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Eagle Owl *Bubo bubo* dispersal patterns and the importance of floaters for the stability of breeding populations

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Dispersionsmuster und die Bedeutung von Nichtbrütern (»floatern«) für die Stabilität von Brutpopulationen des Uhus *Bubo bubo*

Die Arbeit präsentiert vorläufige Daten zur Dispersionsdynamik des Uhus. Nach einer ersten Phase der aktiven Suche nach einem Ansiedlungsgebiet sind Uhus innerhalb eng begrenzter Reviere relativ standorttreu. Die räumliche und zeitliche Überschneidung der Aktivitätsräume von einzelnen Individuen wurde untersucht. Darüber hinaus werden die Ergebnisse einer individuenbasierten Simulation vorgestellt, die die entscheidenden Beziehungen zwischen dem Nichtbrüter- und brütenden Anteil innerhalb einer Population zeigen.

Keywords: breeding population, *Bubo bubo*, dispersal, Eagle Owl, floater, settlement area

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Introduction

Despite a large amount of theoretical and empirical studies on dispersal (e.g. Clobert et al. 2001, Nathan 2001, Paradis et al. 2002), several aspects of such animal movements are still unknown (Bennets et al. 2001). For example, few information are available on individual variation in dispersal behaviour, feeding strategies during dispersal, choice of settlement areas (i.e. temporary settling zones used by floaters during dispersal) and the process of floater integration within the breeding portion of a population.

In addition, few studies have been focused on the relationship between the nonbreeding segment of the population in the settlement areas (i.e. floaters) and the dynamics of the breeding pairs in the reproductive areas (Danchin & Cam 2002, Penteriani et al. 2005a,b).

Floaters (Brown 1969) refer to nonbreeding individuals that wander widely in *a secretive life* searching breeding opportunities. Moreover, settlement areas are usually unknown for most species and, for this reason: (a) the ecology and behaviour of nonterritorial individuals were poorly studied; and, as a consequence, (b) settlement areas were less protected than breeding territories. The effects of habitat loss, mortality rates, extinction probability and environmental stochasticity have frequently been ignored for floaters, but it is now essential to give more importance to this "invisible" and "undetectable" piece of animal populations. Population conditions (e.g. density, breeding performance, mortality) have been mostly checked on the breeding communities, but both habitat destruction and decreasing survival rates can also affect settlement areas and floaters, respectively. Finally, negative factors acting on floaters showed to strongly impact on the whole population trajectories (Penteriani et al. 2005a,b).

The aim of this study was two-fold. First, we presented preliminary information on some characteristics of the dispersal process of Eagle

Owls *Bubo bubo* in south-western Spain, that is: (a) the movement patterns in the dispersal searching paths; (b) the different settlement areas used by floaters; and (c) the integration rates of juveniles into the breeding population. Finally, we presented the outputs of an individual-based simulation to show: (a) the effects of an increase in floater mortality on the number of breeding pairs within breeding territories; and (b) the relationship between the availability of settlement areas and floater survival during dispersal.

Methods

A radiotracking study on Eagle Owl dispersal started in 2003 in the Sierra Norte (Sierra Morena massif), 20 km north of Seville (south-western Spain; for more details see Penteriani et al. 2005c). A combination of direct and indirect census methods (see Penteriani et al. 2001, 2002, 2003) allowed to detect the whole breeding pairs of our study area (46.91 km^2), where the density was of 36 pairs/100 km^2. The mean nearest neighbour distance (NND) between nests averaged 940.7 ± 387.1 m (range = 427.8-1621.5 m), that is the densest breeding population reported for the Eagle Owl in Europe (reviewed in Marchesi et al. 2002). We tagged by harness mounted backpacks of 30 g (Biotrack Ltd, Wareham BH20 5AJ, Dorset, UK) 8 juveniles in 2003, 17 in 2004 and 29 in 2005, but only data recorded during 2003 and 2004 are presented. Radios were equipped with mercury posture sensors that allowed us to record the activity patterns during all-night-long radiotracking of focal individuals. Locations of radio-marked animals were determined by triangulation using 3-element hand-held Yagi-antennas with Stabo (XR-100) portable receivers.

Tab. 1. Dates and ages of dispersal of Eagle Owls (*Bubo bubo*) in south-western Spain (Sierra Norte of Seville) during the 2003 and 2004 breeding seasons.

	2003	2004
Juveniles monitored	8	17
Earliest dispersal date	21 July	30 July
Latest dispersal date	3 October	30 October
Mean dispersal date	17 August	24 August
Earliest dispersal age (days)	144	131
Latest dispersal age (days)	204	222
Mean dispersal age (days)	162	170

To collect information on dispersal distances and patterns, as well as number of available settling zones in the study area, we recorded the exact position of each individual weekly. In addition to such single locations, and to assess Eagle Owl behaviour during dispersal, focal individuals were also monitored continuously from one hour before sunset to one hour after sunrise. We did continuous radiotracking two times per week throughout the whole years. Topographical 1:25 000 maps and GPS were used to plot the fixes. Triangulations were analysed by GIS software ArcView 3.2. We used the extension "Nearest Features v. 3.6 d" (Jenness 2002) to calculate dispersal distances. We identified 50 % core areas (i.e. the core area of activity) by Adaptative Kernel Countouring (Worton 1989) and, successively, we calculated overlap between them. We used least squares cross validation to select the smoothing width of core areas because it minimizes the estimated error for a given sample (Silverman 1986). This method was generated by the extension "Home Range" (Rodgers & Carr 2002). Also if methods of home-range analysis are generally considered as not useful to represent dispersal areas (Doerr & Doerr 2005), we considered that, due to the characteristics of owl settlements, such methods were helpful to represent spatial segregation between dispersal areas.

To test how floaters survival influences the dynamics of the whole population and explains puzzling decreases of breeding populations, we developed an individual-based simulation model (see Penteriani et al. 2005a,b for information on the simulation characteristics) to assess the consequences of: (a) an increase in mortality (from 5 to 30%) within settlement areas on the breeding population; and (2) availability of settlement areas on floater survival, in a array of situations, ranging from 2 to 15 settlement areas, for 1 to 15 floaters.

Results

Dispersal patterns. Most of the radiotagged juveniles stayed in their natal territories until the end of August. Main dispersal features were similar between 2003 and 2004 (Tab. 1). The mean dispersal distance among the years was 9.1 ± 8.2 km (range = 1.6-34.9 km). Dispersal distances were significantly different between years ($z = -2.0$, $p = 0.04$, $n = 9,6$; Mann-Whitney U-test), being higher in the last year.

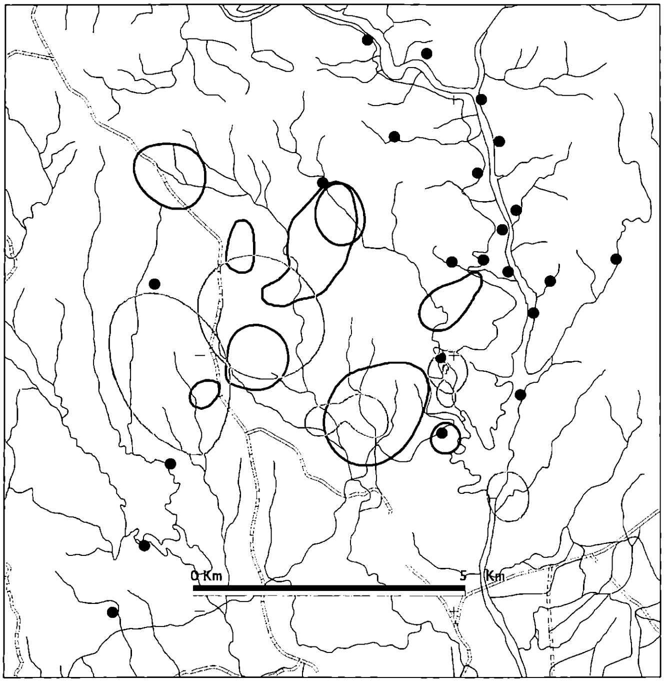

Fig. 1. An example of the spatial overlap among the 50 % core areas of ten Eagle Owl settlement areas during dispersal. Black contours represent the settlements of six owls tagged in 2003, whereas grey contours delimit the settlement areas of four owls marked in 2004. Black spots are occupied nests. – *Beispiel für die räumliche Überschneidung zwischen den 50 %-Kernrevieren (s. Methode) von 10 Uhus während des Dispersals. Schwarze Linien: Reviere von sechs im Jahr 2003 telemetrierten Uhus, graue Linien: Reviere von vier im Jahr 2004 telemetrierten Uhus. Punkte: besetzte Horste.*

Ten (40 %) of the 25 tagged owls died during the first two years of the study. 40 % of marked floaters settled and started reproduction in a breeding territory with ≥1 year of life; two mates of a breeding pair became from two different nests, separated by less than 500 m.

Settlement areas of different floaters overlapped broadly (Fig. 1). On average, core areas (i.e. the smallest area used by individuals) overlapped of more than 50 % (highest overlap = 98 %). Spatial overlap not always corresponded to temporal overlap, that is a same area was not always used in a synchronous way by more than one floater.

After the beginnings of dispersal (i.e. approx the first six months), during which owls were searching for an area in which to settle (Fig. 2), they remained in a relative stable and well-delimited area. At this moment, floater movements were similar to the movements of a territorial eagle owl (i.e. short movements within the settlement area and intensive use of focal areas; Delgado & Penteriani, unpublished data).

Floater dynamics affect breeding populations. Concerning the results of the simulation, we detected a significant decrease in the mean number of pairs in breeding territories when floater mortality within settlement areas varied from 5 to 30 %. In fact, the number of breeding pairs decreased by approx. five times when mortality within settlement areas increased from 5 to 30 %. In situation of low floater mortality (5 %), adult mortality in the breeding segment of the population was compensated for the demographic contribution of dispersers.

Finally, the probability that a floater survive during dispersal seemed to be strictly dependent to the number of available settlement areas ($r_s = 0.69$, $p = 0.0001$, $n = 210$; Fig. 3). That is, the higher the number of favourable settlement areas, the higher the number of individuals that can survive during dispersal.

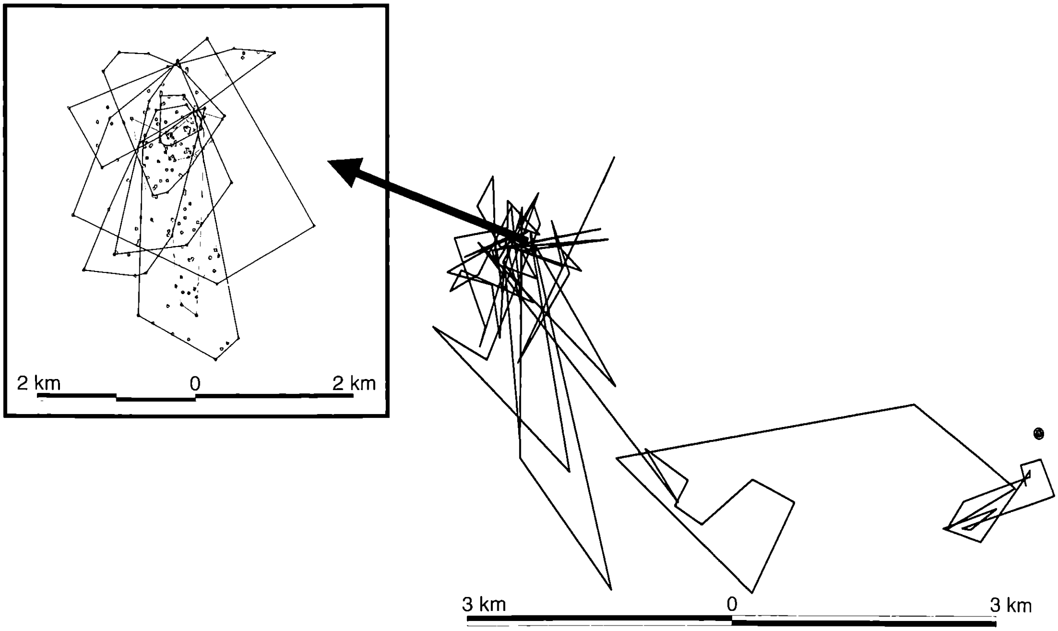

Fig. 2. Movement patterns of a same floater from the nest to his stable settlement area, as obtained by weekly localisations. In the upper detail are showed the movements recorded during continuous tracking (n = 13 nights). – *Aktivitätsmuster eines Nichtbrüters (»floaters«) vom Nest zu seinem Ansiedlungsgebiet, ermittelt anhand von wöchentlichen Ortungen. Das Detail (oben) zeigt die Ortsbewegungen während einer kontinuierlichen Telemetriephase von 13 Nächten.*

Discussion

Our preliminary data seem to highlight that, during dispersal, Eagle Owls quite rapidly shifted from an active "searching phase" (in which they explore for a settlement area) to a stable settlement in a well delimited area, moment in which they became relatively sedentary. Moreover, we found a spatial and, in many cases, temporal overlap among different individuals. These might have important conservation consequences. In fact, the effort to identify settlement areas by radiotracking is compensated by: (a) the temporal stability of such settlement areas; and (b) the fact that a same area can be used by several individuals over time.

Our simulation results highlighted the link between the dynamics within settlement and breeding areas. Floater survival, extremely dependent on the availability of settlement areas, influences the whole population persistence (Penteriani et al. 2005a,b), which is in agreement with earlier theoretical and empirical works (Klomp & Furness 1992, Ruxton et al. 1997, Casagrandi & Gatto 2002, Etienne et al. 2002). Therefore, it is crucial to consider the floater portion of a population when modelling population dynamics, the rate of floater mortality being able to shape population trajectories and persistence. We previously showed (Penteriani et al. 2005b) that, because fecundity is density-dependent, the breeding performance of a population is less sensitive to the initial increase in floater mortality. That is, at the beginning of a population decline due to high mortality of floaters, the relatively stable fecundity could generate the false impression that the population is healthy, even if some breeding territories are lost. Because the earliest deserted territories are in general the low quality ones (Liberatori & Penteriani 2001, Sergio & Newton 2003), the risk of extinction of the population could be overlooked. The definitive decline of breeding performance (and populations) will occur when mortality in the settlement areas makes mate replacement more and more difficult due of the lack of new individuals available to occupy empty territories. But such effect can become appreciable in the breeding sector of the population after more than 20 years (Penteriani et al. 2005b). Therefore, monitoring no more than the breeding

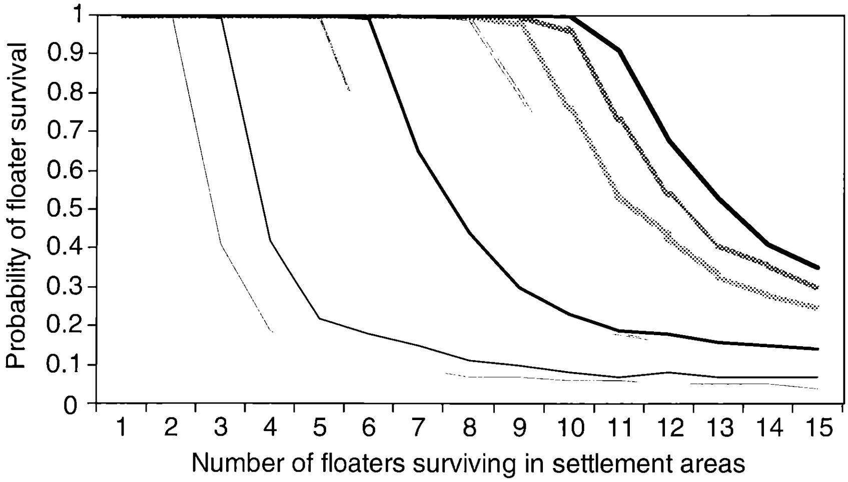

Fig. 3. The number of floaters that can survive during dispersal is highly dependent on the availability of settlement areas. The different line colours represent the survival probability for different number of individuals (from 1 to 15) depending on the number of available settlement areas, these latter ranging from light and thin grey (2 areas only) to bold and solid black (15 areas). – *Die Anzahl der Nichtbrüter (»floater«), die während des Dispersals überleben können ist vor allem von der Verfügbarkeit besiedelbarer Reviere abhängig. Die unterschiedlichen Linienfarben repräsentieren die Überlebenswahrscheinlichkeit für unterschiedliche Individuenzahlen (von 1 bis 15) in Abhängigkeit von der Verfügbarkeit besiedelbarer Reviere (von 2 Revieren – dünne graue Linien, bis 15 Reviere – fette schwarze Linie).*

portion of a population can be dangerous for the population conservation.

Generally, because the areas where dispersers settle in the dispersal stage are unknown or difficult to detect, fewer efforts are devoted to the conservation of these sites than to breeding territories, which can result in less successful conservation efforts. In many European countries (e.g. France, Germany and Italy), in which there are large areas occupied by human settlements, Eagle Owl floaters can experience high mortality rates (e.g. deaths by electrocution and car collision). Therefore, the main risk could be that conservation efforts are ineffective because they are focused on breeding areas only, when the real problem is located in the unknown settlement areas. In this case, the absence of information on the location of settlement areas and on the dynamics of individuals within them catch us unprepared to stop the progress of population declines.

To conclude, there is a critical need for empirical data on the area used during dispersal, because the information on the location of settlement areas and dispersal dynamics may represent the real solution to conservation concerns. The lack of such empirical data, largely due to the difficulty to track dispersing individuals over large territories, can be solved by radiotracking techniques. In many situations, the economic efforts required by radiotracking are today not higher than the ones required by the prospecting of breeding sites to collect information about the population breeding performance.

Summary

Preliminary data on main dispersal features of Eagle Owls are presented. After a first phase of active searching for a settlement area, Eagle Owls settled in well delimited zones and became relatively sedentary. Within settlement areas, both spatial and temporal overlap among different individuals were detected. Moreover, we reported the outputs of an individual-based simulation showing the crucial link between the floater and breeder portions of a same population.

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