos azarosos con direccionalidad, de percolación, y un largo etc.) han tratado de analizar y predecir los desplazamientos de los animales durante la dispersión, la mayoría de ellos han encontrado importantes limitaciones, sobre todo a la hora de predecir patrones de movimientos a largas escalas temporales y al no considerar que el comportamiento de los animales puede variar con el transcurso del tiempo. Además, aunque muchos de estos modelos de movimientos tienen un soporte empírico, generalmente procede de estudios experimentales a pequeñas escalas temporales y como modelos biológicos insectos, que seguramente muestran una menor complejidad y variabilidad que animales vertebrados moviéndose a través de hábitats reales y heterogéneos. De hecho, durante la dispersión, el movimiento de los animales se encuentra afectado por numerosas y complejas interacciones entre varios factores, como la estructura y composición del hábitat, la condición física de los individuos, la densidad, la predación, la disponibilidad de recursos, las capacidades de aprendizaje y las habilidades cognitivas, etc.

La complejidad que conlleva el proceso de la dispersión, las diferentes estrategias de comportamiento y las diferentes rutas
evolutivas que conlleva son los elementos principales que han guiado mi curiosidad científica hacia este tema, interesándome especialmente en aquellas especies y sistemas hasta ahora menos estudiados. En el transcurso de esta tesis hemos investigado los efectos que tienen las características del hábitat, la calidad de los individuos y las habilidades cognitivas y las capacidades de aprendizaje sobre los movimientos (centrándonos en el comportamiento) de la dispersión de una especie de larga vida, el búho real (*Bubo* *bubo*). En el primer capítulo hacemos una detallada revisión de la importancia de los floaters en la estructura, dinámica y persistencia de las poblaciones. Dado que la gran importancia que puede tener la fase previa a la dispersión, es decir, la etapa de postfledging, en el destino de los animales, dedicamos un capítulo al estudio y descripción de los patrones de movimientos durante el periodo en el que los individuos, ya habiendo abandonado el nido, permanecen bajo los cuidados parentales. Posteriormente nos sumergimos completamente en el propio proceso de la dispersión. De este modo, ya en el capítulo cuatro analizamos el comportamiento de los animales durante los desplazamientos realizados en la fase de búsqueda y, teniendo en cuenta la complejidad y variabilidad observada en el comportamiento de los individuos, comparamos la fiabilidad de los modelos de movimientos azarosos a la hora de predecir la distribución de los organismos. En el siguiente capítulo realizamos un estudio para analizar el efecto de la interacción entre los factores ambientales y aquellos propios de la calidad de los individuos en los patrones de movimientos. También estuvimos interesados en estudiar la red espacial que caracterizaban la dispersión y la importancia de la conectividad, con el objetivo de conocer si las rutas descritas por los dispersantes eran óptimas o fruto del azar. Por otro lado, dado que los patrones finales de asentamiento son el resultado de las variaciones en el comportamiento, los costes y riesgos a lo largo de la dispersión y la estructura del hábitat, exploramos dónde, cuándo y cómo los individuos buscan y seleccionan áreas estables de asentamiento. Por último, investigamos el efecto aprendizaje y el grado de familiaridad con el entorno en las estrategias de dispersión.

Esta tesis está basada en 7 manuscritos originales, actualmente en revisión en revistas del SCI. En todos los artículos he contribuido al
desarrollo y concepción del estudio, he participado en la recogida, análisis e interpretación de los datos, así como en su escritura.

1.2 Floaters, el Lado Luminoso y Oscura de las Poblaciones Animales

La dinámica y el futuro de los individuos no-reproductores (es decir, los floaters) durante las diferentes fases de la dispersión son elementos cruciales en la regulación de la estructura, trayectoria, distribución espacio-temporal, en la estabilidad y en los riesgos de extinción de las poblaciones animales. Durante los últimos treinta años, la ecología de las poblaciones animales ha experimentado un marcado cambio desde una ciencia más simple y genérica (principalmente basada en la porción reproductora de las poblaciones) a un campo de investigación más complejo y estructurado formado a su vez por diferentes ramas específicas de investigación. Un ejemplo de este cambio ha sido comprender las diferentes piezas que forman las poblaciones animales, las metapoblaciones. Ahora, tenemos la posibilidad de continuar en la misma dirección, dando un paso adelante en esta complejidad para devolver a la porción no-reproductora de la población, los floaters, su verdadero e importante valor en el contexto de la dinámica de la población global. Los dispersantes y su destino durante las fases de la dispersión han sido frecuentemente olvidados en el pasado, a pesar de su importancia.

Recientemente, se ha demostrado cómo la permanencia de la porción reproductora de una población es estrictamente dependiente de la dinámica de los floaters en sus áreas de asentamiento, del número de áreas de asentamiento disponibles y de los recursos tróficos en ellas, así como de diferentes tipos de fluctuaciones (simétricas vs. asimétricas) entre la porción reproductora y no-reproductora de una misma población. También se ha demostrado como la disponibilidad de presa juega un papel fundamental en los patrones de dispersión observados entre diferentes áreas de asentamiento y cómo un incremento en la tasa de mortalidad en las áreas de asentamiento es capaz de determinar un
perverso e impredecible "efecto mariposa" en los individuos reproductores de una población. Siguiendo en la misma línea, previos trabajos han mostrado cómo los patrones y la dinámica de la porción reproductora de una población pueden ser la consecuencia de los patrones y la dinámica de los individuos no-reproductores en las áreas de asentamiento.

En esos previos trabajos queda bien reflejada la importancia de considerar las poblaciones de animales como una mezcla indivisible de individuos reproductores y no-reproductores, siendo la dispersión uno de los factores principales en la determinación de la trayectoria de las poblaciones. En muchos casos, la ecología de las poblaciones ha olvidado de recordar la importancia de los floaters como aquellos individuos capaces de entrar como reproductores cuando un territorio o un una potential pareja- dueño de un territorio -se queda disponible. De hecho, los individuos no-territoriales han sido frecuentemente considerados como entidades numéricas, cuyo mayor interés era su tasa de inmigración, llegándose de este modo a ser comúnmente tratados como "semillas de animales" y perdiendo cualquier relación espacio-temporal con la población en la que se habían considerado.

A pesar de la importancia de los individuos no-reproductores en la dinámica y estabilidad de las poblaciones, el interés hacia los dispersantes ha nacido recientemente. Al revisar la bibliografía referente a los dispersantes, no se encuentran más de 70 trabajos centrados en el estudio de los floaters. Aunque las primeras evidencias de la existencia de una importante fracción de individuos no-reproductores, capaces de cubrir las posibles vacantes en los territorios de cría, se remonta a los años 50, hemos tenido que esperar hasta finales de la década de los 70, principios de los 80, para percibir a los floaters como un importante "mundo subterráneo" que vive cerca y afecta la porción reproductora de las poblaciones. Desde esa nueva percepción, los estudios centrados en los floaters estuvieron en un principio básicamente interesados en su comportamiento, en sus estrategias de adaptación y en las posibles consecuencias que podían tener sobre los individuos territoriales como potenciales intrusos. Trabajos más recientes están pasando a integrar a los floaters en la dinámica de las poblaciones, como factores cruciales
para la estructura y trayectoria de las mismas. Pero estos trabajos son sólo, por decirlo de alguna forma, "la punta del iceberg". Mucho queda aún por explorar, como por ejemplo, la compleja relación entre los floaters y sus áreas de asentamiento y la porción reproductora de la misma población, así como las estrategias utilizadas por los dispersantes de especies de larga vida para entrar como reproductores en una población. Además, esta necesidad de una mayor consideración a esta vital y crucial fracción de las poblaciones animales se ve bien reflejada en los estudios teóricos, que generalmente se olvidan de tener en cuenta la dinámica y el comportamiento de los individuos no-territoriales al analizar la viabilidad y la probabilidad de extinción de una población.

Es más, tanto la trayectoria de los floaters (es decir, el futuro de la población) en sus áreas de asentamiento, como la localización y características de las áreas de asentamiento, pueden ofrecer una nueva e innovadora visión en la ecología de la conservación, hasta ahora centrada casi exclusivamente en el sector reproductor de las poblaciones de animales. Nosotros consideramos que, la unión de la potencialidad que ofrecen los nuevos estudios teóricos con el estudio de la dinámica de los floaters y la localización de las áreas de asentamiento, puede ser de vital importancia en la conservación de las poblaciones, con el consecuente impacto socio-económico. Recientes trabajos basados en el radioseguimiento de los jóvenes a lo largo de su dispersión han mostrado que las áreas ocupadas por los floaters son frecuentemente muy diferentes a las áreas de reproducción, siendo las áreas seleccionadas por los dispersantes caracterizadas por tener un alto nivel de antropización. Zonas que, en general, nadie pensaría en incluir en planes de conservación.

Además, debido a la dificultad de localizar las áreas de asentamiento, pocos esfuerzos están dirigidos a su conservación. Trabajos de ecología, análisis de la viabilidad y riesgos de extinción de las poblaciones que no consideren la importancia de los floaters, pueden no llegar a comprender cómo, dónde y por qué decrecen las poblaciones de animales. Cada vez son más los trabajos que incluyen dentro de los planes de conservación los corredores y rutas utilizadas por los individuos no-reproductores, resaltando la importancia crucial de los mismos en la persistencia de las poblaciones.
Para concluir, al estar las poblaciones de animales formadas por reproductores y no-reproductores, nos encontramos con un importante dilema. Por un lado, debido al aumento general de la pérdida de la biodiversidad, nos vemos obligados a identificar los peligros de extinción de las poblaciones en indicadores fáciles de identificar, localizándose los mismos principalmente en las áreas de reproducción. Pero, por otro lado, nos arriesgamos a subestimar la amenaza real cuando el problema de la población no se localiza en la porción reproductora, si no en las áreas de asentamiento. Además, cuando el problema se localiza en las áreas ocupadas por los dispersantes, es difícil darse cuenta de la gravedad de la situación de forma inmediata, y sólo somos capaces de identificarlo cuando la situación ha adquirido un carácter irreversible. Por tanto, a pesar de la dificultad de estudiar la porción de los individuos no-reproductores, es necesario tenerla en cuenta e incrementar los esfuerzos para conservar las áreas de asentamiento utilizadas por los dispersantes. La solución del declive de las poblaciones puede estar localizada en ellas.

En este capítulo hemos hecho una revisión, sólo considerando las poblaciones de aves debido a que las informaciones sobre los individuos no-reproductores de otras poblaciones de animales son muy escasas. La gran cantidad de informaciones empíricas y teóricas sobre poblaciones de aves nos permite la posibilidad de realizar una interesante comparación entre individuos reproductores y floaters. Esta revisión, también si restringida a las poblaciones de aves, puede considerarse como un punto de partida para recoger más y detalladas informaciones de floaters en otras especies. Añadir también, que en este estudio excluimos aquellas informaciones sobre “helpers” e individuos cooperantes de los reproductores, ya que no pueden considerarse como floaters en sentido estricto.

Los puntos más importantes que hemos analizado, discutido y profundizado en esta revisión son:

1. El origen de los floaters: territorialidad, saturación de hábitats y estrategias de adaptación.
2. Dinámica de los floaters en las áreas de asentamiento.
3. Cómo el destino de los floaters durante el proceso de la dispersión puede afectar la estabilidad de las poblaciones reproductoras.
4. Floaters y la regulación por densidad, dependencia en las poblaciones de aves.
5. La dinámica de los individuos no reproductores bajo condiciones extremas, como la falta de recursos.
6. Categorías de edad en poblaciones de aves: aumentos de la tasa de adquisición de territorios por parte de los floaters puede ser una señal de una disminución en la población.
7. Mortalidad en los floaters: efectos en la estabilidad de la población.
8. Los floaters no son semillas de animales: cómo el comportamiento y los patrones de movimientos de los floaters determinan la estructura de la población en su totalidad.
9. Organización social de los floaters.
10. Comportamiento y estrategias de los floaters en su escalada social, es decir, pasar de vivir en un mundo aparentemente olvidado a adquirir una posición de adulto reproductor.
11. Relaciones de competencias entre floaters y adultos territoriales.
12. Teorías de las respuestas territoriales desde la perspectiva de los floaters.
13. Floaters activos vs. pasivos
14. Cuando los floaters se convierten en problemáticos competidores y determinan (a) aumentos de la tasa de copulación extra-pareja; (b) agresiones y competiciones sexuales entre individuos; (c) incrementos en los niveles de defensa territorial y aumento de los niveles de estrés en los individuos territoriales.
15. Asimetrías y habilidades para competir entre floaters vs. reproductores.
2
Consideraciones metodológicas

MODELO BIOLÓGICO Y ÁREA DE ESTUDIO

Uno de los principales objetivos de la ciencia es el de tratar de explicar los múltiples y diferentes patrones biológicos así como el comportamiento de las especies y de los sistemas biológicos. Cumplir este objetivo no es fácil, sobre todo teniendo en cuenta la impresionante variedad y riqueza que caracteriza el mundo natural. Bajo este escenario, elegir buenos modelos biológicos se convierte en algo fundamental. Pero hoy en día, los modelos biológicos se eligen sólo bajo el criterio impuesto por la necesidad de obtener de la forma más rápida posible resultados (sean cuales sean). Nos olvidamos de la diversidad de respuestas, diversidad que existe en los patrones ecológicos y en el comportamiento de las especies y que no podemos permitir que subyaga en nuestra "cómoda" elección del modelo sobre el que trabajar. Cuanto mayor sea la variedad de modelos en los que nos basemos, más nos acercaremos a la respuesta final, quizás llegando incluso a comprender las reglas que rigen los sistemas biológicos. Es esta enorme variedad y complejidad de patrones que se observan en la naturaleza, de estrategias empleadas, de complejas estructuras, rutas y cruces evolutivos los responsables de que, por llamarla de alguna forma, mi "curiosidad científica" se dirigiera especialmente hacia especies y sistemas que me parecían menos habituales y donde era más fácil tropezarse con resultados originales y novedosos, también si el tema central de estudio ha sido extensamente investigado durante varias décadas:

El búho real (Bubo bubo), perteneciente a la familia Strigidae y orden Estrigiformes, es la rapaz nocturna de mayor tamaño del continente europeo. Es una especie altamente territorial a lo largo de todo el año, sexualmente monomórfica y considerada estrictamente monógama. Se caracteriza por su carácter sedentario, con una alta tasa de reproducción y extremadamente generalista tanto en la dieta como en la selección de del hábitat de nidificación, también caracterizada por el importante impacto sobre otras comunitudes de aves. Este predador, con un estado de conservación vulnerable, presenta una amplia distribución por la
región del Paleártico, pudiéndose observar en una gran variedad de hábitats, desde bosques boreales a zonas desérticas.

El presente estudio fue llevado a cabo en la Sierra Norte (Sierra Morena), localizada a 20 Km al norte de Sevilla (suroeste de España). El sistema lo forma un embalse (Embalse del Gergal, 250 ha), dos valles fluviales correspondientes a los ríos de Cala y Huelva con colinas de entre 60 y 200 m de altitud. El paisaje se encuentra principalmente formado por encinas Quercus ballota, alcornoques Quercus faginea, pinos Pinus pinea, acebuches Olea europea, lentiscos Pistacia lentiscus y pequeñas plantaciones de eucaliptos Eucalyptus sideroxylon. In many areas, scrubland has replaced woodland. El área se caracteriza por una gran riqueza tanto de conejo europeo Oryctolagus cuniculus como de perdices Alectoris.

TOMA DE DATOS

Durante cuatro años (2003-2006) se llevó a cabo el marcaje con radioemisores de 74 jóvenes de búho real (2003: n = 8; 2004: n = 18; 2005: n = 26; 2006: n = 22) nacidos en 12 nidos diferentes. Los individuos fueron marcados cuando alcanzaron 35 días de edad, con un emisor de mochila de 30 g (Biotelemetry Ltd, Wareham BH20 5AJ, Dorset, UK). Este peso correspondió al 3% del valor más bajo del peso adulto registrado en nuestra área de estudio (1500 g; medio = 1761 ± 231.7 g; n = 17 búhos adultos), tal y como es recomendado por U. S. Geological Survey Bird Banding Laboratory. Gracias a un sensor de mercurio, y a través de sus cambios de frecuencia, estos emisores permitieron no sólo localizar la posición de los animales, si no además registrar sus ritmos de actividad. Dado que a esa edad los individuos no han completado su crecimiento, los emisores fueron colocados de tal forma que se expandían a medida que el animal aumentaba de tamaño. Tras cuatro años de radiotrackamiento continuo de 17 adultos reproductores y 74 dispersantes de búho real, nunca se ha registrado ningún efecto adverso que pudiera ser directamente atribuido a la colocación de los emisores. Tanto la manipulación como el marcaje de búhos se realizó bajo la autorización de la Junta de Andalucía - Consejería de Medio Ambiente (permiso No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02).
MÉTODOS PARA LA DETERMINACIÓN DEL SEXO Y DE LA CALIDAD DE LOS INDIVIDUOS

Los jóvenes de búhos fueron datados siguiendo los métodos descritos en Penteriani et al. (2005d) y sexados a través de análisis genéticos del ADN procedente de muestras de sangre (Griffiths et al. 1998). La calidad de los jóvenes de búho se determinó en base a diferentes parámetros morfológicos, biométricos, bioquímicos y sanguíneos. Las A través de las medidas morfológicas y biométricas se calculó el índice de condición física (BCI) que, separando el peso asociado al tamaño del animal con el de otros aspectos puramente relacionados a las reservas de energía, refleja la condición física de los individuos. Búhos con valores más altos de BCI son los que se encuentran en mejor condición física (Green 2001).

Para la obtención de las medidas bioquímicas se tomaron muestras de sangre, que fueron conservadas en tubos de heparina a 4ºC hasta llegar al laboratorio. Una vez allí, las muestras fueron centrífugadas durante 10 minutos a 4000 rpm para conseguir la separación del plasma. De las muestras de plasma, almacenadas a -78ºC, se calcularon las concentraciones de colesterol, triglicéridos, ácido úrico, glicerol y proteínas totales a través de un espectrofotómetro (Screenpoint 2, COR SRL, Ginestra Florentina, Italy) y un paquete comercial (Biolabo). Trabajos anteriores han demostrado que estos parámetros bioquímicos son buenos indicadores de la calidad de los individuos en aves (e.g. Alonso-Alvarez et al. 2002).

Además de las muestras de sangre, se realizaron frots (fijados con el método Giemsa) para medir tanto la respuesta inmunitaria como los niveles de estrés y salud de los individuos. Con tal objetivo, y siguiendo los métodos descritos en Figuerola et al. (1999), estimamos: (a) la cantidad total de leucocitos, a través del recuento de 20 campos a 40 x, y extrapolando el número de leucocitos encontrados a un total de 100 campos. La estima obtenida se asume que es equivalente al número total de leucocitos por μl de sangre; (b) la proporción de los diferentes tipos de células blancas (eosinófilos, linfocitos, monocitos y heterófilos); y (3) los niveles de presencia del parásito Leucocytozoon spp.
MÉTODOS DE RADIOSEGUIMIENTO

El radio seguimiento de los jóvenes de búho comenzó desde el momento en que los diferentes individuos marcados abandonaron el nido, meses antes del inicio de la dispersión (es decir, durante la etapa postfledging). Durante este período se llevaron a cabo sesiones de radio seguimiento intensivo dos veces por semana. Durante cada sesión, cada nido fue visitado en el intervalo de una hora a lo largo de toda la noche (desde una hora antes del anochecer hasta una hora después del amanecer), realizándose la localización de cada uno de los búhos. En total se obtuvieron 1962 localizaciones.

Los jóvenes fueron seguidos desde que comenzaron la dispersión hasta que la batería del emisor se acabó o hasta que el individuo murió. Durante el período de la dispersión se llevaron a cabo dos métodos de radio seguimiento, a dos escalas temporales diferentes, (a) durante el período de actividad nocturna; los individuos fueron seguidos de forma individual y continua a lo largo de toda la noche, desde una hora antes del anochecer hasta una hora después del amanecer (tiempo medio de cada sesión ± SD = 11.28 ± 2.13 hrs) durante 163 sesiones y una duración total de 1840.25 horas. Durante las sesiones de radio seguimiento continuo, el animal fue localizado (número medio de localizaciones por sesión continua de radio seguimiento ± SD = 18 ± 4.62) cada vez que se detectó un cambio en la frecuencia de la señal del emisor, registrándose de esta forma cada movimiento del animal durante su período de actividad. Dichos cambios de frecuencia fueron registrados a través de una antena fija colocada en el techo del vehículo. Para las localizaciones de los animales se empleó una antena de mano Yagi compuesta por tres elementos, conectada a un receptor portátil ICOM (IC-R20); y (b) localizaciones semanales: cuando los animales se encontraban en sus posaderos diurnos, para obtener informaciones a una mayor escala de los patrones generales de movimientos durante el proceso de la dispersión. Los datos de radio seguimiento fueron ploteados en mapas 1:25 000 y analizados a través de los programas de sistema de información geográfica ArcView v 3.2 y ArcGis v 9.0 (ESRI).
3

¿Cómo exploran los pollos su entorno desde que abandonan el nido hasta que comienzan la dispersión?

Hasta ahora, la mayoría de los estudios que se han centrado en el análisis de los movimientos de los animales han explorado aspectos relacionados sobre todo con los movimientos de animales territoriales en su dominio vital, las estrategias de búsqueda de hábitats favorables, la obligada respuesta frente a la fragmentación de hábitats y las estrategias de caza en ambientes heterogéneos. Del mismo modo, y fruto del reconocido efecto que tienen los dispersantes en la población reproductora, esta rama de la ecología también ha realizado grandes esfuerzos en comprender el proceso de la dispersión. Sin embargo, pocos son los trabajos que han analizado los patrones espaciales y temporales de los movimientos de los animales antes de comenzar dispersión, cuando todavía se encuentran en su territorio natal y, en mayor o menor medida, aún dependen de los cuidados parentales. En aves, esta fase se conoce con el término de periodo de dependencia, periodo fundamental en el ciclo de vida de los animales dado que las experiencias que cada individuo viva en él puede tener importantes consecuencias directas en su futuro. Durante el periodo de dependencia, los animales tienen que, gradualmente, desarrollar sus capacidades de vuelo, alcanzar una condición física óptima para el inicio de la dispersión y adquirir informaciones tanto de su entorno más cercano como de los individuos de su misma especie (es decir, de sus conspecificos). De hecho, un aumento de la tasa de mortalidad durante el periodo de dependencia puede tener, a largo plazo, serias consecuencias en la sección reproductora de la población, debido a la consecuente e inevitable disminución en el número total de floaters.

A pesar de su importancia, esta etapa ha sido poco estudiada, siendo por tanto las informaciones sobre ella muy escasas y generalmente vinculadas con aspectos relacionados con la supervivencia y con los factores que determinan su duración. Sin embargo, el conocimiento de los patrones de movimientos durante el periodo de dependencia podría ser una de las herramientas más útiles para
llegar a comprender esta fase del ciclo biológico de las aves, y tener de este modo una visión más real de los posibles riesgos que tienen que afrontar los individuos durante esta etapa.

Nuestro objetivo en este capítulo fue analizar y describir los patrones de movimientos durante el período de dependencia. En concreto, nuestro interés estuvo centrado en: (1) estudiar las características esenciales de los movimientos, las interacciones familiares y el uso del espacio a lo largo de dicho período; e (2) investigar la posible evolución en los patrones de movimientos a lo largo del tiempo. Para ello, a través del radio seguimiento (ver Consideraciones metodológicas para más detalles), recogimos la localización de 41 individuos procedentes de 13 nidos diferentes a lo largo de dos años (2004 y 2005) y analizamos las siguientes características: (a) distancia media entre sucesivas localizaciones, (b) distancia media entre cada localización y el nido, (c) distancia media entre las localizaciones de individuos pertenecientes a una misma familia, recogidas simultáneamente y (d) área utilizada durante el período de dependencia o FFAs. Por último, para estudiar el patrón espacial y temporal de los movimientos, estimamos (e) la dimensión fractal (D), como medida absoluta de la tortuosidad de cada una de las trayectorias descritas por los jóvenes; y (f) el estadístico CRW qui nos informa acerca de la similitud del movimiento de los animales con uno realizado al azar.

A través del análisis de los patrones de movimientos a lo largo del período de dependencia detectamos la existencia de cambios significativos en el comportamiento de los individuos. Tras abandonar el nido, los jóvenes de búhos se movieron a través de pequeños desplazamientos, centralizando sus actividades y prospectando un área pequeña en las vecindades de su nido. Tras pocas semanas, el patrón de los movimientos de los individuos experimentó un marcado cambio, desplazándose trayectorias más largas, localizándose con mayor frecuencia lejos del nido y prospectando áreas mayores. Aunque el área prospectada por los jóvenes fue aumentando a lo largo del período de dependencia, siempre incluyeron el nido. Es decir, el nido parece ser un elemento muy importante a lo largo de toda la fase. El cambio en los patrones de movimientos podría estar íntimamente relacionado con el aumento en las capacidades de vuelo que van adquiriendo los
individuos a lo largo de este período. Cuando los jóvenes abandonan el
nido no están completamente capacitados para volar, y los
desplazamientos son principalmente realizados a través de pasos y
saltos. A lo largo de las semanas, los individuos van aumentando sus
capacidades de vuelo. En cuanto a las interacciones familiares, mientras
durante las primeras semanas se observó que hermanos del mismo
núcleo familiar permanecían juntos prácticamente a lo largo de todas las
noches, la distancia entre ellos fue aumentando progresivamente a
medida que transcurrieron las semanas. Sin embargo, aunque la distancia
entre hermanos aumentó durante el período de dependencia, jóvenes de
diferentes sexos tendieron a permanecer a una menor distancia, vínculo
que, además, no se disolvió forzosamente en las primeras fases de la
dispersión.

Durante el período de dependencia, los jóvenes se movieron según un
patrón desorientado, probablemente debido a que: (a) a esta edad los
jóvenes se encuentran protegidos y alimentados por los padres; (b) tras
abandonar el nido, los jóvenes se encuentran inmersos en un hábitat
desconocido, entorno que exploran al azar; y (c) sus habilidades para
volar y su rango de percepción no están completamente desarrollados.
Ante tales circunstancias, los movimientos no-orientados pueden
representar una buena estrategia para explorar áreas desconocidas. Si,
tras abandonar el nido, las trayectorias descritas por los búhos se
caracterizaron por su tortuosidad, a lo largo de las semanas y a medida
que los individuos se aproximaban al período de independencia (es
decir, al inicio de la dispersión), fueron adquiriendo un diseño más
recto, posiblemente asociado al incremento en el rango de percepción de
los jóvenes. El rango de percepción, es decir, la distancia máxima a la
que un animal es capaz de percibir el ambiente, representa la ventana
de información del individuo. Cuando los animales se mueven con
movimientos no-orientados, los mecanismos de comportamiento que
gobiernan los patrones de movimientos suelen actuar a pequeñas
escales espaciales, escalas espaciales que a su vez están determinadas
por el rango de percepción. Un incremento en el rango de percepción
podría facilitar que los jóvenes aumenten sus desplazamientos,
 describiendo trayectorias más rectas. Por tanto, la tortuosidad de las
trayectorias podría venir determinada por la interacción entre el grado
de de crecimiento de los jóvenes como de las habilidades cognitivas. A
medida que crecen, los individuos son capaces de desarrollar estos dos aspectos, incrementando su rango de percepción, familiarizándose más con su entorno y, por tanto, explorando de forma más eficiente áreas mayores.

Para concluir, poco se sabe sobre cómo los animales toman las decisiones relacionadas al movimiento durante el periodo de dependencia, ni se tiene un buen conocimiento de cómo las diferentes estrategias de movimientos en esta fase pueden afectar el futuro de los individuos. Pero, dado que esta fase representa una etapa intensiva, cargada de experiencias y aprendizajes, tenemos que tener presente que el comportamiento de los individuos en ella podría tener grandes consecuencias en el siguiente período, fundamental en la vida de los animales y crucial en la dinámica y estructura de las poblaciones, es decir, en la dispersión natal.
4

Estudio del comportamiento ayuda a trasladar los movimientos durante la dispersión hacia patrones espaciales de distribución de floaters

En las últimas décadas, la dispersión ha sido objeto de numerosos estudios, tanto teóricos como empíricos, demostrándose que es un proceso esencial en la dinámica y persistencia de las poblaciones. Sin embargo, aún los numerosos estudios realizados y la amplia bibliografía existente, el proceso de la dispersión aún representa una laguna en nuestro conocimiento sobre la ecología animal. Esta falta de conocimiento se debe principalmente a que, mientras la mayoría de los trabajos empíricos se han centrado en el estudiar las posibles diferencias en las estrategias de dispersión relacionadas con el sexo, entre poblaciones, y en función de la estructura y composición del ambiente o de la especie, las a veces simples asunciones de los modelos teóricos no han tenido siempre en cuenta factores claves del comportamiento de los animales que pueden influir fuertemente en este proceso. A pesar de ser un complejo proceso, en el que el comportamiento de los individuos es un elemento fundamental, la dispersión ha sido frecuentemente considerada como una estrategia fija para cada especie.

La dispersión puede ser subdividida en tres fases secuenciales, pero diferentes en cuanto a su comportamiento: (1) inicio, cuando los individuos abandonan su lugar de nacimiento, (2) transferencia o fase de búsqueda, comprende los movimientos realizados por los floaters cuando exploran áreas durante un tiempo variable antes de encontrar una nueva área en la que definitivamente asentarse, y (3) parada, cuando los floaters se asientan en un área de forma más estable, es decir, cuando encuentran un área en la que pasarán el periodo de tiempo más largo del proceso de la dispersión o cuando los dispersantes entran finalmente como reproductores. Pocos son los trabajos empíricos que han tenido en cuenta estas tres etapas. Del mismo modo, y aún existiendo un fuerte vínculo entre la dinámica de los floaters en las áreas de asentamiento y el equilibrio y persistencia de la población reproductora, son también escasos los trabajos que han estudiado la relación entre estos dos sectores de una población. Dado que la
selección de las áreas de asentamiento, las distancias de dispersión y la tasa de supervivencia de los dispersantes pueden depender en gran medida de las estrategias de movimientos que los individuos empleen una vez que abandonen su territorio natal, el comportamiento de los movimientos durante la dispersión puede tener importantes consecuencias tanto a nivel de poblaciones, de comunidades y de ecosistemas. Es por tanto necesario identificar los elementos claves del comportamiento que afectan los movimientos de los dispersantes. Aunque muchos trabajos han tratado de cuantificar el patrón de los movimientos durante la dispersión, pocos han sido diseñados para intentar comprender el comportamiento de los animales moviéndose a largas escalas de tiempo, siendo este uno de los grandes problemas que han tenido muchos de los diferentes enfoques que han sido utilizados para analizar y modelar el movimiento de los animales durante la dispersión ha sido el de las escalas temporales. Generalmente estos enfoques no han considerado que, a lo largo del tiempo, se pueda dar un cambio en el comportamiento de los individuos en los patrones de movimientos. Como consecuencia, las teorías sobre la dispersión y, por tanto, de la distribución y abundancia de los individuos, se han basado en innumerables ocasiones en asunciones poco realistas para representar y predecir la dinámica del proceso de la dispersión.

En este capítulo, nuestro objetivo principal fue el de caracterizar el comportamiento de los floaters durante la fase de búsqueda, a través del análisis de las distancias, duración y los ángulos de giro entre los desplazamientos. Por otro lado, y a través del índice de residencia (Turchin 1991), evaluamos la precisión y realismo de los modelos random walk (como ejemplo de uno de los modelos más utilizados a la hora de analizar los patrones de movimientos de los animales) a la hora de predecir la distribución espacial de las poblaciones animales. El índice de residencia postula que la densidad de individuos en un área es directamente proporcional al tiempo que los mismos permanecen en dicho área. Para ello seguimos 33 jóvenes dispersantes de búhos real marcados con radioemisores (ver Consideraciones metodológicas para más detalles), localizándolos semanalmente desde el momento en que abandonaron el nido (inicio de la dispersión) hasta que entraron en la fase final de la dispersión, es decir, hasta que encontraron un área nueva en la que se asentaron.

174
El primer paso fue determinar, para cada floater, cada una de las diferentes fases de la dispersión. Consideramos que los jóvenes de búho habían comenzado la dispersión cuando la distancia entre cada localización y el nido dejó de fluctuar entre valores bajos para aumentar de forma considerable alcanzando valores mayores a la distancia total recorrida por cada individuo a lo largo de la dispersión. Del mismo modo, para identificar el momento exacto en el que cada individuo se asentaba, comparamos la distancia entre pasos sucesivos respecto a la distancia total recorrida previamente. En el momento en el que los dispersantes se asentaban y se estabilizaban en una zona, la distancia entre los pasos sucesivos tomó valores inferiores a la distancia viajada hasta entonces, sin seguir el individuo avanzando con sus desplazamientos. El período comprendido entre el inicio y el final de la dispersión corresponde a la fase de búsqueda. Una vez identificada la fase de transferencia o búsqueda, caracterizamos los diferentes patrones de comportamiento de los individuos. Para ello creamos una ventana temporal (comprendida por localizaciones recogidas de forma secuencial en el período en un mes) que la fuimos moviendo a lo largo de la fase de búsqueda. En cada bloque mensual, medimos la distancia total y calculamos tanto la distancia neta en cada uno de ellos como la distancia entre cada bloque y el nido. De esa forma, observamos que cada trayectoria recorrida por cada dispersante podía dividirse en dos fases diferentes, reflejando dos estados de comportamiento: (1) un estado intensivo, en el que la distancia total en cada bloque mensual era mayor que la distancia neta, y (2) un estado extensivo, en el que la distancia total fluctuaba alrededor de la distancia neta calculada por cada bloque o era menor que la distancia neta respecto al nido. Para poder relacionar los diferentes estados de comportamiento con el patrón de los movimientos de los individuos, calculamos y analizamos la distribución de algunas variables, como la distancia media entre pasos, la duración de los desplazamientos y el ángulo medio entre sucesivos pasos. Finalmente, con el objetivo de estimar el índice de residencia y comparar los valores predichos de la distribución de una población al aplicar modelos random walk con valores reales observados, calculamos el grado de solapamiento entre los individuos durante los dos estados de comportamiento, a través del mínimo
polígono convexo descrito en cada uno de los estados del comportamiento.

El análisis de los patrones de movimientos durante la fase de búsqueda indicó la presencia de importantes cambios en el comportamiento de los individuos, en función a diferentes factores, como la escala espacial de los desplazamientos, la configuración de las trayectorias, la respuesta individual a la presencia de individuos de la misma especie y las variaciones intra-individual de los tipos de movimientos. Mientras que algunos individuos (35%) mostraron exclusivamente un tipo de comportamiento, permaneciendo durante toda la fase de búsqueda en el estado intensivo, otros (15%), adoptaron durante toda la etapa de búsqueda un comportamiento extensivo. Este tipo de comportamientos o personalidades extremas han sido previamente documentados en vertebrados, bajo la denominación de animales tímidos y atrevidos, respectivamente. En general, los individuos atrevidos son animales más agresivos y con una gran capacidad de adaptación frente a diferentes estímulos externos. Por el contrario, los individuos tímidos actúan con más precaución, siendo a su vez, más sensibles a los estímulos externos. Nuestros resultados apoyaron la idea de que la dispersión es el resultado de varios tipos de movimientos claramente diferenciables, estando unos asociados a las actividades diarias de los animales y otros más directos y asociados a aquellos encaminados a realizar grandes desplazamientos con el fin de encontrar un área de asentamiento nueva y estable. Previos trabajos empíricos han demostrado que los individuos con personalidades más atrevidas suelen desplazarse mayores distancias, correspondiéndose en nuestro estudio a aquellos dispersantes que permanecieron constantemente en estado extensivo, y que se desplazaron mayores distancias a través de trayectorias más rectas. Por el contrario, los individuos tímidos son aquellos que expresaron exclusivamente un estado intensivo, con pequeños desplazamientos a través de trayectorias tortuosas. Por último, pero no por ello menos importante, observamos que el 52% de los dispersantes mostraron una transición entre los dos estado de comportamiento. Durante el estado intensivo se observó un alto solapamiento entre los individuos, solapamiento que disminuyó en el estado extensivo, con la consecuente notable reducción de la densidad de los individuos, debido a que los dispersantes se desplazaron a zonas
más exclusivas y aisladas. Con una alta densidad de conspecificos, la mejor opción para una especie territorial es localizar un área particular lo más rápido posible, área que puede ser alcanzada de forma rápida y eficaz a través de movimientos a grandes distancias y describiendo trayectorias rectas. Desde una perspectiva adaptativa, cabe esperar que los individuos sean capaces de ajustar su comportamiento en función de las diferentes condiciones. Nuestro trabajo apoya la idea de que, dado que no existe una única estrategia adecuada para todas las situaciones, la dispersión debe ser considerada como un proceso dimórfico, con individuos más sedentarios que restringen sus movimientos, y otros con una mayor tendencia a realizar grandes desplazamientos.

El índice de residencia predice que, si la distribución de los individuos en una población es el resultado de movimientos azarosos, la distribución de las poblaciones animales deberá seguir una distribución ideal libre (IFD). Cuando aplicamos el índice de residencia a nuestro escenario, encontramos que éste no predecía correctamente la distribución final de los individuos. Sin embargo, la distribución real que observamos sí parecía seguir el modelo postulado por Fretwell y Lucas, en el que los dispersantes parecen desplazarse libremente desde áreas con una mayor agregación a áreas menos densas, aparentemente sin el efecto de ningún factor restrictivo. Este resultado es muy importante dado que, aunque no se cumplan las predicciones de modelos random walk, la distribución de los organismos puede ajustarse a una IFD. Mirando nuestros resultados, nos parece importante resaltar el hecho de que una misma especie, en función del estatus social de los individuos (floaters vs. reproductores) puede presentar tanto una distribución libre como una despótica a lo largo del ciclo de vida. Durante la dispersión, los búhos no son territoriales y, por tanto, pueden distribuirse libremente en el espacio. Sin embargo, cuando los individuos adquieren el carácter territorial propio de los adultos reproductores, la distribución de los individuos no es sólo limitada por factores externos como la distribución de los recursos, si no también por factores sociales, como el fuerte carácter territorial.

Al contrario de lo que predice el índice de residencia, la densidad de individuos en los diferentes parches fue negativamente proporcional al tiempo medio que los organismos permanecieron en el área. Las
densidades más altas de jóvenes fueron observadas en aquellas áreas donde permanecieron menos tiempo. Generalmente, los modelos de difusión consideran estrategias pasivas de dispersión, no incluyendo algunos mecanismos que se pueden generar como consecuencia de factores fundamentales en la distribución espacial de los animales, como la densidad o la presencia de conspecificos. El aumento de las interacciones entre individuos en situaciones de alta densidad puede reducirse a través de cambios en el comportamiento de los patrones de los movimientos, normalmente dirigidos a una disminución de la densidad de población. Nuestros resultados mostraron una estrategia de dispersión activa, con el consecuente intercambio equilibrado, en relación inversa a la densidad de organismos, entre floaters durante la fase de búsqueda.

Generalmente, las premisas básicas de los modelos random walk son fáciles de controlar bajo condiciones experimentales. Aunque se ha demostrado que los modelos random walk son válidos para una gran variedad de pequeños y pasivos organismos, es debatible si este enfoque es adecuado para describir situaciones o especies más complejas, especialmente cuando se tiene en cuenta el comportamiento de los individuos. Por ejemplo, los modelos random walk podrían ser idóneos para modelar los movimientos observados en el estado intensivo, pero no aquellos directos y a grandes distancias. De hecho, como son los movimientos intensivos los más fáciles de registrar, estudios centrados en la estimación de parámetros de la dispersión puede estar sesgados y obviar los movimientos directos, a una mayor distancia. Un asunción importante de los modelos random walk, siendo una de las principales causas de que el modelo no prediga correctamente nuestra población, es que los organismos se mueven de forma constante a lo largo del tiempo. El comportamiento de los animales puede estar influenciado por una inmensa cantidad de factores y sus interacciones, siendo uno la escala temporal. Por tanto, es importante entender el comportamiento de los animales en relación al movimiento y tener presente que puede existir una variación a lo largo del tiempo, pasos fundamentales para acercarnos más a la realidad y entender la distribución espacial de los individuos, la dinámica y persistencia de las poblaciones animales.
5

Factores claves determinantes en los movimientos de los animales

En las últimas décadas, un tema central en la ecología ha sido analizar qué factores determinan los patrones de los movimientos de los animales. Se ha demostrado que el movimiento de las animales depende de las interacciones entre múltiples factores, tanto de bióticos como abióticos. Sin embargo, dada la tremenda complejidad de tales interacciones, los trabajos que han tratado de cuantificar los patrones de movimientos han tenido generalmente que simplificar el número de factores, eliminando de este modo diferentes e importantes interacciones ecológicas. Así, los trabajos que han estudiado el efecto de la estructura y composición del hábitat generalmente no han considerado factores de naturaleza biótica, mientras que los trabajos realizados para estudiar el efecto de los factores bióticos han asumido que los animales se movían por en ambiente irreal, continuo y homogéneo que no afectaba el patrón de los movimientos. Pero, como anteriormente hemos mencionado, el movimiento de los animales es el resultado de múltiples interacciones de factores internos y externos, y por tanto debe ser el reflejo de la compleja mezcla entre las decisiones a nivel de comportamiento, la calidad del individuo y las propiedades físicas del ambiente por el que se mueven los animales. Sin embargo, existen pocos trabajos que hayan considerado el efecto de esta compleja interacción.

El objetivo de este trabajo fue explorar cómo las interacciones entre los factores externos e internos afectan los patrones de los movimientos durante el proceso de la dispersión en sistemas naturales. Durante la dispersión, los animales se desplazan a través de diferentes áreas de asentamiento hasta que encuentran un área más estable en la que se asientan o entran como reproductores. A lo largo de cuatro años, observamos cómo, las diferentes áreas de asentamiento, eran exploradas por individuos de diferente procedencia, de diferente sexo y de diferente calidad física. Es decir, encontramos en la dispersión un escenario natural que nos daba la oportunidad de comparar los patrones de los movimientos de diferentes individuos explorando el mismo hábitat, así como del mismo individuo moviéndose en diferentes
ambientes. Podríamos esperar que, si los patrones de movimientos están principalmente influenciados por (1) el hábitat, los patrones de los movimientos de los diferentes dispersantes deberían ser más similares cuando exploran las mismas áreas de asentamiento; o (2) condición individual, los patrones de movimientos de los distintos individuos deberían ser diferentes, también cuando los mismos exploran áreas comunes.

Para testar estas hipótesis, caracterizamos los patrones de los movimientos (estimando la dimensión fractal y el parámetro CRWdet) de 39 individuos procedentes de 12 nidos diferentes, marcados y seguidos de forma intensiva y continua a lo largo de las noches (ver consideraciones metodológicas para más detalles). De cada uno de las noches estimamos el punto medio de las localizaciones observadas (es decir, de los movimientos observados del animal) y calculamos la distancia entre esos puntos centrales para todas las posibles combinaciones de noches, descartando aquellas del mismo individuo. De la misma forma, para cada una de esas combinaciones, calculamos la diferencia de los valores de los parámetros descriptores de los patrones de movimientos. La comparación de los patrones de los movimientos realizados por diferentes búhos fue llevada a cabo a través de un método similar a los correlogramas, en el que representamos el valor de la diferencia de las características de los movimientos de las diferentes parejas de búhos en función de la distancia a la que se encontraban las áreas que habían explorado. Por otro lado, para comparar los patrones de los movimientos de un mismo individuo cuando exploraba diferentes áreas, utilizamos modelos lineares generalizados en los que, al tener medidas repetidas de un mismo individuo y, para evitar posibles problemas de pseudoreplicación, introdujimos el individuo como factor azaroso. Finalmente, el efecto de la condición individual y del sexo sobre los patrones de movimientos (ver consideraciones metodológicas para más detalles) fue también analizado a través de modelos lineares.

Los resultados revelaron que (1) la tortuosidad de las trayectorias descritas por los animales dependía fuertemente de la estructura del hábitat, siendo aquellas trayectorias descritas por diferentes individuos más similares cuando explotaron áreas comunes que cuando explotaron áreas más distantes. El efecto de la calidad del individuo no parecía
tener fuertes efectos sobre la tortuosidad descritas por los animales en sus desplazamientos, ya que el mismo animal adoptó diferentes trayectorias en diferentes hábitats. Estos resultados demostraron claramente que la tortuosidad de las trayectorias es un reflejo de la estructura del hábitat; (2) el parámetro CRW\text{Diff} no se vio influenciado ni por los factores bióticos ni por el hábitat; y por último (3) detectamos un efecto en la velocidad de los movimientos, estuvo determinada por la interacción entre la condición física de los individuos y el sexo, siendo los individuos de mejor calidad y, especialmente las hembras, las que se desplazaron a mayor velocidad. Apoyando previos trabajos, nuestro estudio demuestra la importancia del hábitat en la determinación de los patrones de los movimientos de los animales. Los movimientos de los animales son el reflejo de la capacidad que tienen los individuos para cambiar frente a diferentes componentes estructurales del ambiente. Aunque, indudablemente, numerosos son los procesos y factores pueden influenciar los patrones de movimientos, la complejidad y heterogeneidad del ambiente parece tener un efecto muy importante. Aunque previos trabajos experimentales han demostrado la importancia del hábitat en los movimientos, la mayoría han sido llevados a cabo bajo condiciones muy simples y diferentes de sistemas naturales, donde cabe esperarse complejas respuestas de comportamiento a las características del hábitat. Además, la mayoría de ellos han tratado de analizar el efecto de factores concretos, como la fragmentación del hábitat, la distribución y composición de parches, la presencia y distribución de recursos, la presencia de barreras y la conectividad. Sin embargo, nosotros no analizamos el efecto concreto de un factor a nivel individual, si no del ambiente en su totalidad.

Un resultado interesante es que, aunque el hábitat parece tener una importante influencia en las características de los movimientos (ej., la tortuosidad de las trayectorias), no parece afectar los mecanismos que rigen dichos patrones. Los tres parámetros que resultaron significativos en nuestros análisis reflejan dos aspectos diferentes de los movimientos: las características (ej., la tortuosidad y la velocidad) y los mecanismos que rigen (analizados a través de la estimación del estadístico CRW\text{Diff}). En base a la relación natural entre patrones y procesos ecológicos sabemos que, mientras los procesos describen lo que los animales hacen, los patrones proporcionan detalles de cómo lo hacen. Es razonable pensar que animales moviéndose por un motivo en
particular, utilizan el mismo mecanismo, independientemente del hábitat en el que se encuentren. Sin embargo, mientras se mueven por ese determinado mecanismo, los animales interactúan con su entorno para alcanzar su objetivo, siendo el resultado de esa interacción el origen de los diferentes patrones observados.

Ni la estructura general ni los aspectos del comportamiento relacionados con el movimiento parecieron estar relacionados por la calidad física de los individuos. Una pequeña excepción vino dada por el efecto conjunto de la condición física y el sexo en la velocidad de los desplazamientos. La velocidad es un factor clave en muchos procesos relacionados con el comportamiento de los animales, como la caza y el uso del espacio. En concreto, los búhos se caracterizan por ser predadores "a la espera", no empleando tácticas de persecución, en las que los periodos de espera o pausa representan un factor fundamental para el éxito de la captura de la presa. De hecho, movimientos intermitentes son beneficiosos para los animales, ya que les permite tanto de obtener más informaciones sobre el entorno y ahorrar reservas energéticas. Por tanto, búhos en mejores condiciones físicas (y especialmente hembras, presentando esta especie dimorfismo sexual) no necesitan moverse tan rápido como aquellos en peores condiciones físicas.

Para concluir, este estudio representa un fuerte apoyo de la importancia que tiene el hábitat como factor determinante de los patrones de movimientos. Debido a la importancia de los movimientos a diferentes niveles ecológicos, incrementar nuestro conocimiento y entender cómo los animales se mueven en su entorno natural, e interactúan con el ambiente físico es fundamental para comprender muchos procesos ecológicos y evolutivos.
6

Rutas hacia la dispersión animal: extendiendo el enfoque de la teoría de grafos

La conectividad funcional se puede definir como el resultado de múltiples interacciones entre el comportamiento de los individuos y las características del hábitat por el que los animales se mueven, siendo uno de los conceptos más importantes vinculado al proceso de la dispersión. A pesar de la falta de datos empíricos, muchos trabajos han estudiado la dispersión bajo el enfoque del análisis del movimiento de los animales durante la fase de búsqueda. En concreto, una de las aproximaciones más utilizadas han sido los modelos random walk y sus aproximaciones. Aunque se ha comprobado la efectividad de estos modelos para predecir la distribución de los animales a pequeñas escalas temporales, tienden a fallar al considerar escalas temporales mayores debido principalmente a que no tienen en cuenta (a) la posibilidad de cambios en el comportamiento de los animales a lo largo de su ciclo de vida y la influencia que estos cambios en el comportamiento pueden tener en los patrones de movimientos; y (b) que los patrones de movimientos pueden cambiar bajo diferentes condiciones ambientales. Desde el reconocimiento de la gran influencia que tienen tanto la naturaleza como la configuración espacial de la matriz por la que se mueven los animales, ha aumentado la importancia de las escalas espaciales. De hecho, los movimientos no sólo dependen de los organismos, si no también del ambiente por el que se mueven. Mientras muchos autores han aplicado métodos matemáticos para analizar el movimiento de los animales y cómo los individuos responden a la heterogeneidad espacial, numerosos modelos de dispersión espacialmente explícitos han sido desarrollados. Estos métodos y modelos permiten la integración de la relación entre el individuo y el ambiente, y han sido más o menos aceptados en función de las diferentes escuelas y tendencias creadas en la rama de la ecología del movimiento.

Sin embargo, aunque el éxito de la dispersión depende en gran medida tanto de la distancia que los individuos tienen que atravesar
como del tiempo que para ello tengan que invertir, la conectividad especial intrínseca al ambiente ha sido ampliamente reconocida como una pieza fundamental y determinante de la dispersión, pero generalmente ha sido poco considerada en tales estudios. La conectividad es, además, una de las propiedades más importante de la teoría de grafos. Considerando el ambiente como una serie de parches interconectados, la teoría de grafos postula la posibilidad de un flujo ecológico a través de ellos a través de mecanismos como, por ejemplo, la dispersión de los animales. Dado que la conectividad es una característica común de tanto la dispersión como de la teoría de grafos, esta última podría representar una herramienta con una alta potencialidad para ayudarnos a comprender algunos aspectos fundamentales del proceso de la dispersión, como por ejemplo, el patrón de movimientos entre parches, las características de las redes espaciales por las que se mueven los animales, la localización de nodos vitales y corredores que conecten diferentes metapoblaciones, etc. Siendo, desde una perspectiva puramente espacial, el diseño de rutas rápidas y óptimas, uno de los problemas que ha habido para el desarrollo de diferentes aplicaciones, y dado que la dispersión puede desde la perspectiva de un proceso que los animales tienen que optimizar, las propiedades de la teoría de grafos pueden proporcionarnos una herramienta elemental y óptima para su estudio.

La teoría de grafos ha sido aplicada a numerosas disciplinas, especialmente para la detección de flujos eficientes y rutas que conforman diferentes redes espaciales. Sin embargo, a pesar de su alta potencialidad en aplicaciones ecológicas (ej., estudios de conectividad, metapoblaciones y conservación), su aplicación no ha sido aún ampliamente difundida, especialmente en el estudio de la dispersión animal. En este trabajo mostramos la potencia y aplicabilidad de la teoría de grafos en el estudio del proceso de la dispersión. Nuestro primer paso fue analizar el patrón de movimientos durante la fase de búsqueda de la dispersión (es decir, los movimientos de los animales desde que abandonan el nido hasta que encuentran un nuevo área donde asentarse) mediante la aplicación de la teoría de grafos. En primer lugar simplificamos el complejo patrón de movimientos observado, convirtiéndolo en un patrón espacial de ocupación bien definido, a través de un análisis "box-counting". Posteriormente, procedimos a la
construcción de la red espacial que caracterizaba la dispersión, en la que los nodos representaron los parches ocupados y los enlaces correspondieron a los movimientos entre parches realizados por los dispersantes. Finalmente, y en ese escenario espacial, comparamos la ruta real observada con tanto rutas óptimas como con rutas generadas al azar, con el objetivo de aumentar nuestro conocimiento sobre la estrategia de movimientos empleada durante la dispersión. Como paso adicional investigamos el posible papel que puede tener el viento en las rutas seguidas durante la dispersión.

Con tales objetivos, utilizamos los datos de 42 jóvenes de búho real desde que abandonaron el nido hasta que encontraron un área de asentamiento definitiva. El primer paso fue trasladar el patrón de movimientos observados durante la dispersión a uno de ocupación del espacio. Para ello utilizamos análisis “box-counting”, en el que usamos parches de diferentes tamaños que al menos incluían la localización de un individuo. Posteriormente, para analizar el patrón de ocupación de los parches a lo largo de diferentes escalas espaciales, representamos el tamaño de los parches respecto al número de parches que fueron ocupados. El tamaño de parches que nos dio una mayor variabilidad en el número de individuos que los ocupaba fue de 1 km². Para tamaños más pequeños, un elevado número de parches fueron ocupados por solo un individuo, mientras que para tamaños más grandes, pocos parches resultaron ocupados. Una vez obtenido el patrón de ocupación espacial, procedimos a la construcción de la red espacial observada durante la dispersión, en la que (1) los nodos representaron los parches ocupados; y (2) los enlaces los movimientos de los animales entre los diferentes parches. El primer paso fue definir la importancia de cada nodo, en función del número de individuos que lo habían visitado. Para que el análisis fuera lo más conservativo posible, sólo consideramos como ocupación de un parche la primera vez que un individuo lo visitaba, descartando la posibilidad que un individuo volviese a ocupar consecutivamente un mismo nodo.

Una vez caracterizada la red espacial descrita por los dispersantes, la comparamos con rutas óptimas y generadas al azar. Consideramos como ruta óptima aquella que, formada por el mínimo número de parches y, siguiendo la misma dirección que observamos a lo largo de la dispersión, unía los territorios natales con las áreas de asentamiento.
finales. Las rutas generadas al azar fueron constituidas por un número de nodos resultado de movimientos entre parches generados al azar. Tanto en las rutas óptimas como en las azarosas, hicimos que los individuos sólo pudieran ocupar los parches que habíamos observado ocupados en la realidad, generando de esta forma un modelo nulo muy conservativo. La comparación entre la ruta real con la óptima y la generada al azar se llevó a cabo contando el número de parches ocupados por diferentes dispersantes. Por último, analizamos la dirección de los movimientos entre parches y la comparamos con la dirección del viento predominante en el área y en el momento en el que los jóvenes deciden abandonar el territorio natal.

Los dispersantes mostraron un patrón de ocupación especial heterogéneo durante la dispersión, en el que (a) sólo una fracción del hábitat disponible fue ocupada por los diferentes individuos y en el (b) los parches ocupados fueron visitados de diferente forma, es decir, mientras que la mayoría de los parches fueron ocupados sólo por un individuo, pocos fueron visitados por el 25% de los dispersantes a lo largo de su dispersión. Es decir, los parches utilizados en las rutas de los jóvenes mostrando una heterogeneidad en cuanto a su función. Las rutas observadas durante la dispersión fueron significativamente diferentes a las generadas por azar, indicando que los dispersantes no se mueven siguiendo patrones determinados por factores al azar. Sin embargo, al comparar las rutas reales con las optimizadas comprobamos cómo los dispersantes utilizaban más nodos que los que cabría esperar si estuvieran siguiendo las rutas más óptimas. Cuando analizamos la dirección general seguida por los jóvenes, comprobamos que era prácticamente la misma que la dirección del viento predominante en el área de estudio en el periodo en el que comienza la dispersión.

En metapoblaciones, la conectividad es principalmente analizada desde el punto de vista de tasa de migración entre hábitats, es decir, la probabilidad de que por ejemplo un parche sea o no sea ocupado durante la dispersión. Esta idea implica que no todos los parches o hábitats presentan la misma conectividad. Nuestros resultados mostraron un claro flujo anisotrópico, en el que los dispersantes tuvieron preferencia a dispersarse en una dirección. Ímplica a esta dirección sesgada nos encontramos con importantes evidencias empíricas de un
patrón de dispersión del que sólo teóricamente se habla hablado, es decir, de un patrón de dispersión asimétrico. Este resultado es especialmente interesante tanto en el contexto de metapoblaciones como en la dinámica de fuentes-sumideros. Por otro lado, la conectividad es también considerada como un elemento esencial en las redes formadas por áreas protegidas, estando estrictamente vinculada la persistencia de las mismas con el éxito de la dispersión de los animales, éxito que, como ya hemos mencionado, depende de la accesibilidad entre los parches. Como consecuencia, se convierte en una necesidad urgente el desarrollar herramientas que nos permitan evaluar la conectividad de redes formadas por áreas que tengan un especial interés para la conservación. A largo de los años, se han ido desarrollando diferentes técnicas para evaluar la conectividad del paisaje y el impacto de la fragmentación del hábitat. Del mismo modo, numerosos datos empíricos se han utilizado para estimar los costes que tienen los cuando tienen que moverse por hábitats fragmentados. Una de las teorías más recientes, ya considerada como en una herramienta de gran utilidad, es la teoría de grafos. Sin embargo, hasta ahora han sido pocos los datos empíricos que han testado y resaltado su potencialidad. Nuestros datos empíricos ofrecen, de este modo, una oportunidad única para representar un patrón real de dispersión, patrón que se encuentra caracterizado por la presencia de nodos, y enlaces entre ellos, de vital importancia. La pérdida de esos nodos y enlaces puede suponer una dispersión no exitosa, con importantes consecuencias en tanto la estructura como en la persistencia de las poblaciones. Gracias a los trabajos empíricos podemos obtener informaciones esenciales para explorar, a través de posteriores simulaciones, qué importancia tienen los diferentes elementos que constituyen el esqueleto de la red de la dispersión en la dinámica de las metapoblaciones, como por ejemplo, que consecuencias implicaría la pérdida de algunos de esos nodos vitales o la ruptura de los enlaces que los conectan. Por ejemplo, nuestros resultados empíricos se ajustan al modelo teórico de conectividad asimétrica teóricamente postulado por Vuilleumier and Possingham (2006). En este tipo de sistemas, la viabilidad de las metapoblaciones depende en gran medida del número de parches conectados. Por tanto si, como consecuencia de un evento estocástico, se produce la pérdida de nodos vitales, o si los enlaces (es decir, las rutas) que conectan los territorios de cría con las áreas de asentamientos desaparecen, es posible esperar un serio declive de
nuestra población. Sólo el conocimiento de las rutas reales seguidas durante la dispersión pueden proporcionarnos las herramientas necesarias para llevar a cabo eficaces planes de manejo y conservación, en los que no sólo es importante el número de parches implicados, si no también la función de los mismos (es decir, nodos donantes vs. receptores). En los sistemas asimétricos, como el observado en nuestra población, tanto el destino de sólo los parches donadores (es decir, los territorios de cría) o sólo los parches receptores (es decir, las áreas de asentamiento) puede ser determinante en la dinámica de las poblaciones.

Este tipo de estrategias de dispersión puede ser el resultado de que exista una mayor facilidad para moverse en una determinada dirección. En nuestro sistema, uno de los factores que podría contribuir a este tipo de patrones asimétricos es el viento. Este no es el primer trabajo que resalta la posibilidad de que animales, aparentemente activos, realicen una dispersión que sea el resultado final de la mezcla entre estrategias activas (lleveda a cabo por decisiones que adopta el animal) y pasivas (en las que factores como el viento desempeñan un papel clave), siendo este tipo de influencias esenciales para entender el efecto de la dispersión en la dinámica de las poblaciones. Comprendiendo tanto (1) la influencia de factores como el viento en la determinación de los patrones de dispersión de las especies y, por tanto, la direccionalidad de los vientos predominantes; como de (3) la estructura (ej. la conectividad entre los nodos) y las características de las redes espaciales descritas a lo largo del proceso de dispersión, favorecidas a su vez por la dirección del viento, podremos aproximarnos cada vez más a la explicación de los patrones de distribución de las especies.

Apoyándonos en los resultados obtenidos en este trabajo, nos gustaría concluir resaltando la idea de que, estudios de poblaciones que no consideren la complejidad del proceso de la dispersión pueden llegar a conclusiones erróneas al tratar de explicar cómo y por qué las poblaciones animales decercen.
Exploración del efecto de las estrategias de movimiento, los factores fisiológicos y ambientales en el patrón de asentamiento durante la dispersión

Las poblaciones animales son una mezcla de individuos reproductores y dispersantes, en las que el proceso de la dispersión es determinante de su dinámica, su distribución espacio-temporal, su estabilidad y la probabilidad de extinción.

Aquellas zonas ocupadas por el mayor período de tiempo a lo largo del proceso de dispersión, y en las que a veces los dispersantes adquieren el status de reproductores y comienzan a criar, se conocen como áreas de asentamiento. Estas áreas de asentamiento tienen una importancia crucial ya que, tanto la decisión de los animales de asentarse como la selección de las áreas de asentamiento puede afectar: (a) la condición de los individuos; (b) el comportamiento social dentro de las poblaciones; y (c) la competición por los lugares de cría. A pesar de su importancia, debido a la dificultad de detectarlas, las áreas de asentamiento han sido en innumerables ocasiones consideradas poco importantes, si no completamente ignoradas en muchos estudios realizados para analizar la persistencia de las poblaciones.

Pero no sólo son importantes las áreas de asentamiento, si no también las estrategias de movimientos que siguen los animales durante su búsqueda. Debido a que los costes y los beneficios durante la dispersión pueden variar no sólo a un nivel interespecífico, si no también entre los diferentes individuos, es esperable que exista una plasticidad en las estrategias de dispersión seguidas por los diferentes dispersantes. Por ejemplo, Zollner & Lima (1999) encontraron que la estrategia de dispersión más efectiva era aquella compuesta fundamentalmente por movimientos cercanos a los rectos. En particular, los movimientos más cercanos a los rectos (no perfectamente rectos), debido a que (1) permiten que los animales se muevan sin que el ambiente por el que lo hacen pase desapercibido, y (2) evita
exploraciones redundantes de las mismas áreas. Estas estrategias de movimiento a lo largo de la dispersión pueden variar, sin embargo, en función de de diferentes factores, como los riesgos durante el proceso de dispersión, la condición física de los individuos, el rango de percepción y la distribución y la densidad de los parches. De hecho, el ambiente físico por el que se mueven los animales es muy variable y puede afectar la habilidad de los animales para dispersarse, varias características de los movimientos durante el proceso y los procesos de colonización. Esas respuestas en el comportamiento pueden, a su vez, afectar la selección del hábitat por parte de los dispersantes. Por tanto, las rutas que describen los individuos durante la dispersión tienen una importancia crucial.

Estudios recientes sobre selección de hábitat han tratado de investigar cuáles son las señales esenciales que guían a los dispersantes durante su búsqueda hacia nuevas áreas. Aunque son muchos los mecanismos de comportamiento que parecen estar implicados, todos se caracterizan por aumentar la calidad de los individuos después de asentarse. Sin embargo, algunos trabajos han demostrado que existen otras señales también pueden guiar a los animales en la selección de las áreas de asentamiento, como las conocidas tramas ecológicas.

En este trabajo, nuestro objetivo principal es explorar (1) cómo, cuándo y dónde los animales buscan áreas de asentamiento; (2) cómo las estrategias a lo largo de las escalas espaciales y temporales están influenciadas tanto por los costes a lo largo de la dispersión como por la estructura del hábitat; y (3) cómo y cuándo los animales deciden dejar de buscar áreas de asentamiento y eligen una en la que definitivamente asentarse. Nuestras hipótesis de partida pueden englobarse en tres grupos:

1. Hipótesis de configuración de las trayectorias: los animales que se mueven a distancias más largas deberían seguir rutas más rectas. Más aún, animales que se mueven con trayectorias más rectas deberían alcanzar las áreas de asentamiento antes que aquellos animales que, por el contrario, siguen trayectorias más tortuosas, disminuyendo de esta forma el tiempo de permanencia en ambientes no favorables.
2. Hipótesis de la habilidad en el movimiento: las diferencias individuales en los patrones de movimiento dependen de la condición física del animal y de la estructura y composición del hábitat. Cuanto mayores sean las distancias que el animal tenga que recorrer o mayor sea el tiempo que tenga que invertir antes de alcanzar un área de asentamiento, mayores serán los costes que tendrá que invertir a lo largo del proceso de la dispersión. Nosotros hipotizamos que los individuos en mejor condición física deberían evitar costes innecesarios, evitando desplazamientos largos a través del empleo de movimientos más rectos y rápidos. Además, dado que moverse a través de ambientes desfavorables puede conllevar graves riesgos, los movimientos más rectos deberían ocurrir más frecuentemente en hábitats más fragmentados, ya que normalmente se caracterizan por ser menos favorables para los animales. Si la primera hipótesis se cumple, y los individuos en mejores condiciones físicas emplean movimientos más rectos, las características individuales y el comportamiento en cuanto a los patrones de movimientos podrían actuar de forma conjunta determinando el éxito de la dispersión.

3. Hipótesis de la experiencia natal: durante la dispersión a través de ambientes desconocidos, los individuos podrían seleccionar el ambiente por el que se mueven en base a las características del hábitat que frecuentaron en su territorio natal. En ese caso, tanto las áreas a lo largo de la fase de búsqueda como las áreas finales de asentamiento deberían tener características comunes (ej., topografía, composición y distribución de parches, tipo de vegetación) a las áreas natales.

El primer paso para testar estas hipótesis fue determinar el momento en el que los búhos decidieron de buscar para asentarse en un área de asentamiento, y localizar espacialmente las diferentes áreas usadas por los diferentes dispersantes. Posteriormente, procedimos al análisis de las estrategias de movimientos durante la fase de búsqueda de los animales en dispersión, a dos escalas espacio-temporales diferentes: (a) una escala pequeña, a través del seguimiento continuo de los animales durante los periodos de actividad; (b) a una escala mayor, mediante un seguimiento semanal, para recoger patrones más generales del proceso global. Junto al análisis de los patrones de movimientos, determinamos la condición física de los animales y realizamos un
análisis del hábitat, con el que obtuvimos características en cuanto a estructura y composición del tanto el hábitat a lo largo de la fase de búsqueda como de las áreas de asentamiento finales.

Los resultados que obtuvimos apoyaron la primera y segunda hipótesis. Es decir, encontramos que los búhos que describieron las trayectorias más rectas se desplazaron mayores distancias a lo largo de la dispersión, alcanzando áreas de asentamiento más alejadas de su territorio natal. Además, los dispersantes que siguieron trayectorias cercanas a rectas (pero no perfectamente rectas) alcanzaron antes esas áreas de asentamiento. Las características del hábitat tuvieron un fuerte efecto sobre las estrategias de movimiento. Aquellos búhos que tuvieron que atravesar ambientes más fragmentados a lo largo de la dispersión, se movieron de forma más recta. Algunas características de la condición física de los individuos tuvieron también un efecto sobre el comportamiento de los animales. Comprobamos que los individuos en mejor condición física eran aquellos que describieron las trayectorias más rectas. Por el contrario, nuestra última hipótesis no se cumplió. Las características del hábitat de las áreas de asentamiento no fueron equiparables a las del área natal. Los resultados de los análisis de hábitat nos llevaron a pensar que los animales podrían estar seleccionando las áreas de asentamiento en base a la experiencia que adquieren a lo largo de la fase de búsqueda, ya que tanto las áreas frecuentadas por los dispersantes durante la búsqueda como las áreas finales en las que se asentaron eran muy similares en cuanto a estructura y composición.

Un resultado muy interesante es el obtenido al haber analizado los patrones de movimientos a dos escalas diferentes, ya que los patrones que observamos son diferentes. A una gran escala, los búhos que siguieron trayectorias más cercanas a las rectas encontraron antes las áreas de asentamiento. Sin embargo, a una escala pequeña, los resultados no reflejan tanto estrategias de dispersión general, si no patrones de uso del espacio. A esta escala pudimos clasificar dos tipos de estrategias: (1) búhos que parecen explorar intensivamente las áreas por las que viaja a lo largo de la dispersión, caracterizados por asentarse más tarde; y (2) individuos que exploran esas áreas de forma más extensiva, pero que de forma general, se asentaron antes. Uno de los mayores problemas en ecología ha sido el tratar de extrapolatar patrones observados a una

192
pequeña escala a escalas más grandes. Numerosos estudios han tratado de analizar la veracidad de esa extrapolación, viendo la dificultad de comprender patrones a grandes escalas a través de informaciones recogidas a escalas más finas. Uno de los principales problemas en esa extrapolación, relacionado con el movimiento de los animales, es que los individuos alteran su comportamiento a lo largo del tiempo, cuando se encuentran bajo diferentes condiciones ambientales o se mueven bajo diferentes motivaciones. Nuestros resultados apoyan previos estudios y resalta la importancia a la hora de considerar las escalas, tanto en el espacio como en el tiempo.

La heterogeneidad de hábitat es un factor determinante en las estrategias de movimientos. Tanto el tiempo como la distancia a la que se desplazan los animales parecen estar determinada por el tipo de hábitat que tienen que atravesar. En general, los movimientos más rectos parecen ser más frecuentes cuando los animales se desplazan por hábitats más fragmentados o poco favorables para los animales. Estas diferencias en las estrategias de movimientos pueden ser explicadas en términos de los costes y los beneficios durante la dispersión. Estudios previos han demostrado que la fragmentación de hábitat puede causar un aumento en los costes a lo largo de la dispersión y, por tanto, largas travesías pueden venir asociadas a altos riesgos de mortalidad.

En un contexto de selección de hábitat, los búhos en dispersión parecieron regirse más por señales (es decir, características del hábitat) que fueron aprendiendo durante la fase de búsqueda, más que por aquellas con las que estuvieron familiarizados durante el período de dependencia en el territorio natal. Son muchos los mecanismos de comportamiento que pueden regir los procesos de selección de hábitat durante la dispersión. En particular, nuestros resultados apoyan previas hipótesis de que el período de búsqueda de áreas de asentamiento es un período de entrenamiento y aprendizaje, durante el que los animales aprenden las características de las áreas más favorables en las que asentarse.

Para concluir, nuestros resultados apoyan la idea de que existe una variación en los movimientos no sólo en función de la especie, si no también dentro del individuo e influenciada por las características del
habitat. Por tanto, cómo los animales se mueven a través de ambientes fragmentados es muy importante para una mejor comprensión del proceso de dispersión, así como para poder predecir el efecto del hábitat en la dinámica de las poblaciones y en la distribución espacial de los organismos.
Niveles de familiaridad durante la dispersión

Las habilidades cognitivas y el nivel de aprendizaje de los animales son aspectos que pueden tener un importante efecto tanto en su comportamiento como en algunas decisiones relacionadas con la selección de hábitat, la elección de la pareja, las estrategias de caza, las interacciones sociales y el uso del espacio. En particular, cualidades como la memoria espacial y la capacidad de aprendizaje permiten a los animales moverse a través del ambiente eficazmente. Sin embargo, los conocimientos acerca de cómo los animales aprenden y adquieren experiencia para moverse son escasos. En general, el aprendizaje espacial puede ser dividido en tres tipos (1) qué, referido a la evaluación de las características esenciales del hábitat (ejemplo, los refugios, las áreas de caza, etc.); (2) dónde, aprendizaje asociado a la localización de las anteriormente citadas características del entorno en el que viven; y (3) cómo, mediante el que los animales adoptan diferentes comportamientos para optimizar la explotación y el uso del hábitat. El aprendizaje no ocurre de forma simultánea, si no que aumenta de forma progresiva en función del tiempo que el animal permanece en un área.

Debido a que el aumento del grado de familiaridad con el entorno, consecuencia directa del aprendizaje, es un factor clave en el movimiento de los animales, en el presente trabajo planteamos las siguientes hipótesis: (1) los patrones de los movimientos deberían ser cualitativamente diferentes cuando los individuos exploran activamente áreas nuevas a cuando se asientan definitivamente en área de forma estable y tienen tiempo suficiente para adquirir los tres tipos de aprendizaje; (2) en las áreas finales de asentamiento, al tener los dispersantes tiempo suficiente para familiarizarse con el entorno, los patrones de movimientos deberían ser más similares al de los adultos reproductores que a los jóvenes en las primeras fases de la dispersión. De hecho, la dispersión representa un escenario óptimo para testar estas hipótesis, ya que cuando los individuos abandonan su territorio natal, exploran activamente áreas diferentes y desconocidas, hasta encontrar una en la que se asientan de forma estable. Dado que en esas áreas finales de asentamiento los dispersantes permanecen durante el periodo
de tiempo más largo a lo largo de todo el proceso de dispersión, pueden aprender y aumentar el nivel de familiaridad con su nuevo entorno. La comparación del comportamiento del movimiento a lo largo del proceso de dispersión es una oportunidad única para aumentar nuestro conocimiento del efecto de la familiaridad en los movimientos de los animales. Para testar las anteriormente citadas hipótesis, utilizamos datos obtenidos a través del radioseguimiento realizado de forma continua e intensiva (ver Consideraciones metodológicas para más detalles) de 40 jóvenes de búhos a lo largo de su dispersión y de 9 adultos reproductores.

Para detectar si los animales habían aprendido el qué, analizamos dos características físicas del hábitat, necesarias para todos los animales: (a) los lugares de cobijo: para comprobar si los animales habían aprendido la posibilidad de utilizar determinados lugares para cobijarse, calculamos la distancia entre el punto inicial y final de cada una de las noches. Si los animales han aprendido la existencia de cobijo en un área, deberían volver a dormir siempre a ellos después de su actividad nocturna, siendo por tanto la distancia entre los puntos iniciales y finales de su período de actividad pequeña; (b) áreas de caza: animales familiarizados con su entorno deberían conocer existencia de zonas donde cazar y explotarlas habitualmente. De cada noche, identificamos las áreas donde los animales cazaban y calculamos su extensión. Animales en las primeras fases de la dispersión, al estar continuamente explorando nuevas áreas, no deberían tener áreas de caza definidas, mientras que tanto los dispersantes asentados en áreas estables como los adultos reproductores deberían concentrar su esfuerzo de caza en áreas más restringidas. En segundo lugar, analizamos cuando los animales habían aprendido el dónde a través de análisis fractales. Para ello estimamos, para cada una de las noches, la variación de la dimensión fractal y la correlación entre la longitud de segmentos adyacentes a lo largo de diferentes escalas espaciales, métodos que nos permitió identificar los diferentes domínios o usos del espacio por parte de los individuos. Animales explorando activamente nuevos y diferentes hábitats vs. animales explotando su ya definido dominio vital representan escenarios muy diferentes, por lo que podríamos esperar que la estructura del movimiento cambie cualitativamente. Por último, para analizar si los animales cambiaban su
forma de usar el espacio (es decir, aprendían el cómo), estimamos varios parámetros para caracterizar los movimientos, como la tortuosidad y la longitud total de las trayectorias, la longitud entre pasos sucesivos y la velocidad del movimiento. Como la dispersión implica altos costes para los individuos, nuestra hipótesis apunta a que los animales en las primeras fases de la dispersión, y con el objetivo de encontrar lo antes posible un área donde asentarse, siguen trayectorias más rectas y se desplazan a mayor velocidad que los animales moviéndose por áreas familiares.

Los resultados de este estudio demostraron cómo los patrones de movimientos experimentan una clara transición desde una fase de exploración en las primeras fases de la dispersión a una fase de explotación cuando los individuos permanecen de manera constante en un área (es decir, tanto los dispersantes en sus áreas de asentamiento como los adultos reproductores). En las primeras etapas de la dispersión, los animales tienen que atravesar áreas desconocidas y, a veces, desfavorables, teniendo poco tiempo para familiarizarse con el entorno. La falta de información en cuanto a conspecificos, recursos y predadores conlleva un alto riesgo, riesgo que los animales pueden reducir a través del aprendizaje y aumentando el grado de familiaridad con el entorno en el que viven. Este proceso quedó bien reflejado por el cambio de comportamiento de los movimientos de los individuos desde las primeras fases de la dispersión a cuando los jóvenes encontraron un área donde asentarse y familiarizarse. Cuando los dispersantes se asentaron de forma más estable en un área, aunque nunca mostraron un comportamiento territorial, presentaron un dominio vital bien definido y explotado de forma similar a como lo hacen los adultos reproductores, dominio vital en el que tienen la ventaja de poder aprender sus características y familiarizarse. Hay que mencionar que previos estudios han demostrado como los beneficios de la familiaridad están vinculados con el aumento de la eficacia de caza, el éxito reproductor y la supervivencia.

Aunque no detectamos ninguna diferencia significativa en el tamaño relativo de las áreas de caza a lo largo de las diferentes fases de la vida de los individuos, los jóvenes a lo largo de la dispersión presentaron en general una zona de caza menos restringida que los adultos, posiblemente debido a las respuestas relativas a las estrategias
de caza de los individuos en función de las características locales del hábitat. Es decir, debido al hecho de que los jóvenes no presentan un comportamiento territorial y pueden, si lo necesitan, desplazarse con mayor facilidad por diferentes áreas de caza, aún solapando con la de otros individuos dispersantes y sin que ellos les suponga un riesgo, el resultado final es la menor delimitación de las mismas.

Existen algunas diferencias claves en los conceptos de territorio y dominio vital. Los dominios vitales son aquellas áreas que los animales explotan día a día, realizando aquellas actividades que les permita obtener los elementos esenciales para su supervivencia. Son áreas en las que, a veces por la distribución parcheada de los recursos, engloban espacios que los animales sólo utilizan para desplazarse de un lado a otro de su dominio vital. Suelen ser, además, grandes extensiones, difíciles de defender en su totalidad. Por el contrario, el concepto de territorio hace referencia exclusivamente a aquellas zonas dentro del dominio vital que son defendidas activamente por los animales que viven en él, evitando cualquier tipo de intrusión. Estas diferencias entre dominio vital y territorio explican algunos comportamientos que observamos en este estudio. Para aumentar la eficacia de la defensa de un territorio, los animales muestran una serie de comportamientos, como agresividad o la capacidad para discriminar entre los que son vecinos y los que representan posibles intrusos. Los floaters no muestran este comportamiento territorial pero, por el contrario, permanecen de forma estable en áreas fijas, como se observa en individuos territoriales, pudiéndose beneficiar viviendo en ellas, ya que pueden familiarizarse con el entorno. La necesidad de los adultos reproductores de expresar un comportamiento territorial puede también explicar las diferencias en la velocidad de los movimientos que mostraron nuestros resultados ya que, por ejemplo, los adultos territoriales tienen que invertir parte de su tiempo en realizar actividades propias del comportamiento territorial (como, en el caso de los búhos cantar) para delimitar el territorio y para comunicar con su pareja. Estas tareas implican largas pausas que no están incluidas en las actividades de los dispersantes. Esta diferencia en la velocidad de los movimientos puede, a su vez, generar diferencias en el grado de percepción de los individuos. La percepción de los animales integra diferentes habilidades sensitivas y puede estar limitada por las
características del hábitat, siendo inversamente proporcional a la velocidad de los movimientos. Al realizar los floats desplazamientos a una mayor velocidad, perciben el ambiente sólo a largas escalas espacioales y, como consecuencia, la estructura de su movimiento queda reflejada un único y gran dominio, como se vio reflejado en el análisis de los fractales. Por el contrario, los adultos territoriales pueden actuar en diferentes y bien establecidos dominios de escala espacial, reflejando cada uno diferentes aspectos de su biología.

En general, los animales pueden moverse según dos tipos de comportamiento, que podemos englobar en estrategias azares y sistemáticas. En las estrategias sistemáticas, que sólo se dan cuando existe un conocimiento previo, las reglas para explotar un área están basadas en planes precisos y controlados. Por el contrario, en las estrategias azares, los animales tienen que moverse con el objetivo de aumentar la probabilidad de localizar diferentes recursos, reemplazando las reglas para explotar los recursos en procesos estocásticos. Aunque no es posible negar la existencia del azar en la naturaleza, las habilidades cognitivas y el aprendizaje podrían disminuir la necesidad de estrategias al azar mediante la creación de, por ejemplo, una mejor capacidad de percibir y, por tanto, aumentando la capacidad de adquirir información procedente de estímulos externos y prediciendo las fluctuaciones de variación y abundancia de recursos.

La dispersión implica altos costes energéticos y riesgos de mortalidad. En general, animales en dispersión a lo largo de hábitats desconocidos y, a veces, desfavorables, suelen describir trayectorias rectas, que les permite atravesar esas áreas de forma más eficaz y localizar una nueva área donde asentarse de forma más rápida. Cuando los animales son familiares con su entorno, como en el caso de dispersantes en sus áreas de asentamiento y de los adultos reproductores, son capaces de regular sus movimientos para explotar su entorno de forma más eficiente. Esta idea es apoyada por nuestros resultados, en los que observamos como los jóvenes asentado en áreas estables ajustan la longitud y tortuosidad de sus trayectorias, mostrando patrones de movimientos más similares a los adultos reproductores que a los jóvenes en las primeras fases de búsqueda de la dispersión.
Para concluir, hay que tener en cuenta que, aunque el grado de familiaridad con el entorno es sólo uno de los múltiples factores que determinan los patrones de movimientos, los resultados que hemos observado podrían deberse no sólo al hecho del aprendizaje progresivo del entorno, si no ser también un reflejo del status social de los individuos.
Conclusiones

Durante esta tesis hemos estudiado la dispersión natal en una especie de larga vida, el búho real, bajo la perspectiva del análisis de los movimientos, integrando por tanto diferentes aspectos de la ecología del comportamiento y de las estrategias evolutivas de la dispersión. Un día, hace ya casi cinco años, decidimos marcar con emisores jóvenes de búho real. Hasta ahora nadie había estudiado la dispersión de esta especie. Y, cuando pensamos en la posibilidad de que éste fuera el tema de tesis, algunos compañeros nos aconsejaron de que no era una buena idea, tanto por la dificultad de seguir animales durante la dispersión a lo largo de largas escalas temporales, como por la dificultad de estudiar una especie de la que prácticamente no se conocía nada en cuanto a su dispersión. Aún así, el riesgo de acabar con pocos, de perder los animales era elevado, no pudimos frenar nuestra curiosidad. Aún así, el primer año marcamos una pequeña muestra, justo para saber la viabilidad de nuestro estudio. Y, a pesar de la dificultad de seguir a estos caprichosos individuos durante miles de kilómetros, a pesar de lo duro de trabajar por la noche, durante numerosas frías noches en la que el tiempo transcurre infinitamente despacio, pronto nos dieron cuenta de la potencialidad de nuestro estudio, con el que podíamos obtener una sorprendente cantidad de informaciones novedosas.

Una especie como el búho real, con una envergadura similar a la de muchas rapaces diurnas de gran tamaño, como el águila imperial o la perdiz, que son capaces de dispersarse a lo largo de distancias del orden de centenares de kilómetros, sólo viajaba decenas de kilómetros a lo largo de su dispersión. Comprobamos, a través de nuestros análisis, que estas distancias de dispersión no eran elegidas al azar, sino que eran el resultado de de diferentes estrategias de comportamiento a lo largo de esta fase. De hecho, observamos que la variación en el comportamiento no sólo se producía entre individuos, si no también dentro del mismo individuo. Al contrario de lo que esperábamos en un principio, nos encontramos con un escenario muy diferente a la visión clásica de los modelos de dispersión, en el que este proceso no consiste en un mecanismo para alejarse de la población natal, si no en el que los dispersantes permanecían flotando cerca y alrededor de su población de
orígen, siendo tanto la búsqueda como el patrón final de asentamiento el resultado de numerosas interacciones entre tácticas de comportamiento, parámetros relativos a la condición física de los individuos y la configuración espacial del ambiente por el que se mueven. Todos estos resultados bien ilustran, en mi opinión, cómo el estudio de la dispersión de diferentes modelos biológicos nos abre las puertas a nuevos horizontes de nuestro conocimiento. Creo que nuestro estudio, con un fuerte soporte empírico, aporta importantes informaciones útiles tanto para una ecología más teórica como para una más aplicada. Sólo con un mejor conocimiento del proceso de la dispersión podremos llegar a alcanzar a entender la relación entre sus causas a nivel individual y sus consecuencias al nivel de poblaciones.

A continuación, voy a resumir brevemente las principales conclusiones de cada uno de los estudios que componen esta tesis:

3 El período de dependencia representa una fase de aprendizaje intensiva que puede tener importantes consecuencias en la posterior fase de la dispersión. Por tanto es importante conocer el comportamiento de los animales moviéndose durante ella. A través del análisis de los patrones de movimientos observamos un cambio gradual en el comportamiento de los individuos, asociado al incremento de las capacidades de vuelo, a las habilidades cognitivas y al aumento en el rango de percepción. Therefore, it is important to have knowledge of movement behaviour patterns during this phase.

4 Los dispersantes muestran diferente patrones de movimientos a lo largo de la fase de búsqueda de la dispersión. Esos cambios de comportamiento fueron observados en las distancias de desplazamiento, la configuración de las trayectorias, la respuesta a conspecíficos y los diferentes tipos de movimientos. Estos resultados resaltan la importancia de considerar el efecto que el tiempo tiene sobre el comportamiento a la hora de realizar modelos predictivos de distribución de poblaciones.

5 El movimiento animal es el resultado de múltiples interacciones entre factores externos e internos, que actúan a diferentes escalas espaciales y temporales. Por tanto, en ambientes naturales y
heterogéneos, el movimiento de los animales es el reflejo del compromiso entre el comportamiento, las diferentes decisiones que los individuos tienen que tomar, la calidad de los mismos y las propiedades físicas del ambiente por el que se desplazan.

Los dispersantes mostraron un patrón de ocupación especial heterogéneo en el que, mientras pocos parches fueron ocupados por muchos individuos, muchos fueron ocupados por uno solo. Las rutas descritas durante la dispersión parecieron ser el reflejo de una solución intermedia entre optimizar los desplazamientos y explorar el ambiente de forma azarosa. Los resultados de nuestros análisis muestran un claro patrón de dispersión asimétrica (fuertemente influenciada por el viento dominante), en el que no sólo el número de parches disponibles, si no también su función pueden tener importantes consecuencias en la dinámica de las poblaciones.

La variación he individual en los patrones de movimientos conlleva variaciones en los patrones finales de asentamiento. Individuos que se dispersaron con trayectorias más rectas, se desplazaron mayores distancias pero tardaron menos tiempo en encontrar un área de asentamiento. La heterogeneidad del hábitat tiene un fuerte efecto en los patrones de movimientos, siendo la distancia y el tiempo de dispersión recorriendo función de la estructura del hábitat. En el contexto de la selección de hábitat, los dispersantes se asentaron en ambientes más parecidos a los visitados durante la dispersión que su territorio natal.

La información sobre el entorno es un elemento fundamental que afecta el movimiento de los animales. Durante la dispersión, los individuos mostraron estrategias de movimientos muy diferentes cuando se encontraron en la fase de búsqueda, moviéndose de forma activa entre diferentes áreas y explorando el entorno, a cuando definitivamente se asentaron en un área de forma más estable, teniendo en ese momento tiempo suficiente para aprender las características esenciales de su entorno, su localización y la mejor forma de explotarlas.
Agradecimientos

Creo que ya no tengo más excusas...ya no tengo más remedio que poner punto y final a este capítulo de mí...pero es que creo que pocas personas (o, no sé, quizás más de las que imagino) comprenderían con la alegría que me levantarla mañana si supiera que el plan es ir al campo, o trampear un adulto, una buena caminata para buscar algún otro nido...también si la mayor parte del camino es atravesando el ‘mundo jabalk’ o el ‘mundo zarza’, o coger la antena y pasarle una noche siguiendo a cualquiera de éstos o durante un buen día soleado buscando bichos en dispersión. Uno de esos días en que recorres centenares de kilómetros, abstraído en tus pensamientos, perdida en tu mundo mientras buscas ese ansiañado pitido (...al menos uno!). Ojalá mañana fuera de nuevo el primer día...

Todavía me cuesta creer que me hayan dado la oportunidad de vivir estos cuatro años de la forma en que lo he hecho. Al primero que me gustaría darle las gracias por, no sé...todo, es a Carlos. ¿Echas de menos esas tardes analizando egagrópilas? Para mí son inolvidables. Una de las pocas personas a la que nunca ha hecho falta explicarle mucho...tú sabías y, también si no estabas de acuerdo, respetabas. Gracias por conocerme tan bien. Creo que eres de las pocas personas que has sabido sacarme de marimarilandia, quizás porque un poco de ti pertenece a ese mundo. La primera vez que te escuché hablando de modelos lineales pensé: ‘¿modelos...qué? ni idea...creo que nunca sabré cómo se hacen’. Y cuando me preguntaste ‘¿qué vas a hacer ahora que has acabado la carrera?’ Pues de nuevo...ni idea. Seguro no una tesis. Y aquí estoy. Me acuerdo un día hablando con Nico, durante una de esas buenas salidas al campo para anillar pajaritos con, quién si no, Manolo Vázquez, que me dijo ‘a mí me pasa lo mismo, pero he pensado que si los demás pueden, ¿por qué no iba a poder hacerlo yo? Y es verdad ¿por qué no? Así Carlos tuvo que casi arrastrarme al despacho de Vincenzo Penteriani. Recuerdo ese día como si fuera ayer. Cuando entre en ese espacio pequeño y conocí a Vincenzo. Perdona VI...pero es que tendrías que ver la cara que tengo ahora mismo, escribiendo esto...una risa! Pero está muy bien poder escribir así...sabiendo que, al menos esto, no va ser rechazado por un referee!!! Aunque...a este ritmo...me van a
acabar rechazando hasta el capítulo de Agradecimientos... entonces sí que me podría presentar el Ignobel, no?

Ese mismo año, y mientras esperaba a que se resolviese la beca, Andy me contrató para trabajar con Héctor en el Laboratorio de Ecología Acuática. Los dos me enseñaron muchas cosas. Me sorprendió el día que Héctor me dio las gracias por el trabajo que estábamos haciendo... pero si las gracias sólo puedo dártelas yo! He disfrutado mucho trabajando contigo y descubrir, a través de la lupa, que existe un mundo sinfín invisible para la mayoría de las personas. Tú y Andy, que siempre me ha demostrado un cariño muy especial, me enseñasteis a ver que, detrás de lo que aparentemente podría ser ‘contar gusanos’, se esconden hipótesis ecológicas, miles de preguntas por contestar... Y, porque no sólo el trabajo con vosotros fue limpiar y analizar muestras, si no que siempre estuve acompañado de interesantes conversaciones, la maquinaria que mueve mi curiosidad por el saber siempre estuvo funcionando. También por aquel entonces recibí el apoyo de Miguel Ferrer, dejándome solicitar la tesis bajo su dirección, ya que el contrato que Vincenzo tenía en aquel momento era menor que el tiempo de duración de lo que sería mi beca. Pero un día me llegó un mensaje de Ví al móvil... le había concedido una beca de la junta... y luego llegó mi beca y un poco más tarde un proyecto del Ministerio... ya teníamos todos los ingredientes que garantizaban nuestros próximos cinco años trabajando juntos! A todas las personas que nos han dado esta oportunidad, GRACIAS.

Un día, volviendo del campo en una de nuestras primeras salidas, Vincenzo vio un cartel publicitario que decía ‘nadie sabe más de la noche...’ era de Licor43, que utilizaba como logo un baño (Virginianus... pero a efectos prácticos no importa, no?) y tuvo la genial idea de ir a Madrid, donde nos reunimos con las responsables del departamento de marketing de Licor43, Piera y Gema. La idea era que, si ellos nos apoyaban económicamente, nosotros podríamos crear un vínculo en su página web en el que la gente tuviera la oportunidad de apadrinar uno de los baños reales que teníamos marcados y de los que recibirían informaciones periódicas de su vida. Tanto a Piera como a Gema les pareció una idea buenísima. Y así fue cómo nació el proyecto “Apadrina tu baño”, en el que participaron más de 7000 personas procedentes de
todo el mundo. Gracias a todas esas personas por la ilusión y entusiasmo que mostraron durante todo esos años. Y gracias a Piera y a Gema por su cariño y apoyo a lo largo del proyecto. También quería darle las gracias al grupo de EMASEA, en especial a Carmelo Scott y Ana Vassanta. No podría imaginar cómo hubiera sido el trabajo en el campo sin su ayuda. Gracias por habernos facilitado el acceso a la Ruta del Agua y por habernos permitido el uso de vuestras instalaciones en el embalse El Gergal. Gracias también, por vuestra inicial ayuda económica y, cómo no, por las invitaciones a esas copiosas comidas en la Feria...

Las salidas al campo estuvieron en innumerables ocasiones aliñadas por la agradable compañía de algunos personajes. Al primer tramo nos acompañaron Enrique Luque, Javier Balbontín, Eva Casado y Carlos Alonso... fue divertidísimo. En cinco minutos el búho estaba en la trampa. No os podéis imaginar lo divertido que le tomamos!!! Que si el ala, la cola, el antebrazo... que si hay que pesarlo... Carlos diciendo de medirle, no me acuerdo cómo, el nivel de carotenoides del color enarbolado de los ojos... Vincenzo diciendo de medirle hasta las uñas! y de cómo no de recoger muestras de las plumas que formaban parte de la mancha blanca de la garganta... vamos, que nos hizo falta hacer canto al bicho para grabarlo!!! Y... primer error colocado... ¿Cómo se movía un búho? Las primeras lecciones de radioseguimiento fueron impartidas por Javier Balbontín... que nos cuenta cara de asombro al levantar la antena y escuchar esa señal... que emoción!!! Teníamos la posibilidad de poder saber, por primera vez, dónde estaba en cada momento este búho, podíamos saber qué hacía... sin pensar, claro, que años más tarde me iba a dar hasta fatiga esta antena de los... que no es broma, esta antena ha sido mi fiel compañera en toda esta travesía. Por eso, me gustaría darle las gracias a Biotrack, por todos los buenos servicios que nos ha prestado durante estos años, y que espero que sean por muchos años más. Mucha gente ha sentido curiosidad en saber que era ‘pasar una noche siguiendo a un búho’... Vincenzo? Te doy una última oportunidad: antes de que consiga una beca post-doctoral (mucho o poco?). Uno de los más sorprendidos cuando me acompañó al campo fue Alfredo Valido, que cuando salió el sol, después de una noche de radioseguimiento intensivo, no hacía más que repetirme: ‘y esto lo haces todas las noches?... tú estás loca chiquilla!’ ¿las noches más divertidas? Con Paola Bartolomei. En realidad Paola se convirtió, desde el primer
segundo que nos conocimos en mi sorrelina. Casi podría acordarme de todo, desde el primer día que entró por el despacho con su maravilla sonrisa ‘80 dientes’ y gritando ‘ciaol’, subiendo su maleta de 180 kg por las escaleras de Federico, del primer día que fuimos a ver un nido de búho, los nunca-logrados trampos, krs y kms de carretera y miles de noches compartidas. Del día que se plantó el traje de flamenca hasta esos buenos ratitos en la cocina, con una cervecita y un cigarrillo mientras preparábamos una cena rica... gracias por seguir compartiendo todo conmigo. En este momento me gustaría pararme un momento para hacerlos notar un sutil detalle, el deterioro que ha sufrido mi castellano a lo largo de estos años. Frases como la que antes he dicho... ‘una cena rica’ es un ejemplo típico de una frase muy utilizada por todo el grupo al que pertenezco... pero las hay mucho peores, como ‘hoy me hago la noche’... empezando por Vincenzo, Stefano y Giulia, Mario y Marzia, Fabrizio, Paola, Carlotta, Sara, Letizia, Nicola, Eleonora, Enmanuel y Sara... me he visto, sin comerlo ni beberlo, inmersa en un mundo de mafiosos... porque de verdad que son todos unos mafiosos! Y si no... ¿qué me dices de la foto de Carlotta, Leti? Creo que debería de respirar del ataque de risa que nos entró el día que la vimos. Pero eso sí, con la que más imaginación he tenido que tener para entenderla ha sido, y es, con Leti. Demasiado curiosa por el castellano. Cuando hablas con ella tienes que estar completamente concentrada, porque en el momento en que menos te lo esperas, cuando no sabe cómo decir algo se para y te dice ‘Mary, ayúdame’ (tono muy imperativo)... tienes que estar más atenta que en clase. Al final estamos casi hemos llegado a una forma de comunicación compartida, en la que cada uno dice un pedacito de la misma frase. Me encanta meterme con ella... y hacerle refín. Al principio no te caía muy bien, eh? ya te he dicho que eres una ‘stronzza’... ahora no sé qué piensas, pero a mí me encanta estar contigo; salir al campo, cervecitas, viajes... todo juntas. Espero que disfrutes de todo como lo he disfrutado yo, y espero que lo podamos disfrutar juntas.

El grupo también ha contado con la presencia de personas de otras nacionalidades, como los estudiantes de Reading (UK), Robert y Lindy; de Portugal, Rui; y, menos mal, algún que otro español, mi voluntario, Paula y Antonio Conejo. Con Rui volví al análisis de egagrófilas... esta vez en mi casa, que se convirtió temporalmente en un museo de huesos. La cara de la gente cuando venía a casa a tomar una cervecita y se
encontraba con esqueletos de conejos, perdices y ratas... que risa! Para mí han sido días muy especiales, analizando esa montaña de huesos con buena musiquita, un buen vino de Portugal, un café malo español (como diría él), y con la buena compañía de ese canijo... que si no te acordabas donde colocar un hueso, sólo tenías que mirar tu cuerpo... Cuando salíamos al campo para recoger egagrolíscas parecíamos las mujeres de la limpieza, íbamos a los nidos y los dejábamos la mar de limpios. Pues sí, vivir con Rui ha sido una experiencia inolvidable. De las noches con mi voluntario tengo también muy buenos recuerdos. Me costó trabajo volver a acostumbrarme a pasarlas sola. Pero estoy segura que te sentirás más satisfecho con tus quehaceres políticos... gracias por haberte dedicado tu tiempo, también sí para ello a veces tenías que decir alguna ‘mentirijilla’.

También han sido muy divertidas las salidas al campo con Fabrizio. Las echo de menos... Los primeros meses no me enteraba de nada. Eran días enteros viendo como os morías de la risa... sólo de veros me entraba a mí también la risa. Al principio pensaba que era por el idioma, pero luego, cuando fui entendiendo un poco más el italiano, supe que no entiendía nada porque todas vuestras conversaciones eran sin sentido... menudo par de golpos... Me habéis enseñado a que hay que retr en los buenos momentos y hay que llorar de la risa en los malos. Pero sin lugar a duda, nuestra mejor ayudante de campo ha sido Giulia, siempre con ganas de ir al campo, siempre con buen sentido de humor, siempre con ganas de echar unas risas. Fiel y entusiasta de todas nuestras ideas, también si la consecuencia era salir al campo a limpiar caca de búho, con estropajo en mano! Ha participado en todos los experimentos, en trampas, visitas a nidos, escuchas, grabaciones de cantos, radioseguimiento,... siempre curiosa y haciendo preguntas mucho más interesante de las que hacen otras muchas personas que me duplican la edad. Estoy segura de que, si sigues con tu idea, llegarás a ser una gran investigadora... aunque, ya lo sabes, no te podrás librarse de hacer una tesis con cucarachas... Salir con ella al campo ha sido sólo la consecuencia de todo lo que hemos compartido a lo largo de estos años, verdad? Prepárate, porque ruego es Benensoso y espero que lo sea siempre a tu lado... nada hubiera sido lo mismo sin la ayuda de todos los guardias empezando por Francisco, miedo, Francisco el de La Lapa, Francisco el de Borbollón, Francisco el de Burguillos, Pablo, el Largo, José
María, Domingo, todos los cazadores, y todos los dueños que nos han dejado entrar en sus fincas. Siempre con ganas de contarte dónde hay un búho, de conseguirte una llave o decirte cómo la puedes conseguir. Cada uno con su peculiaridad. Pablo nos ha llevado a nidos donde sólo un guárraro tendría ganas de ir. Y el Largo, con sus millones de historias, todavía sigue convencido de que cuando levantas a una hembra con huevos, no es que la haces fracasar y haces una segunda puesta en otro nido, es que ella ‘muda’ los huevos de un sitio a otro. Quizás al que más cariño le he cogido a lo largo de estos años es a Francisco el de La Lapa, tan tímido que casi le da vergüenza mirarte a los ojos... pero siempre con ganas de gastarte una broma, siempre con una sonrisa. Francisco, ¿crees que después de cinco años de trabajo nos merecemos que nos dejen la llave de la finca? Aunque, si te digo la verdad, me gusta que no nos la des, si así tenemos la oportunidad de verte un rato.

En la Estación he tenido la oportunidad de conocer a personas muy interesantes y hacer muy buenos amigos. No me apetece hacer una lista de nombres... todos vosotros sabéis quienes sois. Gracias a todos por tan buenos momentos, por vuestra ayuda, por las cervezas y las no-cervezas compartidas y por hacer del trabajo un lugar de no sólo trabajo. En especial me gustaría darte las gracias a ti. Impresionada por tu infinita tolerancia. Por tu saber estar y por saber sacarme una sonrisa, tan bien en los momentos difíciles. Por haberte acompañado aún en la distancia, y haber compartido conmigo tantas lunas.

Fuera de la Estación, hay otras muchas personas a las que me gustaría agradecerles su incondicional apoyo, confianza e... infinita paciencia a lo largo de, no sólo estos años, si no de muchos más. Mis padres, excepcionales personas, me han enseñado, y me siguen enseñando, cosas tan importantes como saber escuchar, la tolerancia, la humildad, la igualdad, la libertad, el saber valorarse uno mismo... siempre han respetado todas mis decisiones, también si a veces no estaban completamente de acuerdo conmigo. Siempre han estado cuando los he necesitado. Ellos me han enseñado a luchar por lo que uno quiere. Y gracias a ellos aquí estoy, casi cerrando este capítulo. Gran parte de este trabajo no lo hubiera conseguido sin su ayuda... ni por supuesto sin la de mis hermanos. MamaFanny se ha convertido en la mamá del grupo. Siempre preparándonos comidas riquísimas ‘para mí y
para todos mis compañeros... vale, para Vincenzo primero... siempre pendiente de cada detalle y preocupándose de todos nosotros. Y también fuera de casa he encontrado siempre el apoyo de grandes amigos. Bea, Carmen, Luis, Elena, Txiki, Moi, Isa y Rosario, Pablo, Aitor y María... cada uno a su forma, pero todos respetando más horarios y mi ‘tengo que trabajar’ a lo largo de todos estos años.

During these years I have had the pleasure to know three very good Canadian. My very best friend, Gary Bortolotti: I love talk with him about ecology, behaviour and... life; John Fryxell, for his stimulating discussions on ecology and, in particular, on animal movements; and Viliis O. Nams: for everything... for his generosity, his patient with my English, for his interest in our work, because behind the statistics and fractals he show me that there is a... life, for his sense of humor and, the most important, for his infectious laugh.

Estaba esperando llegar al final para hablar de Vincenzo... pero no soy capaz de condensar todo en un párrafo. Lo que me gustaría es dedicarte esta última línea de mi tesis... de forma no muy profesional... porque todo esto es tuyo. Y porque todo esto no acaba nada más que empezar... no? gracias Ví.
REFERENCES


at the University of Reading, 2-5 April 2001). Blackwell

connectivity: a conservation application of graph theory.

Burkey T.V. (1989) Extinction in nature reserves: the effect of
fragmentation and the importance of migration between

Bustamante, J. (1994) Behaviour of colonial Common Kestrels
(Falco tinnunculus) during the postfledging dependence
period in southwestern Spain. Journal of Raptor Research 28:
79-83.

Bustamante, J. & Hiraldo, F. (1990) Factors influencing family
rupture and parent-offspring conflict in the Bick Kite

period of the lesser kestrel (Falco naumanni) in

during the postfledging period in the Egyptian Vulture
Neophron percnopterus (Aves, Accipitridae). Ethology 85:
225-235.

Movement parameters of ungulates and scale-specific
responses to the environment. Journal of Animal Ecology 71:
225-235.

Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001)

consequences of dispersal. Pages 307-335 in: I. Hanski, and
O. E. Gaggiotti eds. Ecology, genetics, and evolution of

University Press.

Foray search: an effective systematic dispersal strategy in

habitat boundaries in two butterfly species: implications for


Penteriani, V. (In press) When similar patterns in time emerge from different initial conditions: equifinality in the breeding performance of animal populations. *Ecological Complexity*. 

- 234 -


Resources’ Centre for Northern Forest Ecosystem Research in Thunder Bay.


UNIVERSIDAD DE SEVILLA

Reunido el tribunal en el día de la fecha, integrado por los abajo firmantes, para evaluar la tesis doctoral de D. FRAIS DE JAR, BELGÁN SÁNCHEZ, titulada "ESTUDIOS DE LA DISPERSIÓN NATAL DE VINO ESPACIO DE LARGA VIDA" se acordó otorgarle la calificación de cum laude sobresaliente por unanimidad.

Sevilla, a 6 de Julio de 2008

Vocal,

D. 

Vocal,

D. 

Vocal,

D. 

Presidente,

D. 

Secretario,

D. 

Doctorando,

D.
La dispersión natal de los animales, así como las diferentes estrategias de comportamiento de los individuos durante esta fase de su ciclo de vida, es un factor clave en la dinámica, la distribución espacio-temporal, en la estabilidad y en la probabilidad de extinción de las (meta)poblaciones. Dado que las decisiones individuales durante la dispersión son el resultado de múltiples y complejas interacciones entre factores externos e internos, a diferentes escalas espaciales y temporales, he centrado mi tesis en el estudio de los efectos que las características del hábitat, la condición física de los individuos, así como sus habilidades cognitivas y de aprendizaje ejercen sobre las estrategias de movimientos durante la dispersión en una especie de larga vida, el búho real (*Bubo bubo*).

*Palabras claves:* análisis fractales, aprendizaje, búho real, estrategias de movimiento, experiencia, familiaridad, redes espaciales complejas, síndromes comportamentales.