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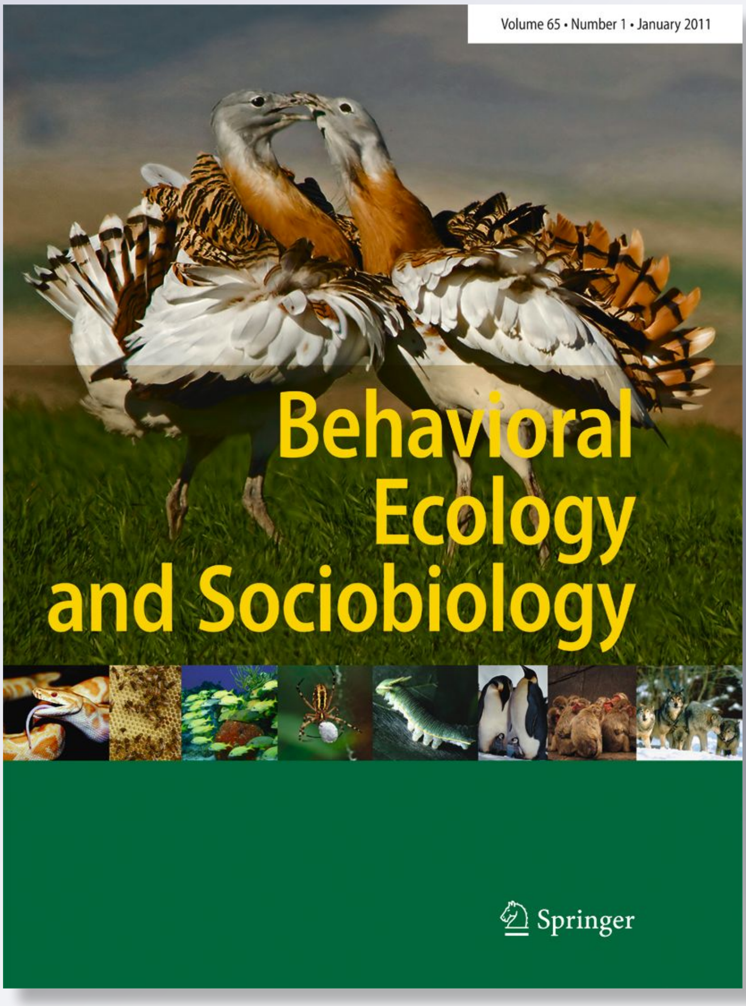

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ORIGINAL PAPER

There is a limbo under the moon: what social interactions tell us about the floaters' underworld

Vincenzo Penteriani · María del Mar Delgado

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Abstract The ultimate and proximate causes of natal dispersal have been extensively investigated, but the behaviour of dispersers in relation to social interactions has been largely neglected. Here, we investigated the social organisation of floating individuals during their dispersal by analysing the behaviour of 40 radio-tagged eagle owls *Bubo bubo* during the wandering and stop phases of dispersal. Unexpectedly, eagle owl floaters mixed with conspecifics independently of their sex, age, phase of dispersal, birthplace, health status and habitat features, showing an 'underworld' of interactions characterised by the absence of obvious social organisation or short-term strategies. Non-breeding owls were not transient floaters that occurred at numerous sites for short periods of time but rather had fairly stable home ranges: they attempted to settle as soon as possible within well-defined home ranges. The spatial distribution pattern of floaters and high rates of home range overlap support the prediction that floating individuals are not spatially segregated, challenging the expectation that dominance by size, age and/or health status may determine the exclusive use of some portions of the dispersal area. Finally, (1) the short distances among conspecifics and the extensive home range overlaps allowed us to discard the possibility that neighbouring floaters represent a real cost during dispersal and (2) floater interactions showed a lack of clear mechanisms for avoidance of kin competition among offspring or inbreeding.

Keywords *Bubo bubo* · Conspecific interactions · Eagle owl · Floaters · Home range · Natal dispersal · Settlement area

Natal dispersal has a number of crucial consequences for population dynamics and stability (Clobert et al. 2001; Bowler and Benton 2005; Ronce 2007). Although there are still many gaps in knowledge and understanding of the ultimate and proximate causes of dispersal, both have been extensively investigated and some of the key mechanisms driving dispersal have been identified. However, the behaviour of dispersers in relation to social interactions has been largely neglected (but see Doerr and Doerr 2005; Griesser et al. 2008; Delgado et al. 2009) despite the fact that social interactions are an essential aspect of dispersal (Doerr and Doerr 2005; Delgado and Penteriani 2008): some dispersal patterns (e.g. dispersal distances and settlement decisions) are not individual behavioural choices per se but arise from conspecific interactions during the different phases of this process (starting, wandering and stop; Clobert et al. 2009). In addition, it has been suggested that dispersal and settlement decisions are the result of interactions between territorial residents and dispersers (e.g. Krebs 1978; Arcese 1987), but there is less information on these types of relationships among dispersers only. This is mainly because of difficulties in accurately measuring individual behaviour during natal dispersal (e.g. Koenig et al. 1996; Clobert et al. 2001; Studds et al. 2008). Therefore,

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there is inadequate knowledge of the behavioural decisions of dispersers (Macdonald and Johnson 2001; Doerr and Doerr 2005) and of their conspecific interactions during their period as floaters. In particular, we lack knowledge of *who*/*what* shapes (*when* and *how*) the 'underworld' of non-breeding individuals (sensu Smith 1978).

Studies on floaters are diverse, and depending on the ecological and behavioural contexts in which animal populations are considered, the term floater can have differing but non-exclusive meanings and implications (Hogstad 1990; Winker 1998; Penteriani et al. 2011). In this study, we defined floaters as the entire pool of dispersing individuals independent of age because: (a) they are sexually mature when less than 1 year old and (b) dispersing owls remained 'floating' in the vicinity of the breeding population during both phases of dispersal (Delgado and Penteriani 2008; Delgado et al. 2010). Although the definition of floaters is not commonly based on their dispersal status, floating individuals moving close to or within nesting sites may also be considered as dispersers until they first reproduce (Penteriani et al. 2011).

Five main questions about floater 'lifestyle' and their possible social organisation were addressed. In the following hypothesis presentations, we will frequently refer to different sections of results (i.e. those that, pooled together, have contributed to answer our questions) because the questions involved the interactions of multiple factors.

1. Do floaters lead a wandering existence with no fixed areas of residence?

Floating individuals may have relatively stable areas of residence and structured social systems (Smith 1978, 1984; Rohner 1996, 1997a; Marra 2000; Tobler and Smith 2004). Three specific types of floater strategies can be distinguished (Matthysen 1989): (1) solitary individuals with a home range overlapping several other conspecific home ranges or parts thereof, (2) paired birds moving across several breeding areas and (3) satellite individuals that may live within the home range occupied by a conspecific but never engage in overt conflicts with the owner. Floaters in a fixed or restricted area will benefit from knowledge of the area and the conspecifics present (including potential mates) and the establishment of social relationships with other floaters (Smith 1978). On this basis, it can be hypothesised that floaters will show: (1) more or less stable home ranges and (2) a well-defined social system structured as a function of the sex and health status of individuals. Findings reported throughout the whole "Results" section relate to both of these hypotheses.

2. Are floating individuals spatially segregated?

Many bird species have distribution patterns involving spatial segregation by sex during the non-breeding period, which is one of the mechanisms proposed to explain sexual habitat segregation relying on dominance (reviewed in Marra 2000). In addition to sexual segregation, large body size, the general health status of individuals and their age may also help floaters to access better or limited resources (Fretwell 1969; Smith and Metcalfe 1997). That is, older individuals and/or those in better condition might have exclusive use of some parts of the dispersal area that are less crowded and where intra-specific competition is less. However, because of the ready availability of rabbits (*Oryctolagus cuniculus*), which are the main prey of eagle owls in our study area (Penteriani et al. 2008), we predicted that spatial segregation would not occur among floaters within the temporary settlement areas (TSA; i.e. stable zones, occupied by floaters for the longest time period across the whole dispersal process or until they become owners of a breeding territory; Penteriani et al. 2011). Findings reported in the "Results" sections "Neighbours on the whole" and "TSA size and overlaps" relate to this prediction.

3. Do neighbouring floaters represent a cost?

If the number of neighbours increases competition for resources, settled dispersers are expected to avoid neighbours (or at least avoid frequent and large overlaps of settlement areas with them) and/or prevent new dispersers from settling in their vicinity. Findings reported in the "Results" sections "Neighbours on the whole" and "TSA size and overlaps" address this issue.

4. Are floaters evaluating future mates during dispersal?

Dispersing individuals in their settlement areas may attempt to establish early mating pair relationships with neighbouring floaters (e.g. Heg et al. 2000). If this occurs, evidence for increased male−female interactions (e.g. closer within the dispersal area, greater TSA overlap) rather than male−male and female−female interactions would be expected. Findings in relation to sex interactions under various scenarios are presented in the "Results" sections "Neighbours on the whole" and "TSA size and overlaps".

5. Do floater distributions during dispersal represent a mechanism of inbreeding avoidance?

Dispersal patterns have the potential to determine kinship structure and spatial assortment of phenotypic traits (van Tienderen and van Noordwijk 1988; Gandon 1999; Ronce et al. 2000). There is also a direct relationship between dispersal patterns and the likelihood of inbreeding (Szulkin and Sheldon 2008), particularly if individuals remain close during dispersal (Motro 1991; Gandon 1999). To increase fitness by avoiding mating with relatives, it is likely that individuals mainly interact with non-kin, and dispersal strategies that increase individual fitness would be expected to be selected (Leturque and Rousset 2002; Roze and Rousset 2005; Szulkin and Sheldon 2008). Consequently, we expected that interactions among siblings (owls from the same birthplace) would be negligible, with contacts among non-relatives being the most common situation. Findings reported in the "Results" sections "Neighbours on the whole" and "TSA size and overlaps" address this issue.

In this study, we addressed the above-described five questions by analysing the behaviour of radio-tagged eagle owls *Bubo bubo* during the wandering and stop phases of dispersal (for general information on eagle owl dispersal, see Delgado et al. 2010 and Penteriani and Delgado 2011). Special emphases were placed on the social structure of dispersers and how their behaviour is affected by (1) conspecifics, (2) the internal state (i.e.,health) of individuals, and (3) abiotic factors (i.e., landscape characteristics). Marked owls were followed within an area of ~70,000 ha (hereafter, the dispersal area; Fig. 1), which represents the domain including the entire area occupied by floating individuals.

Methods

Collection of data from radio-tagged floaters

During the period 2003−2007, we studied the movement and behaviour of 40 juveniles during natal dispersal. Individuals (males = 30, females = 10) from 12 different nest sites in Sierra Morena (southwestern Spain; for more details, see Penteriani et al. 2007) were radio-tagged between 2003 and 2006 (2003: n=6; 2004: n=11; 2005: n=14; 2006: n=9). The owlets were tagged at ~35 days old. For each analysis we used different sub-samples (detailed in the "Results" section), representing those dispersers for which it was possible to collect the specific information sought. Each individual was fitted with a 30-g radio transmitter using a teflon ribbon backpack harness (for more details, see Delgado and Penteriani 2008). The weight of the transmitter was less than 3% of the weight of the smallest adult male (1,550 g; mean±SD = 1,667±104.8 g) and 3.5% of the smallest fledgling weight (850 g; mean± SD = 1,267±226.4 g) at the time of tagging. The owls were aged following Penteriani et al. (2005) and sexed by molecular procedures using DNA extracted from their blood.

Tagged individuals were tracked within the dispersal area at two different temporal scales: nightly and weekly. At the nightly scale (n=178 tracking sessions for a total of 2,010 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 (n_{tot}=3,196) 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), i.e. the number of locations recorded represented the effective movement of an individual during the night. Individuals were tracked on a rotation basis throughout the year. 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 =

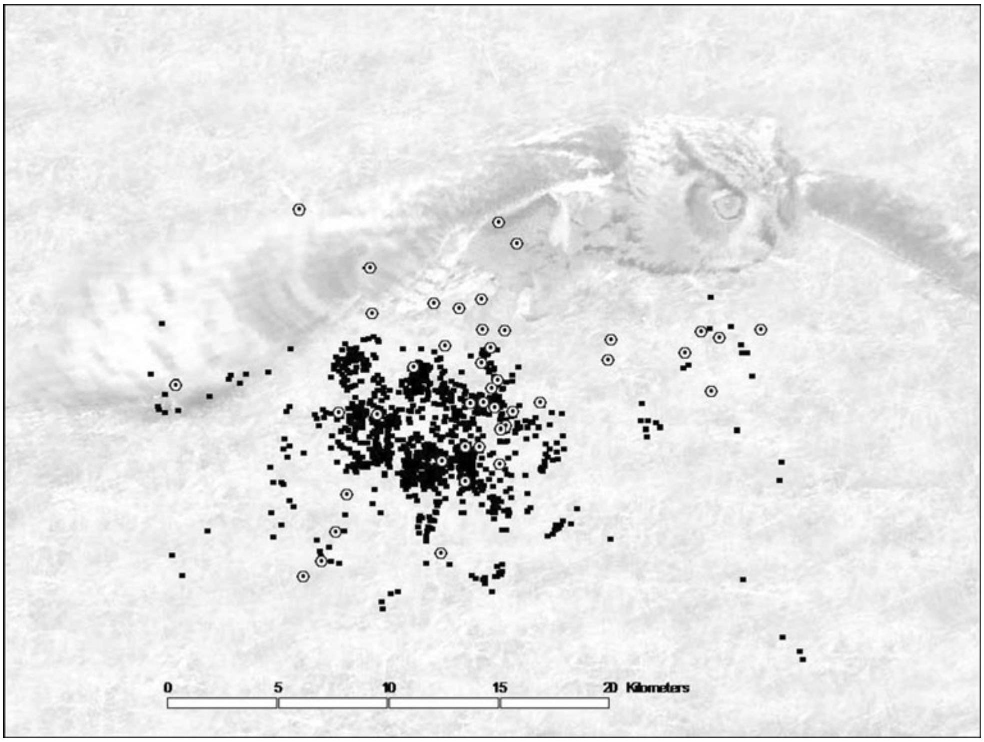

Fig. 1 The study system (~70,000 ha; 2003−2007). *Black squares* represent weekly locations of dispersing eagle owls within the dispersal area. *White dots* with black centres show the location of different breeding sites

1−11, mean±SD = 3.6±2.6; range for females = 1−13, mean±SD = 5.3±4.5). The tracking sessions were relatively evenly distributed among: (1) the dispersal phases (wandering phase: n=68 tracking sessions, 41.7%; stop phase: n=95 tracking sessions, 58.3%) and (2) the dispersal phases of each sex (males$_{\text{wandering}}$: n=47 tracking sessions, 39.8%, range=0−6, mean±SD=1.6±1.4; males$_{\text{stop}}$: 71 tracking sessions, 60.2%, range=0−9, mean±SD=2.4±2.9; females$_{\text{wandering}}$: n=21 tracking sessions, 46.7%, range=1−5, mean±SD=2.1±1.7; females$_{\text{stop}}$: 24 night tracking sessions, 53.3%, range=0−7, mean±SD=2.4±2.8). For weekly scale tracking, on a weekly basis the location of each owl was determined when it was at its daytime roosting site (n_{tot}=1,189 locations).

Locations were determined by triangulation using a three-element hand-held Yagi-antenna connected to an ICOM portable receiver. Based on the accuracy of radio tracking devices (mean accuracy±SE=83.5±49.5 m) and to ensure independence among locations, a distance of 150 m was set as the minimum threshold necessary to distinguish locations while tracking at night. To avoid unnecessary disturbance during continuous tracking, we attempted to maintain a distance of at least 100−300 m from the focal individual, although directly following individuals did not appear to affect their behaviour (i.e. owls appeared to ignore the observer when the latter accidentally went closer to the bird; Delgado and Penteriani, unpublished data).

Internal state of dispersers Dispersal behaviour can be determined by a suite of phenotypic traits (Clobert et al. 2009; Dawideit et al. 2009; Delgado et al. 2010). To account for the effect of individual characteristics in our analyses, we measured several physiological/morphological indices for owls of 35 days of age. The health status of individuals was represented by single morphological (body condition index, BCI) and physiological (haematocrit) parameters, which had previously been found to affect individual dispersal behaviour (i.e. higher values of both BCI and haematocrit represent individuals of better quality; for more details, see Delgado et al. 2010). BCI was estimated by a reduced major axis regression (Green 2001), using log of both body mass (to the nearest 10 g, with 1 kg Pesola scales) and wing length (using a digital calliper, ±0.1 mm).

External cues acting on dispersers To test for the effect of habitat heterogeneity on individual behaviour, we analysed the landscape structure and the composition of habitats to which the owls were exposed during nightly tracking sessions. We evaluated both landscape structure and composition using ArcMap of ARCGIS version 9.0. We reclassified the map into ten simpler land cover elements: urban areas, water bodies, forest, dense scrubland with trees, sparse vegetation with trees, herbaceous vegetation with trees, scrubland, low vegetation, woody crops and herbaceous. We then calculated the proportion of each habitat type within the area traversed by individuals on each night. The calculated areas (in raster format; cell size, 0.5×0.5 km) were used as a basic input data layer for measuring landscape metrics. We used the raster version of FRAGSTATS 3.3 (McGarigal et al. 2002) to calculate the total landscape area, the density of patches (defined as relatively homogeneous areas that differed from the surroundings), the mean patch size, edge density, patch density and Shannon's diversity index.

Social interactions

Temporal window of overlapping floaters and TSAs To determine which individuals were temporally sharing the same or neighbouring areas at the same time (and were thus potentially interacting), we firstly established the temporal window (hereafter, permanence period) in which each owl settled in a given TSA. We considered a TSA to be the area prospected by each individual during each nightly tracking session. For each TSA (n=163, one for each tracking night), we calculated its extent using the 95% minimum convex polygon (see also Fig. 2) and determined its spatial location by estimating the central point of the TSA. The permanence period for an owl in a given TSA was estimated by superimposing the weekly locations onto the TSA: the permanence time for each TSA was therefore the temporal bracket between the first and the last weekly location fitting in such TSA. Because weekly locations represented the daily roost of an individual, from where it commenced its nocturnal activity (Delgado et al. 2009, 2010), an owl still located inside a given TSA during the day(s)/week(s) after its delimitation was considered to have at least partially used this area (Delgado and Penteriani 2008; Delgado et al. 2010). Obviously, conspecific relationships determined in this way represented the minimum social interactions of focal individuals because: (a) other non-tagged owls (i.e. undetected individuals) may have been present in the same area during the same temporal window and (b) the movements of individuals during periods when they were not radio-located were unknown. Because more than one TSA per neighbouring owl can fit the permanence period of a focal owl, the TSA temporally closest to the TSA of the focal owl was the one selected for analyses.

Assessment of the social structure of floaters To evaluate the interactions among temporally overlapping owls, neighbouring individuals were placed into one of two categories: (1) overlapping neighbours (neighbours that had at least partially overlapping TSAs or shared one of the TSA edges with the focal owl during the same temporal

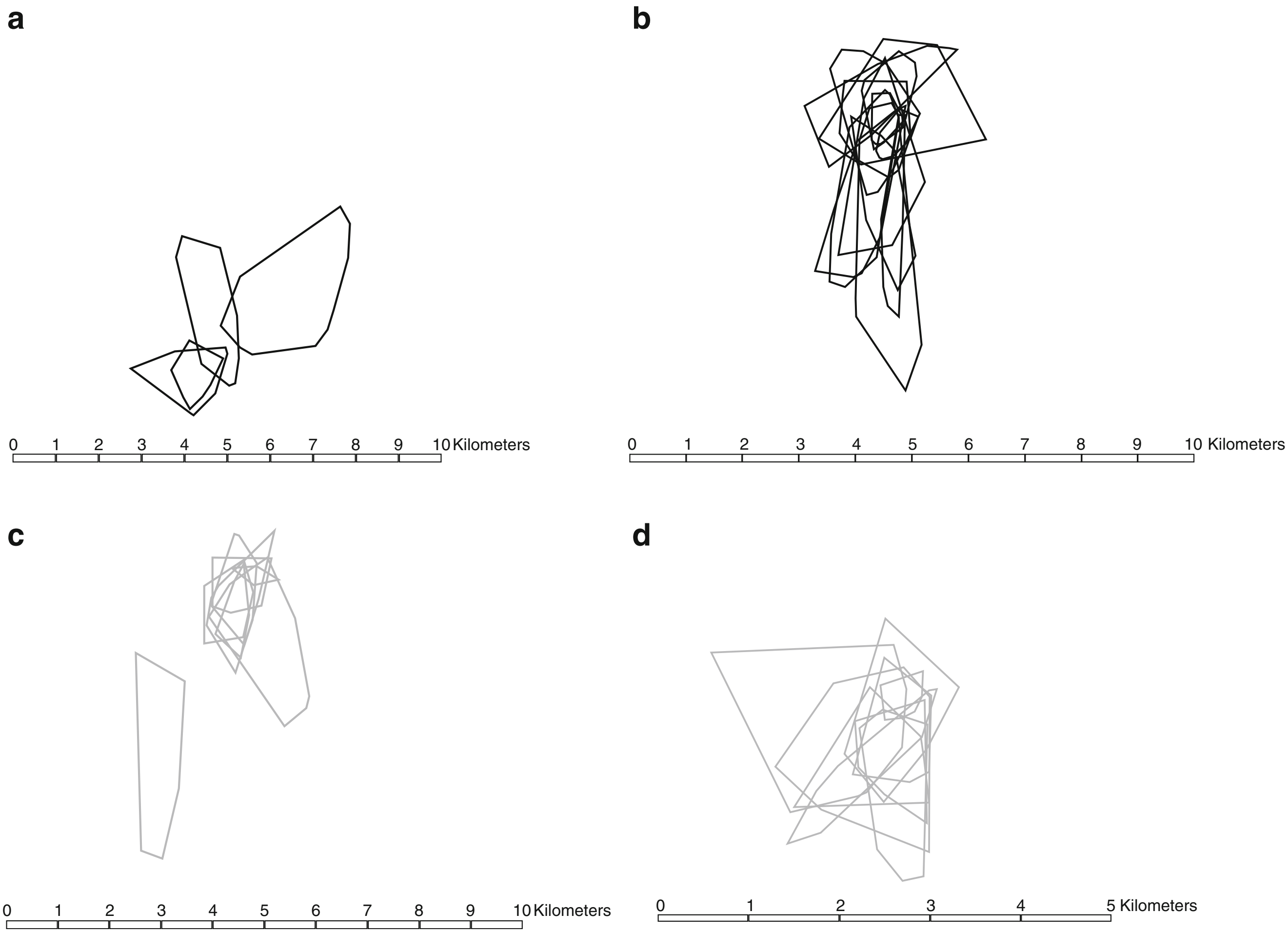

Fig. 2 Four examples of the locations of temporary settlement areas (see the text for details) for two males (*black*, **a** and **b**) and two females (*grey*, **c** and **d**). Each group of polygons (calculated using 95% minimum convex polygons) represents the nightly area occupied by a given individual during dispersal (wandering and stop phase together)

window) and (2) other neighbours, comprising all other tagged owls that were detected during the same temporal window but which did not overlapped in space with the focal owl. Within each temporal window, we calculated: (1) the TSA size and % overlap (calculated with ArcMap of ARCGIS (Geoprocessing Wizard) version 9.0.), which provided information on the level of saturation and potential for interactions among neighbours (Brown et al. 2000); (2) the distance among neighbouring owls, estimated from the activity centres of their nocturnal movements (Delgado et al. 2010) and (3) the number of temporally overlapping individuals, as well as their age, sex, birthplace (i.e. nest of origin) and dispersal phase at the time each was detected. In addition, we considered three types of social interaction: (a) between sexes (male−male, female−female and male−female interactions), (b) among dispersal phases (wandering vs. wandering, stop vs. stop, wandering vs. stop) and (c) among birthplaces (siblings vs. non-siblings). While factors including sex and dispersal phase should represent sources of intra-individual variation in dispersal behaviour, the nest of origin was expected to enable assessment of sibling−sibling vs. sibling−non-sibling differences.

Statistical analyses

We built multi-level linear mixed-effects models to test the effects of social interactions (as defined above), the health status of individuals and external factors on: (1) the permanence period, (2) the number of temporally overlapping neighbours, (3) the distances among nightly activity centres of temporally overlapping owls, (4) the TSA size, (5) the % of TSA overlap established by floaters and (6) the social status of dispersers after the first year of dispersal, i.e. early breeder (10 of the 40 tagged owls started breeding during the reproductive season immediately following their birth) vs. 'forever' floater.

Statistical analyses were performed using SAS. We firstly explored the data for: (1) normality, (2) homogeneity and (3) independence assumption. For the latter, we used

Moran's I test statistic (Moran 1950), which indicates the statistical significance of spatial autocorrelation (*p*-values were never significant). The residuals of dependent variables were all homogeneous and independent, and normally distributed. Because we had repeated measures for the same owls, the data included siblings originating from the same nests in different years. We thus considered individual, nest of origin and year as first-, second- and third-level nested random effects, respectively. Model simplification was by backward selection of variables from the full model, and models were compared using likelihood ratio tests until a minimal adequate model was obtained. All tests were two-tailed and statistical significance was set at $\alpha<0.05$.

Results

The permanence period

The permanence period ranged from several days to approximately 1 year, although mean values were similar among dispersal phases and between sexes (Table 1; ESM 1A and B). In particular: (a) during the wandering and stop phases, individuals showed minimal differences in permanence times and (b) sexes showed similar permanence times in TSAs, with males having shorter permanence times (1 week less on average) than females. As a consequence of these similar patterns, and even though the dispersal phases and numbers of potentially interacting individuals were the unique factors explaining the permanence periods of individuals within their TSAs, their contribution to the overall pattern was very weak (Table 2).

Neighbours on the whole

Similarly, the number of neighbours did not show any strong significant trend (Table 2); however, floaters were surrounded by relatively more neighbours during the wandering phase than in the stop phase (Table 1; ESM 1A; Fig. 3), with the most frequent case being the simultaneous presence of individuals belonging to different dispersal phases (wandering vs. wandering = 27.7%; stop vs. stop = 28.3%; wandering vs. stop = 44%; ESM 1B).

The distances among neighbours during the stop and wandering phases were similar (Table 1; ESM 1A). This homogeneity was also reflected by the absence of significance among the entire set of variables tested, as well as the low contribution of the dispersal phase as an explanatory variable (Table 2). In particular, similar values were recorded for intra-individual distances between: (a) phases (wandering vs. stop = 4.0±2.2 km; wandering vs. wandering = 3.9±2.3 km; stop vs. stop = 3.9±2.1 km; ESM 1B), (b) sexes (male–male = 4.0±2.4 km; female–female = 3.8±2.0 km; male–female = 4.0±

Table 1 Nightly patterns of interactions among eagle owl floaters (n=40 radio-tagged individuals)

	Permanence period[a] ($\bar{x}$ ± SD; range; n)	Neighbours on the whole[b] ($\bar{x}$ ± SD; range; n)	Overall neighbour distances (km) ($\bar{x}$ ± SD; range; n)	TSA size per night (km^2) ($\bar{x}$ ± SD; range; n)	Individuals overlapping TSA[c] ($\bar{x}$ ± SD; range; n)	Overlapping neighbour distances (km)[d] ($\bar{x}$ ± SD; range; n)
Overall patterns	43.2±38.7; 2–283; 152	4.9±2.5; 0–12; 761	4.0±2.2; 0–15.5; 762	2.1±4.2; 0.1–50.2; 162	0.7±0.9; 0–5; 108	1.2±0.7; 0–3.7; 108
Dispersal phase						
Wandering	43.9±45.4; 4–283; 61	5.7±2.7; 0–12; 761	3.9±2.2; 0–15.5; 374	2.9±6.4; 0.2–50.2; 63	1±1.1; 0–5; 108	1.2±0.7; 0–3.7; 63
Stop	42.8±33.7; 2–168; 91	4.3±2.2; 0–11; 761	4.1±2.2; 0.4–15.3; 388	1.6±1.4; 0.1–7.0; 99	0.5±0.7; 0–3; 108	1.1±0.6; 0.4–2.9; 45
Sex						
Male	41.2±32.9; 2–168; 109	4.7±2.5; 0–11; 761	4.0±2.2; 0–15.3; 499	2.3±4.8; 0.1–50.2; 112	0.7±1; 0–5; 108	1.1±0.7; 0–3.7; 80
Female	48.4±50.6; 8–283; 43	5.3±2.6; 2–12; 761	4.0±2.3; 0–15.5; 263	1.8±2.2; 0.1–12.3; 50	0.6±0.8; 0–3; 108	1.4±0.7; 0.5–3.7; 28

[a] Permanence period (days) within the same temporal settlement area

[b] Total number of individuals temporally coincident within the dispersal area

[c] Number of individuals with temporal and spatial overlap of their temporary settlement areas

[d] Neighbours overlapping their temporal settlement areas

Table 2 Significant linear mixed-effects models testing the social interactions among floating eagle owls during dispersal

Social interaction descriptors	Parameter estimate ± SE	F-value	P	% deviance explained
Permanence period (n=696)[a, b]				4.8
Dispersal phase[c]	−15.96±3.70	18.65	<0.0001	
Social interactions: between dispersal phases[d]	−6.23±3.02	3.48	0.016	
	−7.07±3.00	–	–	
Overall number of neighbours	6.19±0.53	137.10	<0.0001	
Intercept	21.57±5.27	–	–	
Neighbours on the whole[e] (n=722)[a]				8.5
Dispersal phase[b]	1.10±0.26	17.79	<0.0001	
Social interactions: between dispersal phases[d]	0.51±0.22	16.67	<0.0001	
	−1.11±0.21	–	–	
Intercept	5.82±0.28	–	–	
Overall neighbour distances (n=737)[a]				1.1
Social interactions: between dispersal phases[d]	−0.14±0.06	4.68	0.01	
	0.07±0.06	–	–	
Intercept	8.08±0.05	–	–	
TSA overlap (n=95)[a, f]				1.5
TSA size[g]	−4.27±1.30	10.75	0.002	
Intercept	34.26±3.61	–	–	

[a] Normal distribution, identity link

[b] Permanence period (days) within the same temporal settlement area

[c] Categorical variable: 1 = wandering phase, 2 = stop phase

[d] Categorical variable: type of social interactions (see text for more details) specifically related to the dispersal phase (three-term category: 1 = wandering vs. wandering, 2 = stop vs. stop, 3 = wandering vs. stop) of potentially interacting individuals

[e] Total number of individuals temporally coincident within the dispersal area

[f] Amount (%) of overlap of temporary settlement areas among individuals

[g] Extension (km^2) of the temporary settlement area

2.0 km; ESM 1B); and (c) siblings (4.2±2.1 km) and non-siblings (3.9±2.2 km; ESM 1B).

TSA size and overlap

The TSA size showed some variation during dispersal, with a relatively small average size per night (~2 km^2; Table 1; ESM 1A). The variation was mostly due to the differing sizes of the TSAs during the two dispersal phases, being larger at the beginning of the process. Although the TSAs were slightly larger for males than females (Table 1; ESM 1A), this difference was not statistically significant. The nightly overlap of TSAs averaged 24.7±22.9% (0−100%; n=108). Throughout the entire dispersal process, owls occupied a mean TSA of 8.5±4.5 km^2, and for individuals followed during both phases of dispersal (n=18) the TSA during the stop phase had an overlap of 39.6±38.5% with the wandering phase TSA (0% overlap = 6 cases, 100% overlap = 2 cases). TSA overlap (Fig. 4) occurred more frequently during the wandering phase than in the stop phase. When all the individuals were in the stop phase, overlap was rarer than during the other phases: wandering vs. wandering = 39.8%; stop vs. stop = 23.2%; wandering vs. stop = 37%; ESM 1B. We did not find any correlation between the set of variables we tested and (a) the numbers of overlapping neighbours, (b) the size of the TSA or (c) the % overlap of TSAs (although Table 2 shows a weak contribution of TSA size, with individuals dispersing in the most crowded areas having the smallest TSAs).

The distances among overlapping individuals showed a similar pattern to the distance among neighbours as a whole (Table 1; ESM 1A and B), and no significant effect of any of the set of tested variables was found. In particular, the distances among overlapping individuals were similar across the phases of dispersal, which was also evident from comparisons of the intra-individual distances among the various dispersal phases (wandering vs. wandering = 1.2±0.8 km; stop vs. stop = 1.1±0.6 km; wandering vs. stop = 1.2±0.6 km; ESM 1B). When spatially overlapping, the distances between males were slightly less than between females (Table 1; ESM 1A). In particular (ESM 1B), both male−male distances (1.0±0.6 km) and female−female

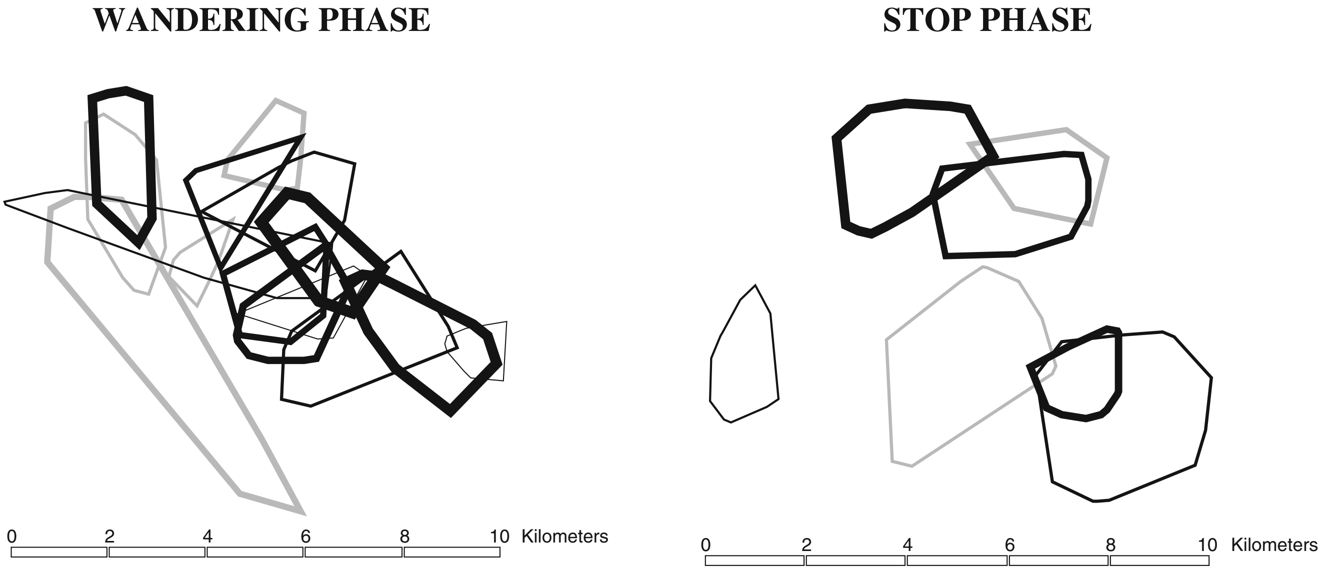

Fig. 3 An example of the spatial distribution of temporal settlement areas of floaters (*black* = males, *grey* = females) sharing the same area during the wandering (n=15) and stop (n=7) phases of natal dispersal (2004–2005). Among the seven individuals in the stop phase, six were the same as in the wandering phase, whereas one arrived in the area during the stop phase. The remaining eight owls in the wandering phase moved to different areas when they reached the stop phase or died

distances (1.1±0.2 km) were less than the male–female distances (1.4±0.7 km). There were minor differences in the distances among owls born in the same nesting area (1.0±0.6 km) relative to the distances among non-siblings (1.2±0.8 km; ESM 1B).

Discussion

During the first 2–2.5 years of life (i.e. the period covered by the lifespan of the transmitters used in the study), eagle owl floaters mixed with conspecifics independently of their sex, age, phase of dispersal, birthplace, health status and habitat features.

The relatively long permanence period of eagle owls inside their relatively small TSAs, as well as their previously reported short dispersal distances (1.5–34.3 km; mean±SD = 6.0±4.2 km; Delgado et al. 2010), suggests that they are not dynamic dispersers actively looking for short-term breeding opportunities as is commonly the case in other bird species (e.g. Heg et al. 2000; Tobler and Smith 2004 and references therein). On the contrary, it seems that eagle owls attempt to settle as soon as possible within well-defined home ranges close to their natal population, similarly to what has been observed for floaters of great horned owls, *Bubo virginianus*, which are the North American ecological equivalent of eagle owls (Rohner 1997b).

During the entire study period, we never detected any prospecting movement from the dispersal area to the natal area or any area potentially suitable for breeding (Delgado et al. 2010, unpublished results). The absence of evident prospecting behaviour aimed at reproduction appears more unusual in view of the fact that the dispersal area in this study is extremely close (if not partially overlapping; see Fig. 1) to one of the most dense breeding populations (~40 pairs/100 km^2) reported for the species within its distribution range. If nest density is able to positively influence the movement behaviour of floaters (Zack and Stutchbury 1992; Rohner 1997a), small clumped nest sites may be easier to monitor than large, scattered territories. Since excursions towards natal areas during dispersal appears to be a regular behaviour in other dispersing raptors (e.g. Ferrer 1993; Walls

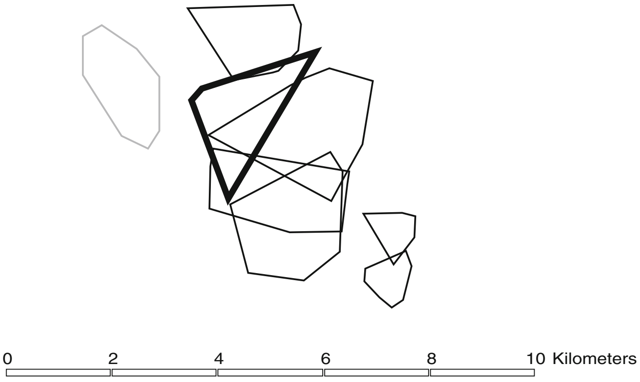

Fig. 4 An example of spatial interactions during the temporal window in which a focal individual (male 093, *boldest black polygon*) temporally overlapped with other floaters (see "Methods" section for more information on the floater temporal windows). The temporary settlement area of the focal male partially overlapped with the settlement areas of three other males (*black polygons*) and was surrounded by the settlement areas of three additional males (*black polygons*) and one female (*grey polygon*)

and Kenward 1998), more research is still needed to find a clear explanation for such apparently 'inert' behaviour during dispersal (see Delgado et al. 2011). However, it can be hypothesised that in short-lived species the high mortality rate of owners confers a high probability that any prospected nest site will become available, increasing the frequency of breeding area checking and quick settlement as a new owner (Stutchbury and Robertson 1985; Smith and Arcese 1989); moreover, lifetime expectancy for reproduction is extremely long in eagle owls (several dozens of years), and the phenomenon we observed may represent queuing for available/best breeding sites. This would be especially important for long-lived individuals, who may have greater lifetime reproductive success than individuals that breed immediately (Smith and Arcese 1989; Hogstad 1999). Queuing and consequent postponement of breeding are linked to fitness benefits and may originate from variations in the saturation or quality of breeding territories (Ekman et al. 1999).

It is also expected that the properties of the breeding population will contribute to shaping the behaviour and fate of floaters. As highlighted by McCarthy (1997, 1999), when (1) individuals disperse simultaneously from multiple nests (because of the saturation of the breeding sector of the population) and (2) the number of dispersers exceeds the availability of nesting sites, the closer that individuals are to the breeding population, the more likely they are to occupy vacant breeding places. Together with the effect of saturation of the breeding population (see also Rohner 1995, 1997b; Rohner and Smith 1996), the safer conditions of the dispersal area (e.g. food abundance and habitat availability in the TSAs; Penteriani et al. 2008) may lead floaters to postpone searching for nesting sites and may reduce active prospecting for breeding opportunities. Because of the relative proximity of TSAs to several breeding territories and in the absence of evident excursions close to the active nests, we could not discount the possibility that floaters obtained information on the saturation of the breeding population directly from the dispersal area.

The distances among conspecifics were generally low and the extent of TSA overlap was relatively high. This suggests that tolerance of conspecifics among eagle owl floaters is high until they reach the status of being territory owners, when male intolerance of intruding males can lead to lethal conflicts (Campioni et al. 2010). It is noteworthy that the percentage of TSA overlap was very similar to that documented for great horned owl floaters (23.3±4.8%; Rohner 1997b). Territoriality is now a well-recognised behaviour in several non-breeding species, and birds seem to actively defend distinct and minimally overlapping territories in response to some limiting resource (Brown et al. 2000). However, the broadly overlapping ranges of floaters in this study suggest a lack of territorial behaviour in non-breeding eagle owls (supporting the prediction that floating individuals are not spatially segregated), challenging the expectation that dominance by size and/or health status may determine the exclusive use of some portions of the dispersal area.

As reported by Rohner (1997a), floaters typically settle: (1) in nesting territories not occupied by a breeding pair, (2) in the spaces between different breeding territories, (3) in habitats unsuitable for breeding and (4) unobtrusively within the home range of territory owners. In view of the evidence of floaters partially sharing the same areas and living within the home range of territory owners, the question arises as to why an individual (independently if a neighbouring floater or a territory owner) would allow an alien individual to share the same resources. Following Smith (1978), this may occur because of a balance among three factors, namely: (a) the benefit to the owner of having floaters nearby, ensuring rapid mate replacement; (b) the disadvantage of sharing the same territorial resource with non-related individuals and (c) the investment in time and energy required to keep neighbours/floaters out of the territory. We suggest that the widespread availability of rabbits in the study area (Penteriani et al. 2008) is one of the most important factors determining tolerant behaviour. Because there was no competition for breeding sites (and consequently for mates) in the dispersal area and the main prey was readily available, floaters were 'neutral', not creating conflict nor being beneficial. Food abundance has previously been shown to influence some dispersal decisions (Coles et al. 2003).

Although the short distances among conspecifics and the extensive TSA overlaps allowed us to discard the possibility that neighbouring floaters represent a real cost during dispersal, it still remains unclear whether floaters took advantage of this proximity to evaluate future mates during dispersal. In fact, sexual interactions (e.g. distances among sexes) were not able to explain the dispersal settlement patterns in our study.

The floater interactions we found in the present study show a lack of clear mechanisms for avoidance of kin competition among offspring (of the same or different sex) or inbreeding (Szulkin and Sheldon 2008), being these causes of dispersal difficult to distinguish (Bowler and Benton 2005). In our study, dispersal did not appear to be associated with any evident mechanism of kin segregation because: (a) nest interactions (sibling−sibling vs. sibling−non-sibling proximity and spatio-temporal coincidences) were similar for the entire set of parameters analysed and (b) the distances separating sibling males from females were too short to prevent inbreeding and justify some kind of benefits with respect to intra-sexual competition (Greenwood 1980; Massot and Clobert 2000).

To sum up, the floating system we analysed highlights, perhaps unexpectedly, an 'underworld' of relationships that can be defined as 'limbo' interactions. That is, interactions apparently characterised by the absence of obvious social organisation or short-term strategies and generally lacking clear social dynamics. As an end consequence, the diverse results, interpretations and views derived from studies of the floater lifestyle point out a need for more studies on floater dynamics in species with different life histories, including short- vs. long-lived species, migrants vs. partially resident vs. territorial species. Such studies will enhance understanding of the factors responsible for determining the occurrence and number of non-breeding individuals as well as their social behaviour.

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The authors declare that they have no conflicts of interest.

The experiments comply with the current laws of the country in which they were performed (we marked owls under the Junta de Andalucía-Consejería de Medio Ambiente authorizations SCFFS-AFR/GGG RS-260/02 and SCFFS-AFR/CMM RS-1904/02)

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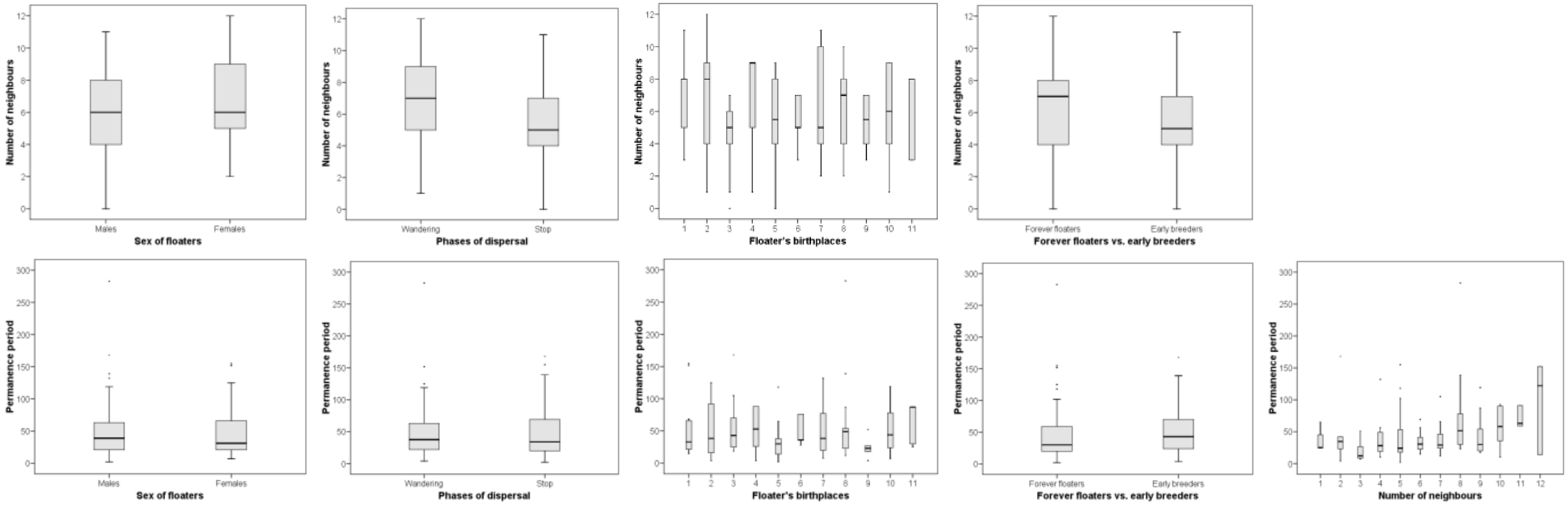
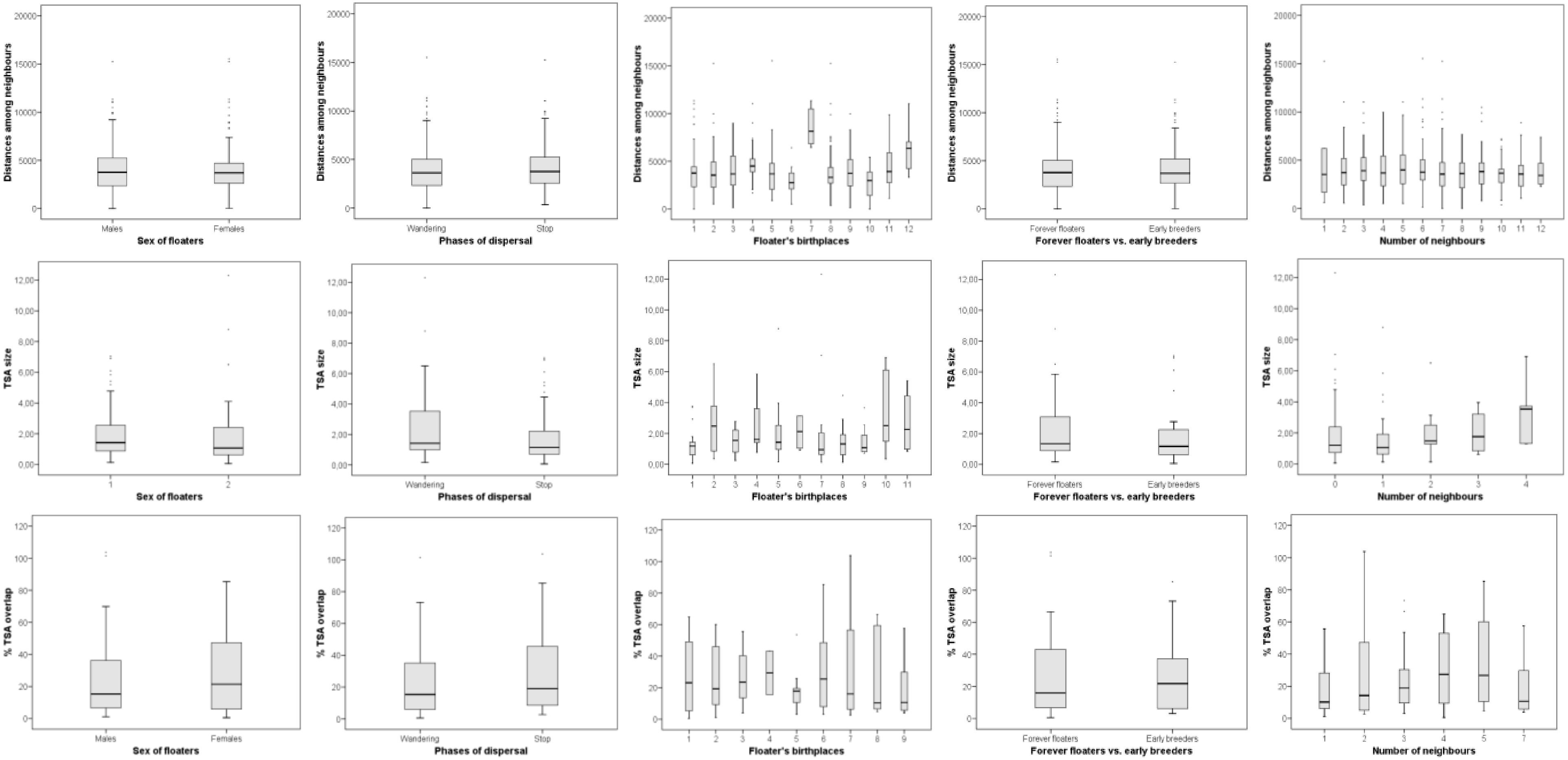
Electronic Supplementary Material 1. Patterns of the number of neighbours, permanence period, distances among neighbours, and size and overlap of temporary settlement areas with respect to the sex, phases of dispersal, birthplace and early breeding attempts of floaters (1A), and for the interactions between sexes, phases of dispersal and birthplace (1B). Although minor but non-significant differences were found (see text), the relationships among floating eagle owls appeared to be independent of the social environment and the various stages of the dispersal process.

ESM 1A




Distances among neighbours
0
5000
10000
15000
20000
Males
Females
Sex of floaters
Wandering
Stop
Phases of dispersal
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Floater's birthplaces
Forever floaters
Early breeders
Forever floaters vs. early breeders
1 2 3 4 5 6 7 8 9 10 11 12
Number of neighbours
TSA size
0,00
2,00
4,00
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1
2
Sex of floaters
Wandering
Stop
Phases of dispersal
1 2 3 4 5 6 7 8 9 10 11
Floater's birthplaces
Forever floaters
Early breeders
Forever floaters vs. early breeders
0 1 2 3 4
Number of neighbours
% TSA overlap
0
20
40
60
80
100
120
Males
Females
Sex of floaters
Wandering
Stop
Phases of dispersal
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Early breeders
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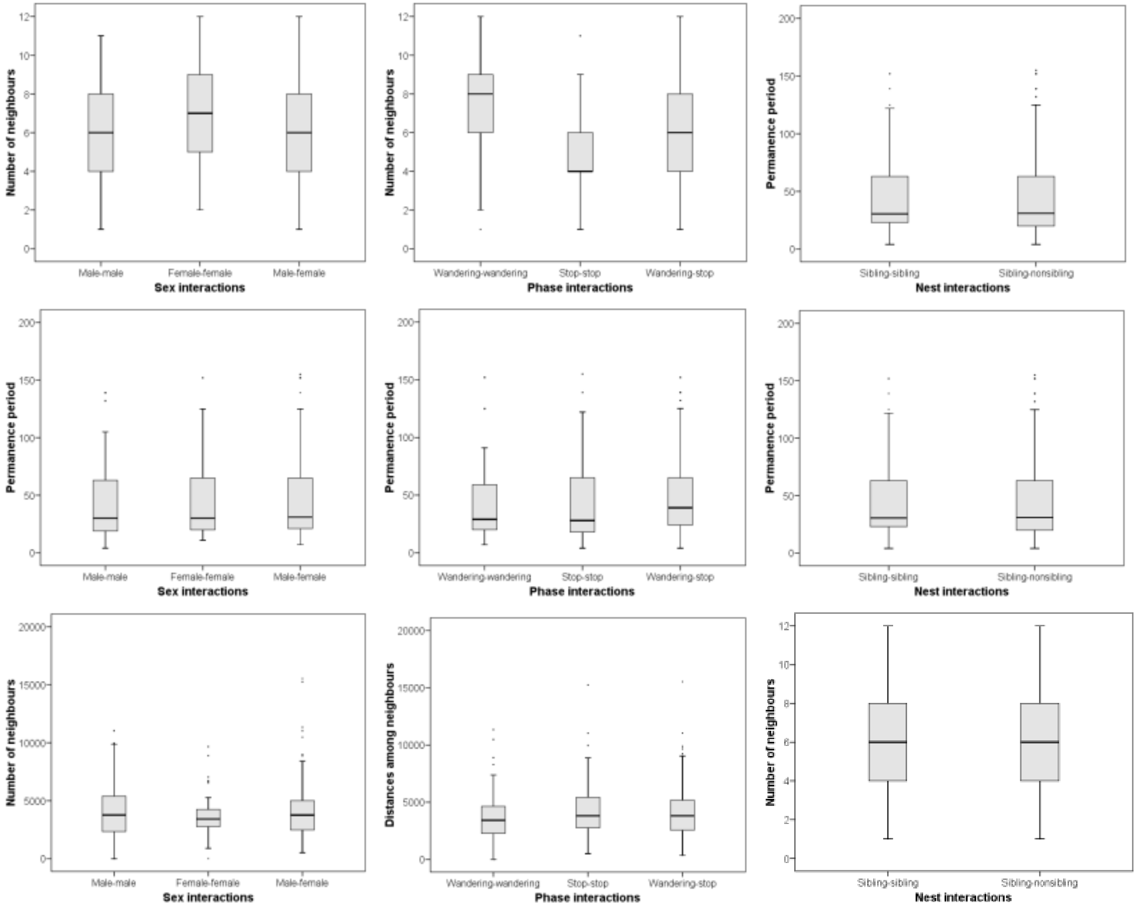
ESM 1B


Number of neighbours
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Phase interactions
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Sibling-nonsibling
Nest interactions
Permanence period
Male-male
Female-female
Male-female
Sex interactions
Permanence period
Wandering-wandering
Stop-stop
Wandering-stop
Phase interactions
Permanence period
Sibling-sibling
Sibling-nonsibling
Nest interactions
Number of neighbours
Male-male
Female-female
Male-female
Sex interactions
Distances among neighbours
Wandering-wandering
Stop-stop
Wandering-stop
Phase interactions
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Sibling-sibling
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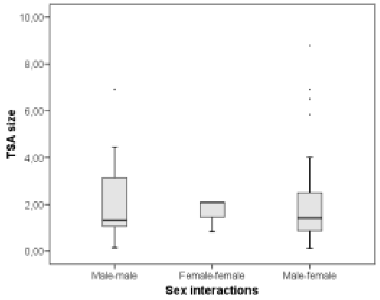
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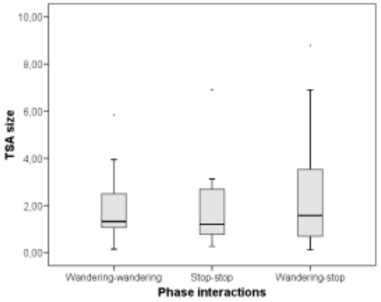
Male-female
Sex interactions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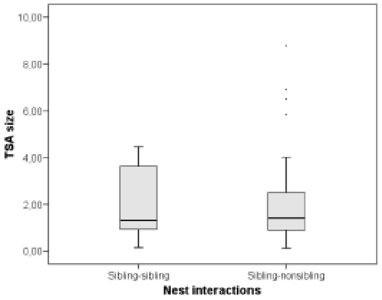
Phase interactions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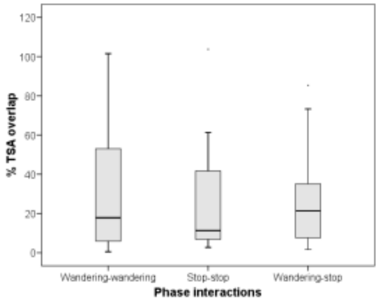
Nest interactions


% TSA overlap
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Wandering-wandering
Stop-stop
Wandering-stop
Phase interactions