Birthplace-dependent dispersal: are directions of natal dispersal determined a priori?

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Sib–sib or, more generally, family resemblance for dispersal seems a widespread characteristic of vertebrates, and the birthplace has the potential to shape the dynamics and features of animal populations. Dispersal studies have often stressed the fundamental link between the fate of dispersers and population dynamics, but few have focused on the dispersal directions of individuals, despite the profound implications that this may have on population distribution, structure, dynamics and viability. We investigated the directions followed by 72 radio-tagged dispersers (43 males and 29 females from 14 nest sites) in an eagle owl Bubo bubo population, and assessed their a) inter-individual distances during dispersal and b) age at dispersal departure. For siblings, as well as potential-siblings (i.e. individuals born in the same nest in different years), the birthplace influenced inter-individual distances and dispersal directions, i.e. dispersers from the same nest moved to similar locations during the study; moreover, in each year, individuals from the same birthplace moved across the same areas in a short time period. Finally, siblings and potential-siblings born in the same nest in different years started dispersal at similar ages. Based on the movement patterns of dispersers we discuss: a) the potential implications of the birthplace-dependent dispersal on the ideal free distribution theory, as well as in terms of kin competition, inbreeding avoidance and population dynamics; and, more generally, b) the effect of the temporal features of the natal dispersal on the concept of habitat suitability vs density of individuals developed by the ideal free distribution theory.

Several hundreds of papers have highlighted the complexity of natal dispersal (hereafter dispersal) and the various behavioural strategies related to its different stages, as well as the implications of dispersal in almost all aspects of ecology and evolution (most recently reviewed by Ronce 2007, Delgado and Penteriani 2008, Clobert et al. 2009). Dispersal directions may have profound implications on population distributions, structure and persistence (Schooley and Wiens 2003, Sharp et al. 2008): the spatial distribution of individuals, their consequent dynamics and associated risks of extinction, the directionality of genetic flows, and the probability of colonization events, are all associated with dispersal directions and the characteristics of animal movements. This raises the question of how these factors are affected by the starting location for this process: the trajectories of dispersing individuals have the potential to be determined a priori by the location of their birthplaces (i.e. birthplace-dependent dispersal).

The existing information on how a common origin might affect dispersal patterns and fates (Newton and Marquiss 1983, Tonkyn and Plissner 1991, Massot and Clobert 2000, Matthysen et al. 2005, 2010, Dale 2010), has stressed the crucial significance of the following for animal populations. a) Some traits determining dispersal patterns are both heritable and under the control of environmental influences (Pasinelli et al. 2004, Matthysen and 2005, Sharp et al. 2008, Doligez et al. 2009). b) Kinship structure, the spatial assortment of phenotypic traits and the likelihood of inbreeding are consequences of dispersal (van Tienderen and van Noordwijk 1988, Ronce et al. 2000, Matthysen et al. 2005, Szulkin and Sheldon 2008). c) Owing to the implications that homogeneous vs heterogeneous dispersal have on spatially structured populations (Doebeli and Ruxton 1998, Vuilleumier and Possingham 2006, Morrissey and de Kerckhove 2009) and source-sink systems (Dias 1996, Kauffman et al. 2004), various population scenarios are possible depending on whether siblings disperse by similar directions. d) Conservation implications may relate dispersal directions to habitat connectivity and fragmentation, habitat selection via conspecific attraction, and habitat-specific demography (Kauffman et al. 2004).

Additionally, as underlined by Holt and Barfield (2001), the process by which multiple dispersers move from a common birthplace and distribute freely can be considered in the context of the Fretwell and Lucas (1970) theory of the ideal free distribution (hereafter IFD), particularly in

relation to the movement of individuals under no territorial constraints (as is the case for dispersers). This can be explained as outlined below.

On one hand, the IFD can be defined as the theoretical model of the spatial distribution of individuals within an environment between locations that differ in quality. In this model, individuals have equal competitive abilities and are free to move (no costs, no interference with other individuals) to the location where their gains are greatest. If average gains per individual are unequal, some individuals will move to a better location until gains equalise, leading to equal intake rates in locations of different quality. Similarly, in this context, dispersal can be defined as the movement whereby an individual leaves its birthplace and, moving from one location to another, reaches an area somewhere else where it settle. In both definitions, the IFD theory and the ecological process of dispersal have two common components: 1) they both have a dynamic connection, the movement, which allows the individuals resident (or born) in one habitat to settle in another; and 2) the underlying assumption that individuals have no apparent constraints when moving across landscapes, i.e. they are free to move anywhere. During dispersal individuals are free to enter any habitat on an equal basis with residents because they do not show territorial behaviour (dispersing individuals may settle as floaters within breeders' territories; Rohner 1997).

Although the original IFD theory has served as a 'null model' for many theoretical and empirical explorations of animal distribution in space, most studies have focused on the IFD from the perspective of spatial distribution and competition for resources (Harper 1982, Kacelnik et al. 1992, Sutherland and Parker 1992, van der Meer and Ens 1997, Hugie and Grand 1998, Cressman and Křivan 2006, Flaxman and Reeve 2006). In attempting to explain individual distributions, successive modifications and tests of the original IFD model have mainly focused on behaviours and dynamics of individuals in a given environment, and not on the way individuals move in the space and reach such environment. As noted by Doncaster (2000), the dynamics of arrival to and departure from habitats have usually been ignored (but see Baguette et al. in press, for negative-density dependent dispersal promoting convergence towards the ideal free distribution when changes in habitat quality happen), despite being essential elements of the IFD. But the ways animals disperse have crucial roles in determining the fate of individuals and are an essential aspect of population studies (Schooley and Wiens 2003, Nathan 2008).

We describe here several movement parameters in the wandering and settlement phases of dispersal (Delgado and Penteriani 2008) in a population of eagle owls Bubo bubo, with the aim to detect if the directions of dispersal may be influenced a priori by the birthplace. This dispersal scenario may allow hypothesizing several implications for animal populations, mainly in the context of IFD, kin competition and inbreeding avoidance, and population dynamics. In particular, we could expect that: a) birthplace-dependent dispersal should represent an important factor affecting spatial patterns of hypothetically ideal-free distributed individuals. Birthplace may be an additive effect contributing to increased asymmetry in individual movements and distribution in those systems in which habitat

heterogeneity has been recognised as the unique source of deviation from symmetric patterns; and b) birthplace-dependent dispersal (as a form of heterogeneous dispersal) might indicate that the likelihood that the dispersal trajectories from the breeding population are uniformly distributed is a remote event.

It is well known that dispersal patterns are the result of both the internal state of dispersers (i.e. phenotype-dependent dispersal) and external factors (i.e. condition-dependent dispersal; Clobert et al. 2009, Delgado et al. 2010). But our main purpose here is to explore the possible influence of the nest location on dispersal and discuss its possible consequence at the level of population, and then we do not attempt to identify the possible different factors determining the birthplace-dependent dispersal (e.g. habitat structure, common ancestors, availability of food resources, intraspecific interactions). In addition, we consider that our scenario represents a conservative situation to recognize an effect of the nest location (in the sense of the original point of departure of dispersers) on dispersal patterns. Even if causal, the birthplace-dependent dispersal has the potential to be due to a biological process (e.g. sibling interactions during dispersal) or only to a simple geometrical effect. Indeed, inter-individual distances may just reflect the location of each nest site within the study area: if we consider siblings with random movements (and within the study area), they will remain closer between them than with individuals from a distant nest. But the features of our study population allow us excluding the presence of a geometrical (e.g. boundary) effect both for inter-individual distances and dispersal directions. Actually, a) the high density of the breeding territories ($^\sim$40 pairs/100 km^2) and, consequently, the short distance between the different active nests (range of distances: from $\mathbf{B}$250 m up to $^\sim$1 km); and b) the use of neighbouring nest sites (i.e. the nest sites were packed together within the same area) for our study purpose, prevented geometrical biases in our results. Furthermore, the peculiar dispersal pattern that we showed previously (i.e. global dispersal directions were associated to the direction of the dominant wind, Delgado et al. 2010), should have the potential to hide an effect of the birthplace, if this latter was not really evident. In fact, because wind strongly determined the whole dispersal directions of the study population, this former could mask an effect of the birthplace because both sibling and non-sibling followed a similar, main direction, the one of the dominant wind.

Study area and methods

From 2003 to 2007 we studied eagle owl dispersal in the Sierra Norte (Sierra Morena hills), 20 km north of Seville (southwest Spain). The scenery is extremely uniform (Delgado et al. 2010) because: a) is mainly composed by a continuous succession of low lying hills, ranging between 60 and 200 m in altitude; b) the absence of main valley systems, mountains or other geomorphologic elements constraining the spatial distribution patterns of individuals. The area is characterised by typical Mediterranean vegetation, mainly dominated by species belonging to the Quercus genus, such as the holm oak Quercus ballota

and gall oak Quercus faginea, mixed with scrublands, grazing of cattle and cultivated fields. Some sectors also inhabit pine trees Pinus pinea, olive trees Olea europea, lentisk Pistacea lentiscus and patches of eucalyptus Eucalyptus sideroxylon woods.

Radiotracking of dispersing individuals

The whole sample (sib and non-sib individuals) was represented by 72 individuals (43 males and 29 females; 2003: n$=$7; 2004: n$=$14; 2005: n$=$19; 2006: n$=$19; 2007: n$=$13) that dispersed from 14 nest sites (owlets from 2 nests were marked during four years, from 4 nests during three years, from 3 nests during two years and from 5 nests during one year). However, for sib–sib measurements our sample was of 49 individuals (30 males and 19 females) from 10 nest sites. At approximately 35 d old these individuals were radio-tagged with a teflon ribbon backpack harness carrying a 30 g radio transmitter (for more information on radio tracking procedures and triangulations see Delgado and Penteriani 2008, Penteriani et al. 2008, Delgado et al. 2009a, 2010). We attempted to locate the owls weekly at their diurnal roosts (n$=$1533 locations; mean time between consecutive owl locations ($\pm$ SD)$=$11$\pm$10 d) from the day dispersal of a particular owl started (mean age at the beginning of dispersal$=$170$\pm$20.5 d-old, range$=$131–232 d-old) to the day: a) it settled in a stable settlement area, i.e. the regions occupied for a fairly long period of time relative to the entire dispersal process, or until the bird becomes an owner of a breeding territory (mean dispersal age at the settlement phase$=$395$\pm$109.9 d-old, range$=$181–640 d-old; see Delgado and Penteriani 2008 for more details on the determination of the different dispersal stages); b) it died; or c) the radio transmitter failed. Accuracy of triangulations was of 83.5$\pm$49.5 m, estimated when, after a radiolocation, we needed to locate where exactly the individual was (e.g. to record the cause of mortality if it died). Dispersal distances ranged from 1.5 to 34.3 km (mean$\pm$SD$=$6.0$\pm$4.2 km). Individuals were aged (days since hatching) following Penteriani et al. (2005a), and were sexed by molecular procedures using DNA extracted from blood.

Characterization of the dispersal pattern

We first estimated the age of individuals at commencement of dispersal (see also Delgado and Penteriani 2008). Second, we calculated the direction of the dispersal trajectories, i.e. the direction of net movement from the natal site to the settlement area (angles were rounded to the nearest 30°). And finally, the between-disperser distances: this enabled representation of all possible combinations of distances between dispersing pairs using individual locations recorded simultaneously, or within a temporal bracket of up to 10 d (i.e. approximately. the mean time between consecutive owl locations). The restricted temporal bracket also allowed detection of possible: a) temporal coincidences in close locations (i.e. spatio-temporal interaction) within the same year; and b) spatial coincidences of different individuals over the years, during the same temporal bracket. Distances between dispersing individuals were recorded in terms of 1) sib–sib distances (n$=$422 paired measurements), 2) distances between potential-sibling, i.e. individuals born in the same breeding site in different years (because of the strong nest site fidelity of the species, when different nests within the same breeding site are used the distances among them are of only some dozens of meters; n$=$960 paired measurements), as well as 3) distances among non-sibling owls (i.e. individuals born in different nesting territories), calculated for both a) the same year only and b) over the whole study period.

Statistical analyses

Linear statistics

Because of the unbalanced structure of the data (i.e. different measurements for the same nest over several years) we built GLMMs (Littell et al. 2002) with a) ages of dispersal departure as the dependent variables and b) inter-individual distances during dispersal. We considered nest, year, sex of dispersing individuals and number of fledglings as the explanatory variables. We first applied a data exploration to verify 1) normality, 2) homogeneity, and 3) independence assumptions. Residuals of inter-distance and ages of dispersal departure were both homogeneous and independent. The residuals of the inter-individual distances model showed a skewed and leptokurtic distribution and this variable was thus modelled using lognormal distribution and the default identity link function (Littell et al. 2002). To test for the effect of the sex of dispersing individuals on the inter-individual distances we considered three categories (i.e. male–male, female–female, male–female distances), differences among sex were then calculated by the LSMEANS statement in SAS. The residuals of the ages of dispersal departure showed a normal distribution and, thus, this variable was modelled using a normal distribution and the default identity link function. The statistical analyses were performed with SAS procedure GLIMMIX. All models were built through a backward stepwise procedure where the least significant terms or interactions were sequentially removed until obtaining a minimal adequate model that only retained significant effects at the 5% probability level. For all analyses, results were reported as the mean $\pm$ SD, and the statistical significance level was set at a $\leq$0.05.

Circular statistics

When multiple factors have the potential to influence angular data like dispersal directions, there is a specific need to adapt statistical methods for such analysis (see the review on statistical methods for circular data of Marchetti and Scapini 2003). In fact, data on dispersal directions represent linear-circular regression models in which the parameters of distribution of the circular variable may depend on several linear explanatory factors (Marchetti and Scapini 2003). Following Presnell et al. (1998), the statistical approach used here is based on a distribution for the directions called projected normal distribution (see Marchetti and Scapini 2003 for more details). Regression models based on the projected normal distribution allow estimating the regression of the circular response on several variables simultaneously by likelihood tests of the effects of the variables, which represent a measure of discrepancy of

models from the null hypothesis of homogeneity (Marchetti and Scapini 2003). Predictor variables were the same as for linear statistics (i.e. nest, year, sex of dispersing individuals and number of fledglings). All analyses were performed using R software 2.9.0 statistical software (R Development Core Team 2009) and showed outputs are the difference between the —2 log likelihoods of the null and explaining model (W), the difference between the degrees of freedom of the null and explaining model (d), and the p value of the explaining model (Marchetti and Scapini 2003).

Results

Close inter-individual distances and similar dispersal ages characterise dispersal of individuals from the same nest

Between-disperser distances were affected by the nest (F$=$23.29, DF$=$885, p$<$0.0001), with the birthplace determining how close individuals remained during the dispersal process, and by the sex (F$=$4.56, DF$=$885, p$<$0.01; LSMEANS: all p$<$0.0001 for the three categories). In particular, although sib–sib distances ranged from 75 m to 38.5 km, the mean distance ($\pm$SD) separating sib–sib over the whole dispersal process was only 5053$\pm$4888 m (n$=$422 paired measurements; Fig. 1). Distances among non-siblings born in the same year were higher (range$=$508 m–40.9 km; mean$\pm$SD$=$7476$\pm$6582 m; n$=$3117 paired measurements). The closest proximity was among male siblings (mean$\pm$SD$=$4204$\pm$3287 m), the next closest was among female siblings (mean$\pm$SD$=$4851$\pm$4958 m), and the furthest was among siblings of the opposite sex (mean$\pm$SD$=$6136$\pm$5978 m). The effect of birthplace also means that dispersing individuals that were born in the same nest during the study years (i.e. potential siblings) also tended to remain closer than non-siblings during dispersal (mean$\pm$SD$=$5072$\pm$4471 m, range$=$79 m to 31.3 km, n$=$960 paired measurements). For these
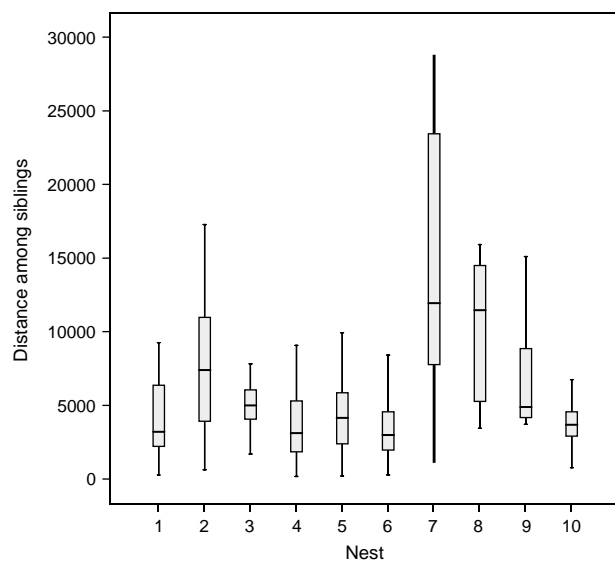
individuals the least distance was among females (mean$\pm$SD$=$3893$\pm$3631 m), the next closest was among males (mean$\pm$SD$=$5281$\pm$4604 m), and the furthest was among individuals of the opposite sex (mean$\pm$SD$=$5438$\pm$4622 m). Again, distances among non-siblings born over the whole study period were higher (range$=$100.2 m–49.8 km; mean$\pm$SD$=$7011$\pm$6341 m; n$=$377462 paired measurements).

It is important to highlight that in assessing inter-individual distances, we only analyzed those locations that were coincident within the 10-d temporal bracket. This not only suggests that individuals from the same birthplace were closer during dispersal, but also that they explore approximately the same areas within a time period of only 1—10 d, and this pattern was observed year after year.

Birthplace also influenced the age at which dispersal started (mean age at the beginning of dispersal$=$170$\pm$20.5 d, range$=$131–232 d), in both siblings (F$=$4.98, DF$=$41, p$=$0.0001) and potential-siblings born in the same natal area (F$=$3.97, DF$=$41, p$=$0.0003), dispersing from their natal place at similar ages. The age of dispersal was also affected by year (F$=$6.68, DF$=$41, p$=$0. 0003).

Individuals from the same nest disperse in similar directions

The short distances found among dispersers from the same nest over the study period suggest that, independently of whether they were real or potential-siblings, individuals born in the same nest frequented nearby to each other areas during dispersal. This pattern was even more evident when analysing the directions of dispersal (Fig. 2). In fact, the birthplace (W$=$39.49, d$=$26, p$=$0.044) seemed to have an important role in determining the direction of dispersal: individuals born in the same nest in different year (i.e. not only siblings) dispersed in similar directions.

Discussion

Results mainly suggest a dispersal scenario where the birthplace influences (at least in part) the distances among individuals and dispersal directions for eagle owls born in the same nest. That is, from year to year dispersers from the same nest dispersed to similar areas. Moreover, for both siblings and potential-siblings, dispersal started at similar ages.

Birthplace has previously been recognised as a postnatal effect (Matthysen et al. 2005) contributing to the sibling's dispersal patterns. Our data support this previous result and suggest that dispersal behaviour of offspring born in the same natal place can be affected by the birthplace location. Birthplace may influence dispersal patterns owing to: a) their relationship with the spatial distribution of possible destinations (van Noordwijk 1984, Arcese 1989); and b) the specific surroundings (Matthysen 2002).

Similarities in sib–sib or other family dispersal patterns seem to be a widespread characteristic in vertebrates (see review in Massot and Clobert 2000). Interfamily variability in dispersal can indicate the non-mutually exclusive

Figure 1. Patterns of natal dispersal of eagle owl siblings, as revealed by inter-individual distances.
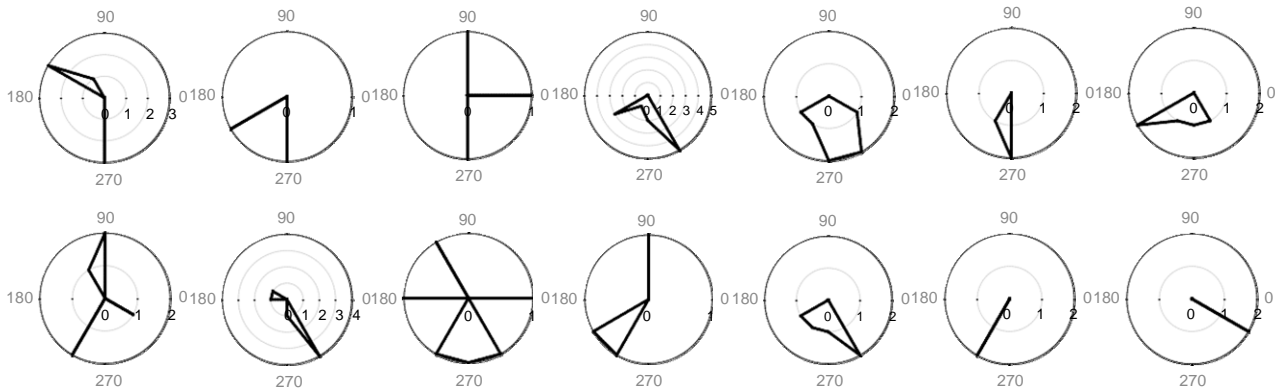
Figure 2. The dispersal directions of individuals from the same nest (each nest is represented by a different polar plot) show that different individuals born in the same nest in different year disperse in similar directions, as shown by the frequencies of angles followed by dispersing eagle owls. Numbers on circles show numbers of individuals following each direction.

influence of a common natal environment and ancestry (genetic determinant of dispersal; Doligez et al. 2009), acting at different times in the offspring life cycle (Massot and Clobert 2000, Pasinelli et al. 2004). The effect of a common parent on dispersal patterns (see also Ronce et al. 2000, Pasinelli et al. 2004) is likely in our biological model due to the long life of eagle owls and their fidelity to the breeding site. A further non-mutually exclusive explanation of the recorded patterns of dispersal of eagle owls may be postfledging behaviour. The siblings association during predispersal activity may influence the similarity of dispersal directions (Alberico et al. 1992). When young owls are >100 d old, eagle owl families may travel considerable distances together (Delgado et al. 2009b), a behaviour that has also been recorded for other birds (Matthysen et al. 2005, 2010, Sharp et al. 2008; but see Newton and Marquiss 1983). This behaviour has the potential to influence both dispersal directions of offspring and their close proximity after the family breakup (i.e. the excursions may have familiarised the offspring with the surroundings of their birthplace; Drent 1984, Matthysen 2002, Matthysen et al. 2005).

Distances among relatives, kin competition & inbreeding avoidance

As one of the key determinants of the geographical distribution of individuals, dispersal has been considered one of the main factors in gene flow patterns (Gandon 1999, Ronce et al. 2000, Clobert et al. 2004, Ronce 2007). 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 should be favoured by selection (Motro 1991, Leturque and Rousset 2002, Roze and Rousset 2005, Szulkin and Sheldon 2008). The dispersal scenario that we highlighted in the present study did not indicate obvious mechanisms for avoidance of kin competition among offspring (of the same or opposite sex), or inbreeding (being these causes of dispersal difficult to separate, Bowler and Benton 2005). This is because: a) a mean between-disperser distance of ca 5 km among both siblings and potential-siblings would not be sufficient

to avoid interactions among individuals of this species, particularly if siblings disperse in the same direction (Fig. 2); and b) the differences in the distances separating males from females can be considered too short to prevent inbreeding, and justify a difference in dispersal costs and benefits with respect to intrasexual competition (Greenwood 1980, Massot and Clobert 2000). This may also be true for potential-siblings because there is a high probability that the parents were the same (although few cases of breeding dispersal has been recorded in the study population; Penteriani and Delgado unpubl.).

Temporal sequences of dispersal and IFD theory

There is a notable relationship between the IFD theory and the fact that bird dispersal is characterised by temporal sequences. Dispersal is: a) a multiphase process that starts from departure from the natal area and, via the wandering phase, ends in a breeding or a temporary settlement area (Delgado and Penteriani 2008, Clobert et al. 2009); and b) a process characterised by temporal waves of emigrations/immigrations that are subsequent to the postfledging dependent period. As shown in this study, individuals from the same natal area start dispersal at similar ages and visit the same areas at approximately the same times. Both these temporal properties are intrinsic to dispersal and highlight that time is an important feature of the process, as shown in Fig. 3. One of the main assumptions of the IFD concerns habitat suitability, which always decreases with bird density; maximum suitability occurs when the density approaches zero (i.e. basic suitability, defined as B_i for the ith habitat, is affected by predators, food density and cover). Fretwell and Lucas (1970) expressed the suitability (S_i) of the ith habitat as a function of B_i and the density d_i:

$$S_i = B_i - f_i (d_i); \ i = 1; 2; \ldots N \qquad (1)$$

where $f_i (d_i)$ expresses the effect of an increase in bird density on reducing suitability; $f_i (d_i)$ always increases with density, S_i always decreases. This equation was assumed to not change with time, and an example for a particular value of i is plotted in Fig. 3A (a redrawing of the original draft of Fretwell and Lucas (1970)). When applying this equation to

(A)

S_I

B_I

$f_I\,(d_I)$

S_I

d_I

(B)

S_I

B_I

$f_I\,(d_I)_{t_1}$

$f_I\,(d_I)_{t_2}$

(a)

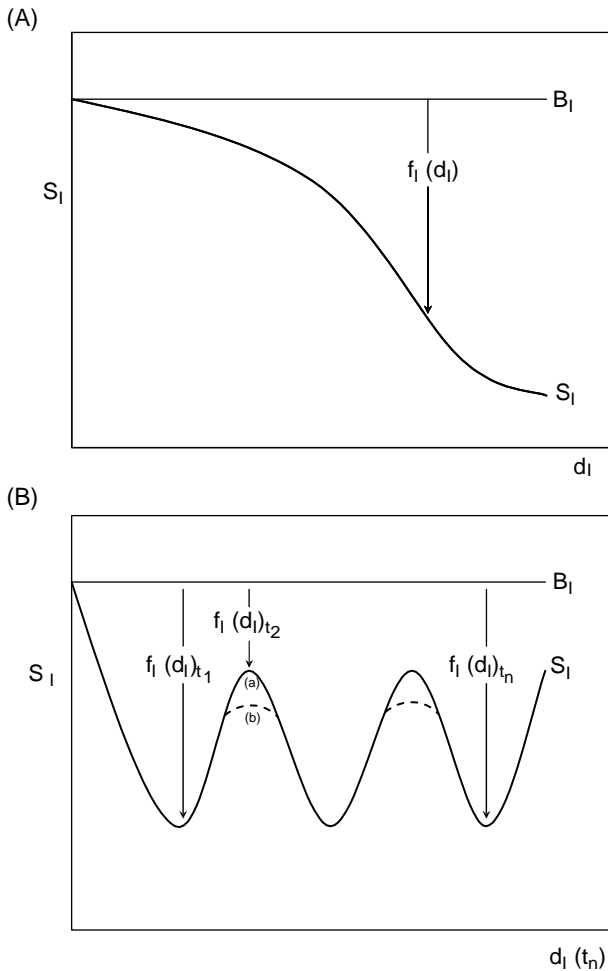(b)

$f_I\,(d_I)_{t_n}$

S_I

$d_I\,(t_n)$

Figure 3. The concept of habitat suitability vs density of individuals (A) according to the ideal-free distribution (a redrawing of the original draft of Fretwell and Lucas 1970) and (B) adjusted to the natal dispersal and its temporal features (see text for more details). In both graphs the suitability (S_I) of the Ith habitat is represented as a function of the basic suitability (B_I) for the Ith habitat and the bird density (d_I), where the term $f_I\,(d_I)$ expresses that an increase in density reduces suitability. With respect to the ideal-free distribution, S_I is assumed to be constant through time (Fretwell and Lucas 1970). However, with respect to dispersal, $f_I\,(d_I)$ is also subject to the effect of the time (t; the period of the year + the phase of dispersal when individuals enter the Ith habitat), so S_I varies through time. The period of the year reflects those variations in habitat suitability linked to the waves of emigrations/immigrations of bird dispersers that are generated after the postfledging dependence period, i.e. when all the offspring of the same population start dispersal more or less at the same time. After these periodic 'invasions', successive displacements and mortality reduce the density of individuals in a given habitat, and this allows it to recover some of its original suitability. However, the recovery is not the same if the habitat was occupied by dispersers in the wandering or settlement phase. Because the former is an exploratory and very dynamic stage of dispersal, individuals make shorter stays. Consequently habitat suitability may recover more in this phase (a, solid line) than during the settlement phase (b, dotted line), when some dispersers usually establish more or less fixed home ranges, increasing the density more permanently in a given habitat.

dispersal, for the temporal features of this process we stress the need for including the effect of time on habitat suitability in the eq. 1, that is:

$$S_i = B_i - f_i\,(d_i)_{ti};\ i = 1; 2;\ \dots N \qquad (2)$$

where $f_i\,(d_i)_{ti}$ expresses varying suitability depending on the time-dependent increase/decrease in the density of dispersers. With respect to time, habitat suitability as a function of density may show more complex variations (Fig. 3B) depending on: 1) the period of the year, with the effect of density being greater in the months succeeding the postfledging dependence period, the density being altered (i.e. conspecific density increases) when all the new-born start the wandering phase and 'invade' habitats; and 2) the phase of dispersal of the individuals entering the ith habitat.

Whereas during the exploratory wandering phase individuals move among different habitats and density increases are generally limited in time (from hours to days), the stop phase in a settlement area indicates permanence, which leads to a longer density increase.

Although we focused here on the temporal features of the dispersal process on habitat suitability only, it is also important to consider the possibility that the density effect may change of sign at temporal intervals. This may be especially true in vertebrates in which clusters of offspring stay together in the early life phases (e.g. to search protection, to exchange information on the environment). Consequently, increased densities may increase habitat quality (when thinking in terms of fitness).

Hypothetically free to distribute individuals constrained by the birthplace, and other non-IFD distributions

When the IFD fails to match field data is mainly because of the simplistic assumptions about the behaviour of individuals (Kacelnik et al. 1992). Successive adjustments of the original model have shown that behavioural properties of real individuals can affect and modify their theoretical distribution (Hugie and Grand 1998). Now, the birthplace-dependent dispersal should be considered an additive factor affecting spatial patterns of hypothetically ideal-free distributed dispersers, and birthplace-dependent movements may be considered as a new type of so-called 'non-IFD movements' (Hugie and Grand 1998).

Heterogeneity among dispersers choices does not necessarily ends up in a non-IFD, the reasoning behind IFD being that individuals are distributing themselves such that every individual achieve equal fitness, i.e. this is not entailing that individuals have to disperse the same way or for similar reasons (McPeek and Holt 1992, Clobert et al. 2009). Nevertheless, several case studies have detected different scenarios in which heterogeneity in dispersal choices can lead to a non IFD (i.e. alteration of the steady-state predicted by ideal free conditions): a) landscape structure and spatial arrangement of habitat patches may affect the species propensity to switch between spatial locations, consequently challenging the assumption that all locations or habitats are equally accessible by dispersers

(Fahrig and Merriam 1994, Diffendorfer et al. 1995); b) because the dynamics of arrival and departure that sustain ideal free distributions may have peculiar dynamic, aggregations may never achieve ideal free model equilibriums if, for example, the system is always under- or over-exploited with respect to resource restoration (Doncaster 2000, Yates et al. 2000); c) the appearance of morphological and behavioural dispersal type (i.e. dispersal syndrome, Clobert et al. 2009) have the potential to engender patterns of individual distribution that are unexpected under the perspective of the IFD (Cote and Clobert 2007); d) when rates of dispersal are driven by kin competition and inbreeding depression (Ronce et al. 2000, Rousset and Billiard 2000, Rousset and Gandon 2002, Roze and Rousset 2005), the interactions among kin have the potential to determine patterns of dispersal that deviate from an IFD; and e) if dispersal is costly, deviations from the IFD can be expected (Leturque and Rousset 2002, Rousset and Gandon 2002).

Finally, it is worth noting that, although the IFD concept has been applied on dispersal among populations, we related it to a 'within population' level. Classical (meta)population systems represent an extreme form of patchiness, their dynamics strictly depending on dispersal (Hanski 1999). But also when looking at the level of a single population, this latter can be spatially structured (i.e. breeders and floaters), which dynamics depend critically upon dispersal patterns. Some mechanisms that work among populations (e.g. information acquisition, habitat matching; Hanski and Saccheri 2006, Benard and McCauley 2008) may decrease the within-population connectivity and, consequently, be responsible of individual/population sector dynamics and persistence.

Birthplace-dependent dispersal as a form of heterogeneous dispersal

There is considerable evidence for heterogeneous dispersal: a) heterogeneous dispersal has been recognised for habitats with unequal carrying capacities determining a balanced dispersal (Doncaster et al. 1997); dispersal is heterogeneous because it can be inversely related to habitat-carrying capacity; and b) the spatial distribution of dispersing individuals is commonly non-random because homogeneous dispersal requires perfectly symmetric environments (Vuilleumier and Possingham 2006). Differences in habitat quality and structure, density of conspecifics, and prey abundance are among the main factors determining heterogeneous flows of individuals (Pulliam 1988). Intriguingly, the common origin of all those factors that engender heterogeneous patterns of dispersal could be found at the birthplace. Birds born at the same nest site may face the same constraints when dispersing and, as shown in our study, should demonstrate heterogeneous dispersal flows. We also showed that the phenomenon of directional dispersal is constant over time, i.e. individuals born in the same birthplace follow similar dispersal directions over the years. These spatial and temporal asymmetries may have

crucial consequences for population structure, dynamics and stability (Kauffman et al. 2004, Vuilleumier and Possingham 2006). If persistence depends on specific non-random directions of dispersal, loss of connection among populations owing to the loss of such specific links of immigrations will increase the risk of reduced viability and extinction. Thus, population persistence is directly related to knowledge of the directions followed by potential immigrants. Dispersal shows annual, temporally limited migration events, so environmental stochasticity coincident with dispersal flows represents an additional process limiting population persistence. Additionally, if environmental stochasticity affecting breeders in a population acts synchronously with its effects on dispersers, the risk of extinction of populations increases (Penteriani et al. 2005b).

Our dispersal scenario showed directional patterns at both the birthplace (all offspring move in a unique direction) and population levels (several directions were never followed by any dispersers): future studies should continue to investigate real dispersal patterns under various environmental scenarios. The assumption that extreme dispersal situations are theoretical artefacts may be erroneous and lead to incorrect interpretations of this ecological process, and predictions of population dynamics. In conclusion, the fate of dispersers seems to be 'assigned' from birth and to depend on the location of the natal site. This is largely a predetermined process, with consequences that may have profound effects in all situations in which dispersal has been shown to have ecological implications.

References

Alberico, J. A. R. et al. 1992. Non-random philopatry of sibling spotted sandpipers Actitis macularia. – Ornis Scand. 23: 504–508.

Arcese, P. 1989. Intrasexual competition, mating system and natal dispersal in song sparrows. – Anim. Behav. 38: 958–979.

Baguette, M. et al. in press. Metapopulation dynamics of the bog fritillary butterfly. Experimental changes in habitat quality induced negative density-dependent dispersal. – Ecography.

Benard, M. F. and McCauley, S. J. 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. – Am. Nat. 171: 553–567.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Clobert, J. et al. 2004. Causes, mechanisms and consequences of dispersal. – In: Hanski, I. and Gaggiotti, O. E. (eds), Ecology, genetics, and evolution of metapopulations. Academic Press, pp. 307–335.

Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and dynamics of spatially structures populations. – Ecol. Lett. 12: 197–209.

Cote, J. and Clobert, J. 2007. Social information and emigration: lessons from immigrants. – Ecol. Lett. 10: 411–417.

Cressman, R. and Křivan, V. 2006. Migration dynamics for the ideal free distribution. – Am. Nat. 168: 384–397.

Dale, S. 2010. Sibling resemblance in natal dispersal distance and direction in the ortolan bunting Emberiza hortulana. – Ibis 152: 292–298.

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

Delgado, M. M. et al. 2009a. Changes of movement patterns from early dispersal to settlement. – Behav. Ecol. Sociobiol. 64: 35–43.

Delgado, M. M. et al. 2009b. How fledglings explore surroundings from fledging to dispersal? A case study with eagle owls. – Ardea 97: 7–15.

Delgado, M. M. et al. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. – J. Anim. Ecol. 79: 620–632.

Dias, P. C. 1996. Sources and sinks in population biology. – Trends Ecol. Evol. 11: 326–330.

Diffendorfer, J. E. et al. 1995. Habitat fragmentation and movements of three small mammals (Simodon, Microtus, and Peromyscus). – Ecology 76: 827–839.

Doebeli, M. and Ruxton, G. D. 1998. Stabilization through spatial pattern formation in metapopulations with long-range dispersal. – Proc. R. Soc. B 265: 1325–1332.

Doligez, B. et al. 2009. 'Heritability' of dispersal propensity in a patchy population. – Proc. R. Soc. B 276: 2829–2836.

Doncaster, C. P. 2000. Extension of ideal free resource use to breeding populations and metapopulations. – Oikos 89: 24–36.

Doncaster, C. P. et al. 1997. Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. – Am. Nat. 150: 425–445.

Drent, P. J. 1984. Mortality and dispersal in summer and its consequences for the density of great tits Parus major at the onset of autumn. – Ardea 1972: 127–162.

Fahrig, L. and Merriam, G. 1994. Conservation of fragmented populations. – Conserv. Biol. 8: 50–59.

Flaxman, S. M. and Reeve, H. K. 2006. Putting competition strategies into ideal free distribution models: habitat selection as a tug of war. – J. Theor. Biol. 243: 587–593.

Fretwell, S. D. and Lucas, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 19: 16–36.

Gandon, S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. – J. Theor. Biol. 200: 345–364.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – Anim. Behav. 28: 1140–1162. Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Hanski, I. and Saccheri, I. 2006. Molecular-level variation affects population growth in a butterfly metapopulation. – PLOS Biol. 4: e129.

Harper, D. G. C. 1982. Competitive foraging in mallards: 'ideal free' ducks. – Anim. Behav. 30: 575–584.

Holt, R. D. and Barfield, M. 2001. On the relationship between the ideal free distribution and the evolution of dispersal. – In: Clobert, J. et al. (eds), Dispersal. Oxford Univ. Press, pp. 83–95.

Hugie, D. M. and Grand, T. C. 1998. Movement between patches, unequal competitors and the ideal free distribution. – Evol. Ecol. 12: 1–19.

Kacelnik, A. et al. 1992. The ideal free distribution and predator–prey populations. – Trends Ecol. Evol. 7: 50–55.

Kauffman, M. J. et al. 2004. Spatial structure, dispersal, and management of a recovering raptor population. – Am. Nat. 164: 582–597.

Leturque, H. and Rousset, F. 2002. Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. – Theor. Popul. Biol. 62: 169–180.

Littell, R. C. et al. 2002. SAS for linear models, 4th ed. – SAS Inst., Cary.

Marchetti, G. M. and Scapini, F. 2003. Use of multiple regression models in the study of sandhopper orientation under natural conditions. – Estuar. Coast. Shelf Sci. 58S: 207–215.

Massot, M. and Clobert, J. 2000. Processes at the origin of similarities in dispersal behaviour among siblings. – J. Evol. Biol. 13: 707–719.

Matthysen, E. 2002. Boundary effects on dispersal between habitat patches by forest birds (Parus major, P. caeruleus). – Landscape Ecol. 17: 509–515.

Matthysen, E. et al. 2005. Do sibling tits (Parus major, P. caeruleus) disperse over similar distances and in similar directions? – Oecologia 143: 301–307.

Matthysen, E. et al. 2010. Family movements before independence influence natal dispersal in a territorial songbird. – Oecologia 162: 591–597.

McPeek, M. A. and Holt, R. D. 1992. The evolution of dispersal in spatially and temporally varying environments. – Am. Nat. 140: 1010–1027.

Morrissey, M. B. and de Kerckhove, D. T. 2009. The maintenance of genetic variation due to asymmetric gene flow in dendritic metapopulations. – Am. Nat. 174: 875–889.

Motro, U. 1991. Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. – Am. Nat. 137: 108–115.

Nathan, R. 2008. An emerging movement ecology paradigm. – Proc. Natl Acad. Sci. USA 105: 19050–19051.

Newton, I. and Marquiss, M. 1983. Dispersal of sparrowhawks between birthplace and breeding place. – J. Anim. Ecol. 52: 463–477.

Pasinelli, G. et al. 2004. Genetic and environmental influences on natal dispersal distances in a resident bird species. – Am. Nat. 164: 660–669.

Penteriani, V. et al. 2005a. Development of chicks and pre-dispersal behaviour of young in the eagle owl Bubo bubo. – Ibis 147: 155–168.

Penteriani, V. et al. 2005b. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. – Oikos 108: 523–534.

Penteriani, V. et al. 2008. Owls and rabbits: predation against substandard individuals of an easy prey. – J. Avian Biol. 39: 215–221.

Presnell, B. et al. 1998. Projected multivariate linear models for directional data. – J. Am. Stat. Assoc. 93: 1068–1077.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.

R Development Core Team 2009. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, <www.R-project.org>.

Rohner, C. 1997. Non-territorial 'floaters' in great horned owls: space use during a cyclic peak of snowshoe hares. – Anim. Behav. 53: 901–912.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Ronce, O. et al. 2000. Kin selection and natal dispersal in an age-structured population. – Theor. Popul. Biol. 58: 143–159.

Rousset, F. and Billiard, S. 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. – J. Evol. Biol. 13: 814–825.

Rousset, F. and Gandon, S. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. – J. Evol. Biol. 15: 515–523.

Roze, D. and Rousset, F. 2005. Inbreeding depression and the evolution of dispersal rates: a multilocus model. – Am. Nat. 166: 708–721.

Schooley, R. L. and Wiens, J. A. 2003. Finding habitat patches and directional connectivity. – Oikos 102: 559–570.

Sharp, S. P. et al. 2008. Natal dispersal and recruitment in a cooperatively breeding bird. – Oikos 117: 1371–1379.

Sutherland, W. J. and Parker, G. A. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. – Anim. Behav. 44: 345–355.

Szulkin, M. and Sheldon, B. C. 2008. Dispersal as a means of inbreeding avoidance in a wild bird population. – Proc. R. Soc. B 275: 703–711.

van der Meer, J. and Ens, B. J. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. – J. Anim. Ecol. 66: 846–858.

van Noordwijk, A. J. 1984. Problems in the analysis of dispersal and a critique on its 'heritability' in the great tit. – J. Anim. Ecol. 53: 533–544.

van Tienderen, P. H. and van Noordwijk, A. J. 1988. Dispersal, kinship and inbreeding in an island population of the great tit. – J. Evol. Biol. 2: 117–137.

Tonkyn, D. W. and Plissner, J. H. 1991. Models of multiple dispersers from the nest: predictions and interference. – Ecology 72: 1721–1730.

Vuilleumier, S. and Possingham, H. P. 2006. Does colonization asymmetry matter in metapopulation? – Proc. R. Soc. B 273: 1637–1642.

Yates, M. G. et al. 2000. Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). – J. Anim. Ecol. 69: 314–322.