Sci Nat (2015) 102:21
DOI 10.1007/s00114-015-1271-x

ORIGINAL PAPER

# Quantifying space use of breeders and floaters of a long-lived species using individual movement data

**Vincenzo Penteriani**[1,2] · **Maria del Mar Delgado**[2,3] · **Letizia Campioni**[4]

Received: 14 November 2014 / Revised: 29 January 2015 / Accepted: 18 March 2015

**Abstract** To date, animal movement studies have mostly analysed the movement behaviours of individuals at specific times of their lives, but we lack detailed information on how individual movements may be affected by the various and different changes that individuals experience throughout their life (e.g. life history phases, experience, age). Here, we attempt to identify differences in home range and movement behaviour between two different statuses, disperser vs. breeder, of a long-lived species (the eagle owl *Bubo bubo*). Information on home range and movement behaviour between different stages of an individual life are crucial for species conservation and management, as well as for basic knowledge on space use and rhythm of activity. Does the transition from an exploratory stage to moving within more familiar surroundings call for changes in the movement behaviour? We observed notable differences during the two stages of the owls' lives, with individuals having different home range behaviours and rhythms of activity depending on their social status. Significant differences in home range behaviour between the sexes began only with the acquisition of a breeding site. Breeders showed larger home ranges than dispersing individuals, although nightly variation of home ranges size was higher for dispersers than for breeders. Finally, dispersers were active throughout the night, whereas breeders displayed a less active movement phase at both the beginning and end of the night. Our results demonstrate it is important to consider individual variations in space use and movement behaviour due to the different life history phases that they attain during their lifetime. The knowledge of the different needs of a species across life stages may represent an important tool for species conservation because each phase of an individual life may need different requirements.

**Keywords** Animal movement · Dispersal · Floaters · Home range behaviour · Rhythms of activity · *Bubo bubo*

## Introduction

Most of the fundamental theories, mechanisms and patterns in which animal ecologists have long been interested are implicitly related to the way animals move. The ideal free distribution, optimal foraging, island biogeography and metapopulation theories, predator–prey interactions, density-dependence reproduction and dispersal, competition and facilitation between species, survival, Allee effect, mating strategies and sperm competition, to name just a few, are the result of animal displacements.

The ubiquitousness of movement in the field of animal ecology explains the interest in this topic and, even more, the emergence of the movement ecology paradigm (Holyoak et al. 2008; Nathan et al. 2008). Although animal movement has been the focus of theoretical and empirical work over the last 25 years (Schick et al. 2008), the movement ecology discipline has developed into a well-recognized branch of

Communicated by: Sven Thatje

✉ Vincenzo Penteriani
penteriani@ebd.csic.es

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

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

[3] Metapopulation Research Group, Department of Biosciences, University of Helsinki, 00014 Helsinki, Finland

[4] Eco-Ethology Research Unit, ISPA, Rua Jardim do Tabacco 34, 1149-041 Lisbon, Portugal

wildlife science during the last decade (Holyoak et al. 2008; Nathan et al. 2008; Morales et al. 2010; Nathan and Giuggioli 2013), rapidly becoming a flourishing area of research embracing almost any aspect of animal ecology.

To date, the main objectives of movement studies have been to relate (a) different environments, phenotypes, past experiences, memories or personalities (e.g. Fraser et al. 2001; Dall et al. 2004; Fauchald and Tveraa 2006; Frair et al. 2007; Fagan et al. 2013) and/or (b) individual quality (Martin et al. 2008, 2012; Delgado et al. 2010) to different individual behaviours, namely: (i) long-distance journeys such as natal dispersal, migration and erratic displacements (e.g. Alerstam 2006; Haydon et al. 2008; Morales et al. 2010), (ii) home range behaviour and, more generally, space use (e.g. Moorcroft et al. 2006; Borger et al. 2008; Smouse et al. 2010; Campioni et al. 2013; Potts et al. 2013); (iii) group movement and consequent dynamics of social animals (e.g. Fryxell et al. 2007; Haydon et al. 2008); (iv) population dynamics and viability (e.g. Patterson et al. 2008; Morales et al. 2010) and (v) applied ecology and conservation practices (e.g. Nathan et al. 2008). These studies have mostly analysed the movement behaviours of individuals at specific times of their life. Yet, we still lack detailed information on how individual movements may be affected by the changes that individuals experience at specific times of their life. In the same way that we cannot calculate fitness for an individual without considering all that occurs across that individual's lifetime, movement cannot be considered fully without better understanding different movement phases.

Different stages characterize individuals during their lifetime, including (i) juvenile dispersal, when individuals facing unknown environments perform exploratory movement behaviours, (ii) the acquisition of a breeding site and mate, which marks the beginning of a life in a more restricted area, (iii) reproduction, during which the individual has to confront new and constraining tasks, as well as (iv) senescence, which may involve an important reduction of activities and a change in social status. Evidence shows that different individuals with the same life history phases may vary in their movement behaviour (e.g. Fraser et al. 2001; Dingemanse et al. 2003; Delgado and Penteriani 2008). Therefore, we expect that individuals of different status (e.g. breeders vs. dispersers) may show an even greater disparity in their movement behaviours.

Here, we attempt to identify differences in home range and movement behaviours of a long-lived species (the eagle owl *Bubo bubo*) between life stages by comparing the disperser vs. the breeder status. Dispersers are mainly juvenile individuals searching for breeding opportunities after they have left their birthplace and started natal dispersal. In contrast, breeders are those individuals that settled on suitable place to reproduce, become owner of a breeding site and mate, thus obtaining a new social status that in most cases will be maintained until death. One basic question exemplifies our approach to understanding changes in movements between life stages: does the transition from an exploratory stage to moving within more limited and familiar surroundings call for changes in the movement behaviour of individuals? We hypothesize that dispersers facing novel environments should exhibit more dynamic and complex space use and activity pattern rhythms than breeders (Borger et al. 2008; Delgado et al. 2009; Berger-Tal and Avgar 2012). Actually, breeders are assumed to have a perfect knowledge of the landscape in which they move, especially in stable environments (Berger-Tal and Avgar 2012) and need to deal with the reproductive duties they acquire when they shift from the solitary lifestyle of a disperser to the status of territory owner and mated individual. By addressing this question, we attempt to identify the key life history traits, behaviours, and external factors determining movement, keeping in mind that the social status of individuals may crucially impact the way in which they use space.

## Methods

With the aim of highlighting differences in home range behaviour and movements depending on the social status of individuals of a same population, below we present separately breeders and dispersers, the latter group being composed of individuals floating in the vicinity of the breeding sector (Penteriani and Delgado 2012). We defined floaters as the entire pool of dispersing individuals independent of age (Penteriani and Delgado 2012) given that (a) they are sexually mature at less than 1 year old and (b) dispersing owls remain 'floating' in the vicinity of the breeding population during dispersal. Although the definition of floaters is not commonly based on their dispersal status, floating individuals moving in the vicinity of, or within, nesting sites may also be considered as dispersers until they first reproduce (Penteriani et al. 2011a).

## Data collection

### The breeding population

The breeding population inhabited a hilly area of the Sierra Norte of Seville (Sierra Morena massif) located in southwestern Spain. From 2004 to 2010, 29 breeding individuals (20 males and 9 females) from 24 nests were radiotracked. We trapped breeding individuals using two different methods (see Penteriani et al. 2007, 2008, 2010, 2011b and Campioni et al. 2013 for more details): (1) by simulating an intrusion using a taxidermic mount and playback of a male call and (2) by utilizing a bow-net placed in the nest when nestlings were 20–35 days old. Each individual was fitted with a 30-g radio-transmitter using a Teflon ribbon backpack harness

(Biotrack, UK; http://www.biotrack.co.uk). The backpack mass was <3 % of the mass of the smallest adult male (1550 g) in our population (mean±SE=1667±105 g). The transmitters included a mercury posture sensor to record individual activity through changes in signal frequency. We followed breeders individually (one focal individual per night) throughout the whole night (from 1 h before sunset to 1 h after sunrise; total time duration=3333 h) during 296 continuous radiotracking sessions (i.e. during the whole night; range per individual=1–25 nights; mean±SD=10.5±6.7 nights; range for males=1–25 nights, mean±SD=12.5±6.9 nights; range for females=2–14 nights, mean±SD=6.4±4.0 nights). We recorded a new location (total number of locations=5298) each time we detected a change in the position of the focal individual (mean number of locations per radiotracking session±SD=17.2±5.2). The continuous radiotracking sessions (mean time duration of a radiotracking session±SD=11.3±1.8 h) were performed year-round. The locations of radiotagged individuals were determined by triangulations using three-element hand-held Yagi antennae (Biotrack) with Stabo (XR-100) portable ICOM receivers (IC-R20). The error in radiotracking localizations (mean±SE=83.5±49.5 m) was calculated by doing fixes of focal transmitters located randomly within the study area by the authors.

## The dispersing population

During the period 2003–2007, we studied the movement and behaviour of 40 juveniles (males=30, females=10) from 12 different nests during natal dispersal in an area of ~70,000 ha located in the vicinity of the breeding population (Penteriani and Delgado 2012). The owlets were tagged when they were ~35 days old and their radiotracking started as soon as they began natal dispersal (at the end of August, mean age at the beginning of dispersal=170±20.5 days, range=131–232 days; Delgado et al. 2010). We used the same radiotracking equipment and procedures detailed above for breeders. At the time of tagging, the weight of the transmitter was still less than 3.5 % of the smallest fledgling's weight (850 g; mean±SD=1267±226.4 g). The owls were aged following Penteriani et al. (2005) and sexed by molecular procedures using DNA extracted from their blood (more details in Bettega et al. 2013). At the nightly temporal scale (*n*=178 tracking sessions for a total of 2010 h), a focal owl was tracked continuously from 1 h before sunset to 1 h after sunrise (the mean time duration of tracking sessions±SD=11.3±2.1 h). Each night, we recorded locations (total number of locations=3196) each time that we detected, by means of a posture mercury sensor, a change in individual posture or position (mean number of locations per radiotracking session±SD=18±4.6). Individuals were tracked on a rotational basis throughout the year, i.e. before to start an additional night of radiotracking for a given owl, we previously performed one radiotracking night for all the other individuals. During the 5-year study period, individuals were tracked on 163 nights (range per individual=1–13, mean±SD=4.1±3.2; range for males=1–11, mean±SD=3.6±2.6; range for females=1–13, mean±SD=5.3±4.5; more details on the distribution of the tracking sessions among the dispersal phases and between sexes in Penteriani and Delgado 2012). In this study, we analysed the behaviour of radiotagged eagle owls during the dispersal phases of wandering (i.e. the first, exploratory phase of natal dispersal) and settlement (i.e. when an individual settles in one or more temporary areas during the dispersal process; see also Delgado and Penteriani 2008; Delgado et al. 2010 and Penteriani and Delgado 2011, 2012).

## Home range behaviour

For each night of radiotracking (i.e. from time since the bird left its nest or resting perch at the beginning of the night to the time it returns to its nest or to a resting perch at the end of the night), we first estimated the home range size through fixed-kernel methods (Worton 1989) using the Animal Movement Extension for ArcView 3.2 (Hooge and Eichenlaub 2000). We calculated the 90 % fixed kernels using the least squares cross-validation procedure (Silverman 1986) to determine the optimal value of the smoothing parameter for a given kernel and sample size (Seaman et al. 1999). The least squares cross-validation process generates the best value of the smoothing parameter for multimodal data with respect to the other methods (Silverman 1986; Worton 1989; Seaman and Powell 1996). To establish home range boundaries, we selected the density isopleth value of 90 % because it better fitted our data (Campioni et al. 2013). In fact, when visually exploring both 90 and 95 % isopleths, the density isopleth values of 95 % over-estimated the areas crossed by tagged individuals (results not shown). For each night and individual we used all data available, focusing more on the biological process that shaped home range internal structure (De Solla et al. 1999) than on obtaining statistical independence of the relocations. This was possible because we followed each focal owl during the entirety of its nocturnal activity, thus recording its full set of movements. In five cases, different individuals bred in the same nesting area in following years, thus representing a 'natural experiment' which allowed the response of different individuals to the same environment to be determined. Different individuals successively occupying the same area might show similar home range and movement behaviour. Second, with the aim of characterising the internal structure of each home range, for each night, we estimated the size of core areas (based on the 50 % isopleth), i.e. those areas most frequently used within the home range. Because it was not always possible to distinguish between the core area of the nest and the core area(s) where individuals foraged, core area(s) represented both nesting and hunting areas (Campioni et al. 2013). Finally, using the Animal Movement Extension for ArcView

3.2, we estimated the percentage of home range area overlap for each night: (a) of neighbouring breeders; (b) of neighbouring floaters; (c) between sexes of neighbouring individuals; (c) between two different individuals occupying the same nesting site; and (d) when home ranges belonged to the interior or the border of the breeding population. For comparisons on home range sizes and overlaps, we also separated the breeding population in two spatially separated sub-units, i.e. the interior (i.e. the area with the highest density of breeding sites, generally <1 km between neighbouring pairs) and the border of the breeding population, which includes the nesting sites closest to the floater settlement areas and a slightly smaller density (generally >1 km between neighbouring pairs).

## Movement behaviour

We first analysed the nocturnal movement behaviour of tagged owls by using two descriptive indices of individual activity rhythms within core areas (Campioni et al. 2013): (1) core area activity, i.e. the time an owl spent inside the core area(s) and (2) individual movement rates, calculated as the movement frequencies within core areas. Core area activity is a measure of the time devoted to main activities, such as hunting, feeding (including nestling/fledgling feeding and female feeding during breeding if the focal owl was a breeding male), and territorial defence. Because night lengths vary over the course of a year, we standardised the core area activities and movement rates per night by dividing them by the total time the individual was active each night. Movement rates within core areas were standardised to account for the total amount of movements performed by the focal individual per night.

We then identified differences in behavioural modes between breeders and floaters. One way to determine behavioural changes along an animals' movement trajectory is to measure the residence time (RT; Barraquand and Benhamou 2008), which is defined as the time required for an animal to cross a circle of a given radius *r*. This tool has been used to identify intensive spatial use, especially area-restricted search, as well as other spatially restricted behaviours (Gurarie et al. submitted). We selected RT because (i) of its simplicity, (ii) it has been demonstrated to be a useful quantity to determine different movement behaviours (but see Barraquand and Benhamou 2008), and (iii) it does not require any *a priori* assumptions. As RT may be sensitive to irregular sampling data, we performed a simple smoothing of the data using linear interpolation to minimize the impact of noisy signals (Calenge 2006), so that the time lag between successive locations was constant (60 min). We selected a radius approximately equal to the mean size of core areas (150 m; Campioni et al. 2013), such that the behavioural partitioning allowed us to directly relate it with different individual activities (e.g. time invested in defending the territory or foraging). As we aim at comparing behavioural modes between breeders and floaters, we combined all trajectories of each category to compute average RT values. RT was implemented with the R package (R Development Core Team 2009) called waddle (Gurarie et al. submitted), which depends on adehabitatLT (Calenge 2006).

## External factors

We used two variables to determine the possible influence of external factors on home range and movement behaviours of breeders and floaters. First, as diet analyses (Penteriani et al. 2008; Campioni et al. 2013; Lourenço et al. submitted) showed that the rabbit *Oryctolagus cuniculus* is the main prey of our eagle owl population (mean biomass percentage of rabbit in the diet±SD=62.0±19.1 %, range 16–94 %), we considered rabbit abundance within the home ranges of tagged individuals as an indicator of habitat quality (González et al. 2008). The relative rabbit abundance was estimated in both breeder and floater home ranges using rabbit faecal pellet counts (i.e. latrine counts). To obtain comparable indices of prey abundance (IKA) for each home range, we drew a circular plot centred on the nest with an area equal to the mean eagle owl home range size in our study population (ca. 200 ha; Campioni et al. 2013). Inside these plots, we walked 2.2-km-long transect lines (total length of transects walked=150 km), recording the number of latrines observed on both sides of each transect within a distance of 4 m (total number of latrines counted=3,440 latrines; mean±SE=20.6±12.4 $\text{km}^{-1}$; range 7.7–46.0 $\text{km}^{-1}$). The IKA was expressed as the number of latrines per km of transect. In addition, we used edge density (i.e., the total length of the patch edge per unit area within each landscape; Elkie et al. 1999) as a proxy for the effect of habitat heterogeneity (Kie et al. 2002; Anderson et al. 2005), which in previous analyses was found to be highly correlated with the home range behaviour of owls (Delgado et al. 2010; Campioni et al. 2013). The GIS application ArcView 3.2 and its extension Patch Analyst (Elkie et al. 1999) were used to estimate this latter measurement.

## Statistical analyses

To test the effects of individual status (breeder vs. floater) and sex, as well as external factors, on home range and movement behaviours, we used multilevel models. Total nightly home range, core area activity and nightly movement rates were modelled with linear mixed-effect models fit by maximum likelihood. To ensure normality, total nightly home range size was log transformed, and core area activity and nightly movement rates were square-root transformed. Following Pinheiro and Bates (2004), the values of random effects were estimated using the Akaike information criterion (AIC). The best random model was found to be the two-term random effect represented by individual nested in nest for the linear mixed-effect models, and three-term random effects represented by night of radiotracking nested in individual nested in nest for the linear mixed-effects models. As suggested by Crawley (2007), model simplification was performed by the backward selection of variables from the full model, and models were compared using likelihood ratio tests until a minimal adequate model was obtained. Residuals of the final models were explored for normality and homogeneity assumptions (except for the generalized linear models). All statistical analyses were performed using R 2.10.1 statistical software (R Development Core Team 2009) with nlme (Pinheiro et al. 2009) and lme4 (Bates and Maechler 2009) packages. Statistical significance was set at $\alpha<0.05$. *t* tests, paired-samples *t* tests and ANOVAs were used to assess differences in home range size and overlap of breeders vs. floaters (as a whole and separated in the two dispersal phases) and between sexes.

## Results

### Home range behaviour

The average breeder home range size ($n=283$ nights, 225 and 58 nights for males and females, respectively) was ~1/3 larger ($t_{27}=-1.69$, $p=0.10$) for females ($n=9$ individuals) than for males ($n=20$ individuals; Table 1). The difference between sexes was even smaller (and not significant) for floaters (Table 1), which showed an inverse pattern, with slightly larger home ranges for males (112 nights and 30 individuals) than for females (50 nights and 10 individuals; Table 1). The size of the home ranges of those breeders located in the interior of the population ($n=13$, mean±SD=$1.8\pm1.4$ km$^2$) was not significantly different ($t_{27}=-1.25$, $p=0.22$) from the home range size of those individuals located on the border ($n=16$, mean±SD=$2.5\pm1.7$ km$^2$). Variations in home range size among different individuals were significantly higher than nightly variations of the same individual: (i) for both breeders ($F_{22,233}=4.09$, $p=0.0001$) and floaters ($F_{36,\,122}=1.70$, $p=0.015$), although in the latter case nightly variations of home range size were larger; and (ii) for different individuals that consecutively occupied the same breeding site ($F_{11,\,101}=2.18$, $p=0.02$).

The percentage of home range overlap among breeders was significantly higher ($t_{2870}=12.83$, $p=0.0001$) than among floaters ($n=192$; Table 1); similarly, the percentage of overlapping area among breeders, wandering and settled floaters was significantly different ($F_{2,2869}=90.64$, $p=0.0001$). Significant differences were also detected in the area of overlap (Table 1) among dispersal phases ($t_{187}=3.01$, $p=0.003$),

**Table 1** Size of home range (km$^2$) and percentage of overlap (%; mean±SD and range) and activity rhythms of breeders ($N=29$) and floaters ($N=40$) of the same eagle owl population

| Home range size (km$^2$) | Overall | Males ($N=20$) | Females ($N=9$) |
|---|---|---|---|
| Breeders | 2.3±4.0 (0.6–44.4) | 2.1±3.9 (0.6–44.4) | 2.8±4.0 (1.2–19.5) |
| | Overall | Males ($N=30$) | Females ($N=10$) |
| Floaters[a] | 1.6±1.3 (0.1–6.9) | 1.6±1.4 (0.1–6.9) | 1.3±1.3 (0.1–6.5) |
| Overlap (%) | Overall | Males | Females |
| Breeders | 20.0±21.3 (0.0–100.0) | 21.1±21.5 (0.0–100.0) | 12.9±18.2 (0.1–100.0) |
| | Overall | Males | Females |
| Floaters[b] | 11.7±19.2 (0.0–85.3) | 10.6±17.8 (0.0–69.9) | 14.2±21.9 (0.0–85.3) |
| Core area activity (min)[c] | Overall | Males | Females |
| Breeders | 257.3±186.9 (0.0–818.0) | 256.2±182.8 (0.0–818.0) | 262.2±205.0 (0.0–715.0) |
| | Overall | Males | Females |
| Floaters | 401.6±151.3 (110.0–761.0) | 409.6±148.3 (149.0–761.0) | 384.1±159.3 (110.0–677.0) |
| Rate of movements in the core areas[d] | Overall | Males | Females |
| Breeders | 4.2±3.7 (0–20) | 4.2±3.5 (0–20) | 4.4±4.4 (0–14) |
| | Overall | Males | Females |
| Floaters | 73.6±35.2 (24.0–127.0) | 82.1±38.6 (24.0–127.0) | 55.0±13.8 (28.0–64.0) |
| Rate of nightly movements[e] | Overall | Males | Females |
| Breeders | 0.03±0.01 (0.01–0.06) | 0.03±0.01 (0.01–0.06) | 0.03±0.01 (0.01–0.04) |
| | Overall | Males | Females |
| Floaters | 0.03±0.01 (0.01–0.05) | 0.03±0.03 (0.01–0.04) | 0.03±0.01 (0.03–0.05) |

[a] Wandering phase, overall: 1.5±1.5 km$^2$ (0.1–6.5 km$^2$); settlement phase, overall: 1.5±1.3 km$^2$ (0.1–6.9 km$^2$)

[b] Wandering phase, overall: 14.7±20.3 % (0–73.3 %); settlement phase, overall: 9.3±18.0 % (0–85.3 %)

[c] The time an individual spent inside the core area(s)

[d] Number of movements within the core area(s)/length of the night

[e] Number of movements/length of the night

with higher values during the wandering (14.7±20.3 %) than the settlement (9.3±18.0 %) phase, but not between male ($n$=133) and female ($n$=59) floaters ($t_{187}$=−0.88, $p$=0.38). The percentage of breeder home range overlap for males ($n$=2319) was twice ($t_{2814}$=12.93, $p$=0.0001) that of females ($n$=497; Table 1). Moreover, the interaction between sexes was also significant ($F_{2,2868}$=49.62, $p$=0.0001; see also Figs. 1, 2 and 3), as the percentage of overlapping area between males (mean±SD=22.7±22.9 %) was higher than between females (14.7±14.8 %) and male–female (13.3±17.9 %). There were no significant differences in the percentage of overlapping area ($t_{2687}$=−0.34, $p$=0.74) between home ranges located in the interior and on the border of the breeding population. In addition: (i) when a paired-samples $t$ test was conducted to compare the home range size between two different occupancies of a same breeding place, there was a significant difference in the scores for only two ($t_8$=−4.16, $p$=0.003 and $t_6$=3.23, $p$=0.02) out of five successive occupancies of a same breeding places and (ii) when comparing the percentage of overlapping area of two different individuals occupying and breeding in the same nesting place, the mean values (mean±SD=40.1±29.6 %, range 0.5–100 %, $n$=935) were significantly higher ($t_{3621}$=−21.85, p=0.0001) than when overlap occurred among neighbouring owls (Table 1).

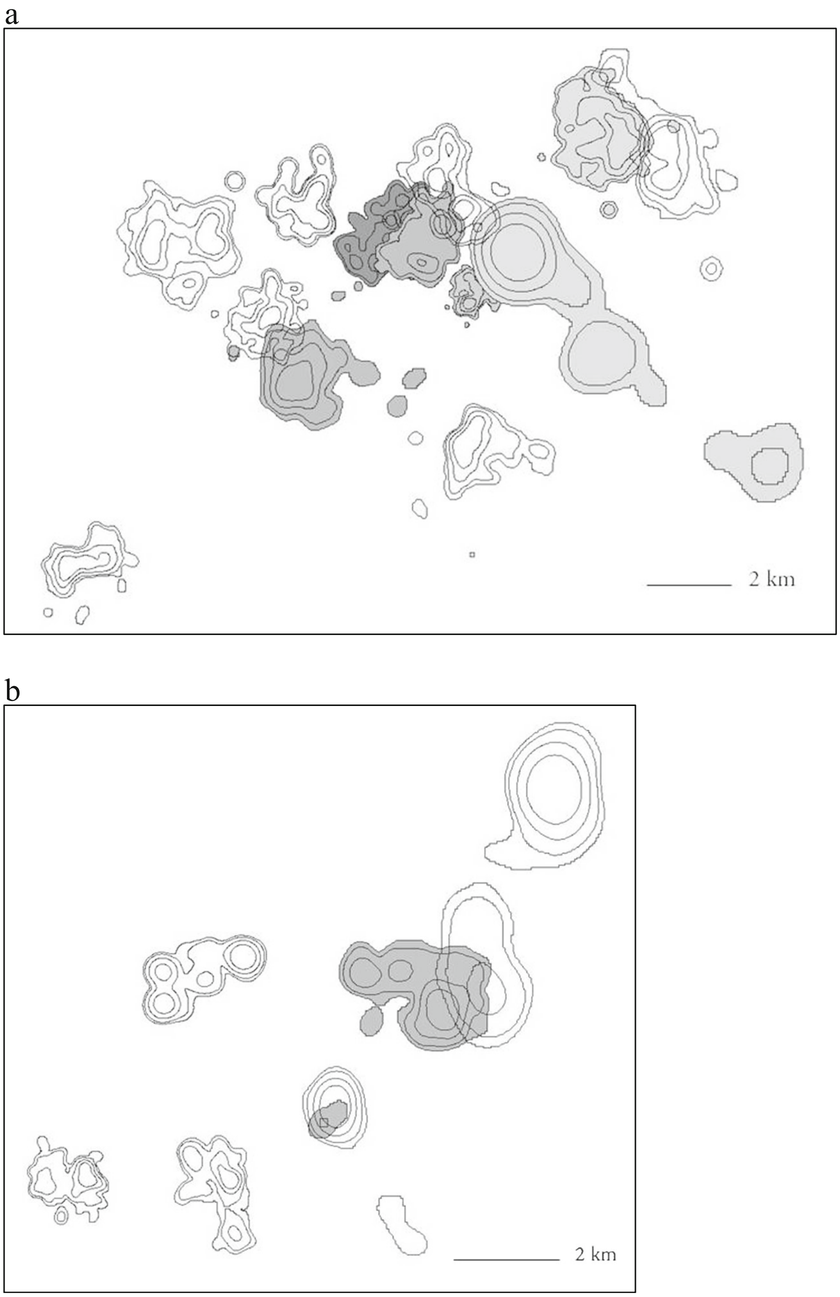
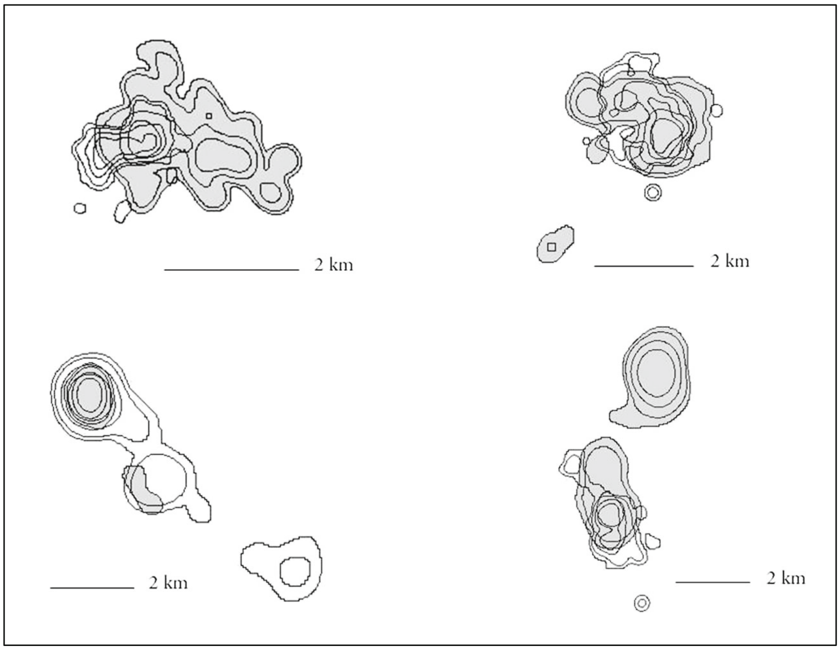


**Fig. 1** Spatial distribution and overlap of home ranges, calculated using the least squares cross-validation procedure (based on 95, 90, 75 and 50 % isopleths) of breeding males (**a**) and females (**b**). *Different shades of grey* are used to differentiate individuals when they overlap each other

**Fig. 2** Example of spatial distribution and overlapping areas of home ranges (based on 95, 90, 75 and 50 % isopleths) between males (*white*) and females (*grey*) of the same pair ($n$=4 pairs)



Finally, the social status of individuals and landscape heterogeneity had an effect on the home range of eagle owls (Table 2): (a) breeders showed larger home ranges than floaters and (b) an increase of landscape heterogeneity (i.e. higher values of edge density) determined smaller home ranges.

### Movement behaviour

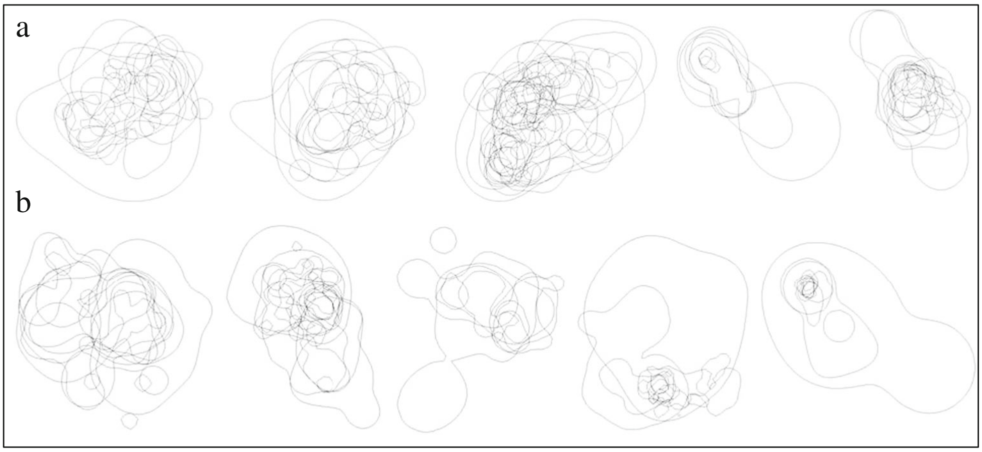
Similarly to home ranges, status and landscape heterogeneity affected individual movement behaviours (Table 2): (a) floaters showed higher activity levels within their core areas than breeders and (b) heterogeneous landscapes increased activity within the core areas (e.g. residing in an area of greater landscape heterogeneity may be more profitable).

The RT analysis revealed a clear distinction between breeder and floater movement behaviours (Fig. 4). Breeders generally switched their movements between a less active phase at the beginning of the night (where residence time took more than an hour) to a more active phase during the central hours of the night (RT=30 min), and finally again to a more stationary phase at the end of the night (RT=1 h). The transition times occurred at 21:00 (A to B) and at 5:00 (B to A; Fig. 4). However, floaters had a unique active phase during the whole night, where RT always took less than an hour.

## Discussion

The classic home range size literature (Andersson 1981; Schoener 1983) has considered resource density (Barraquand and Benhamou 2008) and its spatial distribution (MacDonald 1983), latitudinal gradients (Morellet et al. 2013) and landscape attributes (Kie et al. 2002) among some

**Fig. 3** Some examples of how the different home ranges of a same individual (**a**=males; **b**=females) overlap among the different nights of radiotracking. Males showed a tendency to move more frequently than females in the same area, whereas females showed nightly explorations of areas farther from the core of home ranges more frequently than males



other predictors to explain differences in home range characteristics. Here, through the analysis of the space use of individuals, we demonstrated notable differences during two of the life stages of an eagle owl's life, with individuals displaying different home range behaviours and rhythms of activity depending on their social status (i.e. breeders vs. floaters).

Firstly, appreciable differences in home range behaviour between the sexes began only with the acquisition of a breeding site (no significant intersexual differences were noted among floaters). In addition, the percentage of breeder home range overlap was higher for males than for females and males-females. During their dispersal period, males and females showed similar home range features (see also Penteriani and Delgado 2012), probably because individuals do not have any territorial and/or reproductive objectives when in their dispersal grounds. However, when owls establish a breeding area and mate, their new tasks (which are very different between sexes) may engender differences in home range behaviour, with females (the less territorial sex in eagle owls; Penteriani et al. 2007) being able to move more freely than males and, consequently, having larger home ranges. Space use strategies largely driven by conspecific avoidance are evolutionarily stable (Barraquand and Murrell 2012), as movements driven by conspecific avoidance have the potential to lead to relatively large home ranges with a rather large home range overlap between individuals, which is not the most optimal way of partitioning the resource (Moorcroft et al. 2006). In our study system, we expect that male space use strategies are driven by high conspecific avoidance. However, even though we detected the emergence of considerable home range overlap, males had small home ranges. Our results are consistent with those reported by Barraquand and Murrell (2012), who found that greater territoriality will in general select for small home ranges, in contrast to the carnivore system described by Moorcroft et al. (2006). This is probably due to the fact that space use in eagle owls is modulated through territorial displays of males, and we can assume this sex, given its territorial and reproductive tasks, experiences the highest costs for travelling away from the nest (Barraquand and Murrell 2012). The high frequency of contests among neighbouring males (Delgado and Penteriani 2007) might be determining the high percentage of home range overlap between males, as well as the higher percentage of home range overlap for breeders than for floaters, whose males do not confront each other in vocal duetting or chorus singing. We hypothesise that benefits of social behaviours like territorial displays (e.g. fight avoidance) may become costs when two individuals share a large portion of their home range (e.g. resource depletion): within the shared space individuals compete over resources (Rieucau and Giraldeau 2011).

Secondly, breeders exhibited larger home ranges than floaters, with higher nightly variation of home range size. Again, such variations in home range behaviour may reflect status-dependent needs and constraints, which we suspect are mostly related to the breeding cycle. For example, during their long breeding cycle, male breeders have to establish a home range large enough to provide food not only for themselves, but also the incubating female (who will spend more than one

**Table 2** Linear mixed-effects models fit by maximum likelihood showing the effect of status (breeder vs. floater), sex of the individual and external factors on movement patterns and activity rhythms of eagle owls. Each model has been run for breeders vs. floaters as a whole and breeders vs. wandering floaters vs. settled floaters (see text for more details concerning the phases of natal dispersal)

| | Estimate | SE | DF | *t* | *P* |
|---|---|---|---|---|---|
| [1]Log(total nightly home range[a]) | | | | | |
| Intercept | 0.52 | 0.14 | 287 | 3.77 | <0.0001 |
| Status[b] | 2.09 | 0.23 | 19 | 9.18 | <0.0001 |
| Edge density | −0.01 | 0.00 | 287 | −12.85 | <0.0001 |
| [2]Log(total nightly home range[a]) | | | | | |
| Intercept | 3.15 | 0.30 | 287 | 10.38 | <0.0001 |
| Status[b] | −0.89 | 0.12 | 287 | −7.49 | <0.0001 |
| Edge density | −0.01 | 0.00 | 287 | −11.77 | <0.0001 |
| [1]Sqrt(core area activity[c]) | | | | | |
| Intercept | 18.88 | 0.86 | 287 | 21.94 | <0.0001 |
| Status[b] | | −9.35 | 1.53 19 | −6.12 | <0.0001 |
| Edge density | 0.03 | 0.01 | 287 | 3.74 | <0.0001 |
| [2]Sqrt(core area activity[c]) | | | | | |
| Intercept | 7.03 | 2.01 | 287 | 3.50 | <0.0001 |
| Status[b] | 4.18 | 0.75 | 287 | 5.61 | <0.0001 |
| Edge density | 0.02 | 0.01 | 287 | 2.83 | <0.0001 |
| [1]Sqrt(nightly movement rates[d]) | | | | | |
| Intercept | 0.17 | 0.00 | 287 | 31.00 | <0.0001 |
| Status[b] | 0.01 | 0.00 | 16 | 1.22 | 0.24 |
| Edge density | −0.00 | 0.00 | 287 | −2.03 | 0.06 |
| IKA[e] | 0.00 | 0.00 | 16 | 0.80 | 0.44 |
| Sex | −0.01 | 0.01 | 16 | −0.84 | 0.42 |
| [2]Sqrt(nightly movement rates[d]) | | | | | |
| Intercept | 0.18 | 0.01 | 286 | 19.12 | <0.0001 |
| Status[b] | −0.00 | 0.00 | 286 | −1.11 | 0.27 |
| Edge density | 0.00 | 0.00 | 286 | −2.32 | 0.06 |
| IKA[e] | 0.00 | 0.00 | 18 | 0.99 | 0.33 |
| Sex | −0.00 | 0.01 | 18 | −0.27 | 0.79 |

[1] Model considering the floaters as a whole

[2] Model considering the floaters separated in the two distinct phases of natal dispersal, i.e. wandering and settlement

[a] Total nightly home range for each individual, calculated from the whole set of locations of one night (km$^2$ ) ($N$=257)

[b] Breeder or floater

[c] Time an owl spent inside the core area(s) ($N$=257)

[d] Individual movement frequencies per night ($N$=257)

[e] Index of rabbit abundance

month incubating and most of the nestling period in the nest) and chicks (which may number up to four; Campioni et al. 2013). On the other hand, the characteristics of the floater's home range may mirror the solitary lifestyle of these dispersing individuals (Penteriani and Delgado 2012), which (i) only need to provide food for themselves; (ii) do not have constraining tasks to undertake during the night and (iii) the absence of territorial contests/objectives allows them to move with less restrictions than breeders.

Finally, breeders and floaters exhibited clearly distinct movement behaviours: (i) floaters were always active throughout the night, whereas breeders showed a less active movement phase at both the beginning and end of the night and (ii) floaters displayed higher activity levels within their core areas than breeders. Recent studies have demonstrated that individual specialization in movement patterns exists in animal populations. These differences may be the result of different learning experiences and cognitive abilities, variation in body mass and the energetic state of the individual (e.g. Papastamatiou et al. 2011). In addition to this, different behaviours may correspond to different phases of an individual's life. As different movement behaviours will ultimately reflect

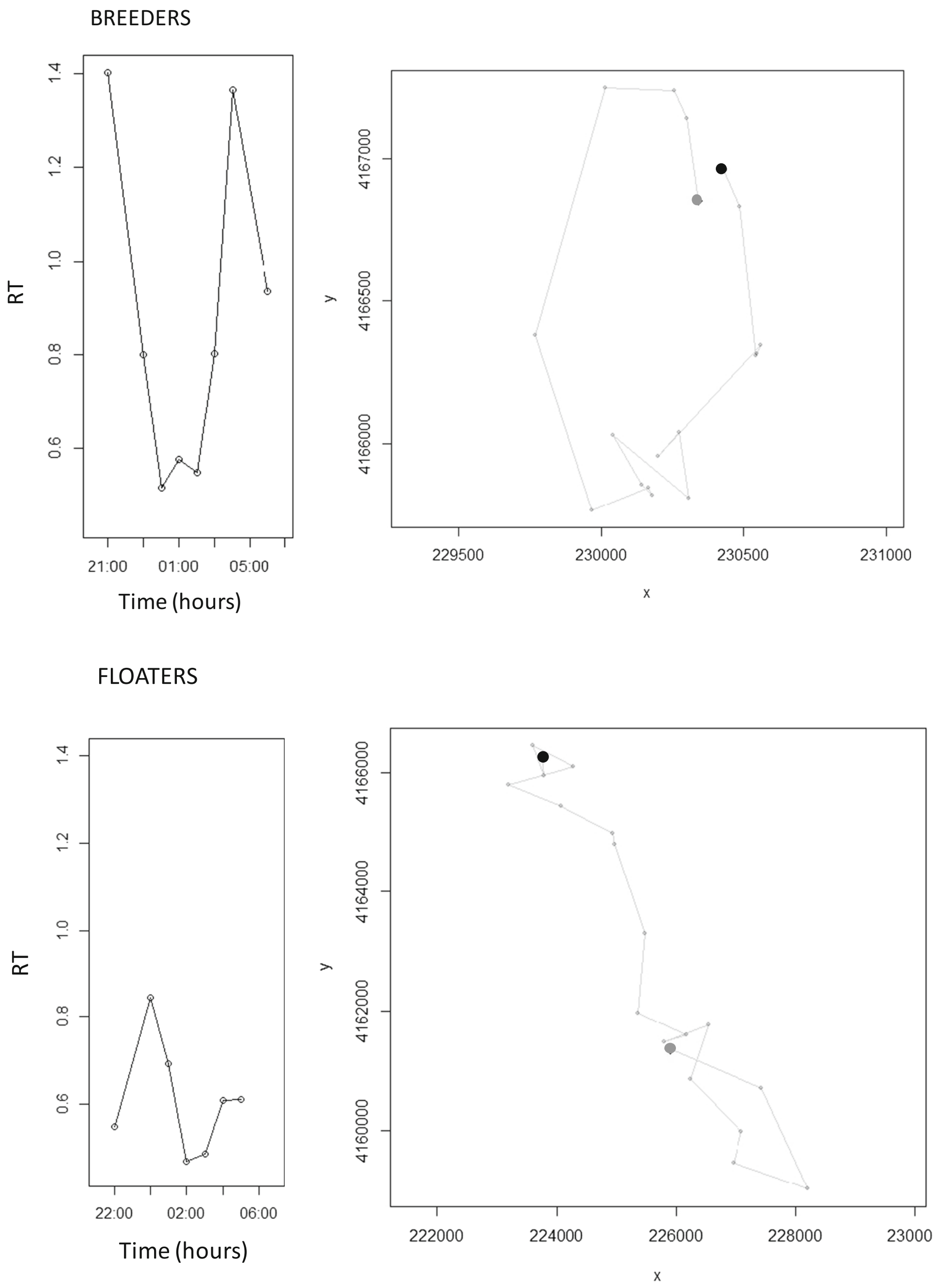


**Fig. 4** On the left are the plots of residence time (RT) values averaged over all nights of tracking breeders (upper panel) and floaters (lower panel) for radius equal to 150 m as a function of time (hours) during the night. On the *right-hand side* are corresponding examples of the movement trajectories for a breeder and a floater. *Black* and *grey dots*, respectively, indicate the starting and ending point of each trajectory

the ability of individuals to react to their experiences as they move (Dall et al. 2005), it is important to understand when and under which circumstances different movement patterns will be displayed. We observed that animals clearly switch their movement behaviours between life stages: for animals confronting novel environments acquiring information about the environment is critical, as informed individuals are more successful than those without the relevant experience in almost all aspects of their life cycle (Berger-Tal and Avgar 2012), e.g. they are better foragers (Rutz et al. 2006). An individual in a novel environment (e.g. a disperser) is expected to first pay a cost (e.g. predation risk, energetic expenditure) for high exploration rates, which in later stages will be superseded by the benefits of information (Berger-Tal and Avgar 2012), e.g. when the disperser settles within a more stable home range or attains reproductive status (Delgado et al. 2009). Such high exploration rates of floaters were clearly highlighted by the RT analysis, which revealed that wandering floaters generally had higher levels of activity throughout the night than breeders. Spatial memory and learning allow animals to move through landscapes as efficiently as possible (Saarenmaa et al. 1988; Vuilleumier and Perrin 2006; Fagan et al. 2013). Individuals are not considered to have a priori information on their surroundings (e.g. Vos et al. 1998; Stamps and Krishnan 1999), and thus, they need time to acquire such knowledge; consequently, they adopt some site-specific mechanisms or rules which allow them to optimally exploit habitat patches (Stamps 1995; Thield and Hoffmeister 2004; Dall et al. 2005). The different levels of information breeders and floaters have concerning their surroundings is what may have been revealed by both (i) the higher activity level of floaters than breeders within core areas and (ii) the RT analysis. Floaters are more active than breeders because they still have an imperfect knowledge of the surroundings in which they move. This may imply that, although juvenile owls are not involved in the costly tasks that characterize reproduction (e.g. finding food for the family, bringing food to the nest several times per night, taking care of chicks), they still have to pay a higher cost than breeders in their day-to-day movements. This is particularly true at the beginning of dispersal, when individuals travel more frequently across unfamiliar areas, which sometimes are unfavourable landscapes where individuals have less time to become familiar with their surroundings (Delgado et al. 2009, 2010). The need of breeders to perform territorial and reproductive tasks, as well as their familiarity with the surroundings of their nest site, could contribute to the reduction in their activity level in comparison to floaters. Breeders spend large amounts of time roosting close to the nest or performing vocal displays on posts located within or close to the core areas of their home range, both for territorial demarcation and mate–mate communication (Penteriani 2002; Delgado and Penteriani 2007; Campioni et al. 2010, 2012). This represents long pauses on strategic posts for territory owners, which are not included in the time budget of floaters that essentially roost, hunt, and survey new areas (Delgado et al. 2009; Penteriani and Delgado 2012).

Animal space use and movement behaviour have been the subject of many detailed studies that have linked the way in which animals move with several spatial, temporal, and individual-level processes. It is well-known that home-range behaviour and movement activities vary with an array of landscapes and other variables such as season, reproduction, availability of food, intra- and inter-specific competition, predation risk, human activities, body size and sex (e.g. McLoughlin and Ferguson 2000; Kie et al. 2002; Jetz et al. 2004; Morales et al. 2005; Börger et al. 2006; Martin et al. 2012). In addition to this, however, we believe it is important to consider individual variations in space use and movement behaviour due to the different statuses that they attain across life stages. Indeed, each individual is the result of a series of complex, reciprocal interactions between factors that can occur throughout its lifetime and are responsible for the emergence of different patterns of behaviour (Sasha et al. 2004; Stamps and Groothuis 2010). The variation among individuals is essential to understand ecological systems (Lomnicki 1988), yet this is not sufficiently captured by the individual's attributes (e.g. sex and age, Börger et al. 2006). Quantifying individual differences in space use requires taking into account the potential influence of social status. By linking space use with the different stages an individual experiences during its life, this work adds to recent advances in the newly emerging movement ecology paradigm.

**Acknowledgments** We thank P. Bartolommei, C. Bettega and R. Lourenço for their help during radiotracking. The research adheres to the legal requirements of the country where it has been carried out. We manipulated and marked owls under Junta de Andalucía-Consejería de Medio Ambiente authorizations No. SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02. The authors do not have any conflict of interest to declare. This work was supported by the Spanish Ministry of Economy and Competitiveness (CGL2012–33240; FEDER co-financing).

**Conflict of interest** The manipulation of individuals (trapping and radiotagging) described in this paper comply with the current laws of the country in which they were performed. The authors declare that they have no conflict of interest.

## References

Alerstam T (2006) Conflicting evidence about long-distance animal navigation. Science 313:791–794

Anderson DP, Forester JD, Turner MG, Frair JL, Merrill EH, Fortin D, Mao JS, Boyce MS (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landsc Ecol 20:257–271

Andersson M (1981) On optimal predator search. Theor Popul Biol 19: 58–86

Barraquand F, Benhamou S (2008) Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. Ecology 89:3336–3348

Barraquand F, Murrell DJ (2012) Evolutionarily stable consumer home range size in relation to resource demography and consumer spatial organization. Theor Ecol 5:567–589

Bates D, Maechler M (2009) lme4: Linear Mixed-Effects Models using S4 Classes. Version 0.999375-31. http://lme4.r-forge.r-project.org/

Berger-Tal O, Avgar T (2012) The glass is half-full: overestimating the quality of a novel environment is advantageous. PLoS One 7: e34578

Bettega C, Campioni L, Delgado MM, Lourenço R, Penteriani V (2013) Brightness features of visual signaling traits in young and adult Eurasian eagle-owls. J Raptor Res 47:197–207

Börger L, Franconi N, Ferretti F, Meschi F, De Michele G, Gantz A, Coulson T (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. Am Nat 168:471–485

Borger L, Dalziel BD, Fryxell JM (2008) Are there general mechanism of animal home range behavior? A review and prospects for future research. Ecol Lett 11:637–650

Calenge C (2006) The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecol Model 197:1035

Campioni L, Delgado MM, Penteriani V (2010) Social status influences microhabitat selection: breeder and floater Eagle Owls *Bubo bubo* use different post sites. Ibis 152:569–579

Campioni L, Lourenço R, Delgado MM, Penteriani V (2012) Breeders and floaters use different habitat cover: should habitat use be a social status-dependent strategy? J Ornithol 153:1215–1223

Campioni L, Delgado MM, Lourenço R, Bastianelli G, Fernández N, Penteriani V (2013) Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. Oecologia 172:371–385

Crawley MJ (2007) The R Book. J. Wiley

Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol Lett 7:734–739

Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20:187–193

De Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. J Anim Ecol 68:221–234

Delgado MM, Penteriani V (2007) Vocal behaviour and neighbour spatial arrangement during vocal displays in Eagle owl (*Bubo bubo*). J Zool 271:3–10

Delgado MM, Penteriani V (2008) Behavioral states help translate dispersal movements into spatial distribution patterns of floaters. Am Nat 172:475–485

Delgado MM, Penteriani V, Nams VO, Campioni L (2009) Changes of movement patterns from early dispersal to settlement. Behav Ecol Sociobiol 64:35–43

Delgado MM, Penteriani V, Revilla E, Nams VO (2010) The effect of phenotypic traits and external cues on natal dispersal movements. J Anim Ecol 79:620–632

Dingemanse NJ, Christiaan B, van Noordwijk AJ, Rutten AL, Drent PJ (2003) Natal dispersal and personalities in great tits (*Parus major*). Proc R Soc Lond B 270:741–747

Elkie P, Rempel R, Carr A (1999) Patch analyst user's manual: a tool for quantifying landscape structure. Ontario Ministry of Natural Resources Northwest Science and Technology. http://flash.lakeheadu.ca/_rrempe/patch/

Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, La Dage L, Schlägel UE, Tang W, Papastamatiou YP, Forester J, Mueller T (2013) Spatial memory and animal movement. Ecol Lett 16:1316–1329

Fauchald P, Tveraa T (2006) Hierarchical patch dynamics and animal movement pattern. Oecologia 149:383–395

Frair JL, Merrill EH, Allen JR, Boyce MS (2007) Know thy enemy: experience affects elk translocation success in risky landscapes. J Wildl Manag 71:541–554

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. Am Nat 158:124–135

Fryxell JM, Mosser A, Sinclair ARE, Packer C (2007) Group formation stabilizes predator–prey dynamics. Nature 449:1041–1044

González LM, Oria J, Sánchez R, Margalida A, Aranda A, Prada L, Caldera J, Molina JI (2008) Status and habitat changes in the endangered Spanish Imperial Eagle *Aquila adalberti* population during 1974–2004: implications for its recovery. Bird Conserv Int 18: 242–259

Gurarie E, Bracis C, Delgado MM, Meckley T, Kojola I, Wagner M (submitted) What is the animal doing? Tools and principles for the behavioral analysis of animal movements

Haydon DT, Morales JM, Yott A, Jenkins DA, Rosatte R, Fryxell JM (2008) Socially informed random walks: incorporating group dynamics into models of population spread and growth. Proc R Soc Lond B 275:1101–1109

Holyoak M, Casagrandi R, Nathan R, Revilla E, Spiegel O (2008) Trends and missing parts in the study of movement ecology. PNAS USA 105:19060–19065

Hooge PN, Eichenlaub B (2000) Animal movement extension to ArcView, version 2.0.3. Biological Science Centre, US Geological Survey, Anchorage, Alaska

Jetz W, Carbone C, Fulford J, Brown JH (2004) The scaling of animal space use. Science 306:266–268

Kie JG, Bowyer RT, Nicholson MC, Boroski BB, Loft ER (2002) Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530–544

Lomnicki A (1988) Population ecology of individuals. Princeton University Press, Princeton

Lourenço R, Delgado MM, Campioni L, Korpimäki E, Penteriani V (submitted) Evaluating the influence of diet-related variables on breeding performance and home range behaviour of a top predator

Macdonald DW (1983) The ecology of carnivore social behaviour. Nature 301:379–384

Martin J, Calenge C, Quenette P-Y, Allainé D (2008) Importance of movement constraints in habitat selection studies. Ecol Model 213: 257–262

Martin J, van Moorter B, Revilla E, Blanchard P, Dray S, Quenette P-Y, Allainé D, Swenson JE (2012) Reciprocal modulation of internal and external factors determines individual movements. J Anim Ecol 82:290–300

McLoughlin PD, Ferguson SH (2000) A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7: 123–130

Moorcroft PR, Lewis MA, Crabtree RL (2006) Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. Proc R Soc Lond B 273:1651–1659

Morales JM, Fortin D, Frair JL, Merrill EH (2005) Adaptive models for large herbivore movements in heterogeneous landscapes. Landsc Ecol 20:301–316

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. Philos Trans R Soc Lond B 365:2289–2301

Morellet N, Bonenfant C, Borger L, Ossi F, Cagnacci F, Heurich M, Kjellander P, Linnell JDC, Nicoloso S, Sustr P, Urbano F, Mysterud A (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. J Anim Ecol 82:1326–1339

Nathan R, Giuggioli L (2013) A milestone for movement ecology research. Mov Ecol 1:1

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltze D, Smouse PE (2008) A movement ecology paradigm for unifying organismal research. PNAS USA 105:19052–19059

Papastamatiou YP, Cartamil DP, Lowe CG, Meyer CG, Wetherbee BM, Holland KN (2011) Scales of orientation, directed walks and movement path structure in sharks. J Anim Ecol 80:864–874

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State–space models of individual animal movement. Trends Ecol Evol 23:87–94

Penteriani V (2002) Variation in the function of Eagle Owl vocal behaviour: territorial defence and intra-pair communication? Ethol Ecol Evol 14:275–281

Penteriani V, Delgado MM (2011) Birthplace-dependent dispersal: are directions of natal dispersal determined a priori? Ecography 34: 729–737

Penteriani V, Delgado MM (2012) There is a limbo under the moon: what social interactions tell us about the floaters' underworld. Behav Ecol Sociobiol 66:317–327

Penteriani V, Delgado MM, Maggio C, Aradis A, Sergio F (2005) Development of chicks and predispersal behaviour of young in the Eagle Owl *Bubo bubo*. Ibis 147:155–168

Penteriani V, Alonso-Alvarez C, Delgado MM, Sergio F (2007) The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. Behav Ecol 18:143–147

Penteriani V, Delgado MM, Maggio C, Alonso-Alvarez C, Holloway GJ (2008) Owls and rabbits: selective predation against substandard individuals by a sit-and-wait predator. J Avian Biol 39:215–221

Penteriani V, Delgado MM, Campioni L, Lourenço R (2010) Moonlight makes owls more chatty. PLoS One 5:e8696

Penteriani V, Ferrer M, Delgado MM (2011a) Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. Anim Conserv 14:233–241

Penteriani V, Kuparinen A, Delgado MM, Lourenço R, Campioni L (2011b) Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. Anim Behav 82:413–420

Pinheiro JC, Bates DM (2004) Mixed-effects Models in S and S-PLUS. Springer, New York

Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Core team (2009) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-96. Vienna: R Foundation for Statistical Computing. http://www.R-project.org

Potts JR, Harris S, Giuggioli L (2013) Quantifying behavioural changes in territorial animals caused by sudden population declines. Am Nat 182:E73–E82

R Development Core Team (2009) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. http://www.R-project.org

Rieucau G, Giraldeau LA (2011) Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. Philos Trans R Soc Lond B 366:949–957

Rutz C, Whittingham MJ, Newton I (2006) Age-dependent diet choice in an avian top predator. Proc R Soc Lond B 273:579–586

Saarenmaa H, Stone ND, Folse LJ, Packard JM, Grant WE, Makela ME, Coulson RN (1988) An artificial intelligence modeling approach to simulating animal/habitat interaction. Ecol Model 44:125–141

Sasha RX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from adaptive perspective. Ecol Lett 7:734–739

Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, Conde DA, Halpin PN, Joppa LN, McClellan CM, Clark JS (2008) Understanding movement data and movement processes: current and emerging directions. Ecol Lett 11:1338–1350

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Seaman DE, Powell RA (1996) An evaluation of the accuracy of Kernel density estimators for home range analysis. Ecology 77:2075–2085

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. J Wildl Manag 63:739–747

Silverman BW (1986) Density estimation for statistics and data analysis. Monographs on statistics and applied probability. Chapman and Hall

Smouse PE, Focardi S, Moorcroft PR, Kie JG, Forester JD, Morales JM (2010) Stochastic modelling of animal movement. Philos Trans R Soc Lond B 365:2201–2211

Stamps JA (1995) Motor learning and home range value. Am Nat 146: 41–58

Stamps JA, Groothuis GG (2010) Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. Philos Trans R Soc Lond B 365:4029–4041

Stamps JA, Krishnan VV (1999) A learning-based model of territory establishment. Q Rev Biol 74:291–318

Thield A, Hoffmeister TS (2004) Knowing your habitat: linking patch encounter rate and patch exploitation in parasitoids. Behav Ecol 15: 419–425

Vos M, Hemerik L, Vet LEM (1998) Patch exploitation by parasitoids *Cotesia rebecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. J Anim Ecol 48:353–371

Vuilleumier S, Perrin N (2006) Effects of cognitive abilities on metapopulation connectivity. Oikos 113:139–147

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168