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Original Article

Evolution of natal and breeding dispersal: when is a territory an asset worth protecting?

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Evolutionary models of dispersal frequently lack explicit reference to the age or sex of the individuals that disperse. This contrasts with reality where dispersal behavior strongly depends on individuals' state, including age. To study why natal dispersal occurs more commonly than breeding dispersal, we investigate the interplay of 2 categories of explanation: the asset-protection principle (APP) and the "multiplier effect" (ME). The APP states that adults in possession of territories should be more reluctant to disperse. According to the ME, the simple fact of being born tells individuals that the site is of high quality, which may promote philopatry. Our model is set in habitats of spatially varying quality and individuals express different dispersal rates depending on state (life-history stage, sex, and quality of residential habitat). The model considers the accuracy of information about habitat quality, the proportion of good quality habitat, and the magnitude of habitat quality variation. We show that the predictions of the APP hold, but only when the "invisible" asset of likely future prospects in the current habitat is taken into account. Effects of the ME are consistently harder to detect, mainly due to density dependency overriding the benefits of habitat quality. We predict higher natal than breeding dispersal when territorial vacancies are scarce, and more variable breeding than natal dispersal when they are common.

Key words: **age-structure, asset-protection principle, dispersal strategies, multiplier effect.**

INTRODUCTION

Dispersal is known to be driven by a range of selection pressures, such as kin competition, inbreeding avoidance, and escaping negative effects of spatiotemporal variation in habitat quality (Hamilton and May 1977; Johnson and Gaines 1990; Bowler and Benton 2005; Roze and Rousset 2005; Ronce 2007; Clobert et al. 2012; Duputié and Massol 2013). General models of dispersal typically consider the effects of these factors in asexual semelparous populations; when considered, the most common categorization of the individuals is their sex (Johnson and Gaines 1990; Gros et al. 2009; Shaw and Kokko 2014). Much less attention has been paid to whether dispersal strategies of individuals depend on age or other stages they have reached in their life history (Starrfelt and Kokko 2012), for example, whether the individual already possesses a breeding territory or whether they have bred successfully (Switzer 1993; Johst and Brandl 1999; Arlt and Pärt 2008; Edelaar and Bolnick 2012).

Dispersing prior to ever breeding, that is, natal dispersal, is in many species more common than breeding dispersal, which occurs between 2 breeding attempts (Greenwood and Harvey 1982; Paradis et al. 1998; Johst and Brandl 1999). Therefore, assumptions of age- or state-independent dispersal clearly contrast with reality. For example, in an extensive British bird data set, natal dispersal distances were larger than breeding dispersal distances for 61 out of those 69 species for which sufficient information of both natal and breeding dispersal was available (Paradis et al. 1998). Some stage-structured dispersal models simply take such patterns as given, such that only juveniles are assumed to disperse (e.g., Ronce et al. 1998, 2000; Schjørring 2002). The focus of this study is on elucidating *why* adults are often less prone to leave. To do so, we investigate the interplay of 2 relevant factors: the asset-protection principle (APP; Clark 1994) and the implicit information of site quality obtained by residing at a natal site ("multiplier effect" [ME]; McNamara and Dall 2011, foreshadowed by Hastings 1983).

In territorial species, breeding dispersal implies that the individual foregoes an opportunity to breed in a territory that it already "owned" (Belichon et al. 1996; Danchin and Cam 2002; Doligez and Pärt 2008), whereas natal individuals do not generally possess

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a breeding site yet. It is therefore tempting to explain the relative scarcity of breeding dispersal with the APP (Clark 1994). This principle was originally phrased in the context of antipredator behavior, but it generalizes to various situations where an individual can risk losing what it already has. In the current context, adults in possession of a site or territory have more to lose if they disperse than juveniles (see also Morris 1982 for a similar statement). However, the accuracy of information about one's territory, as well as the magnitude of habitat quality variation might both matter, as a poor quality territory may not qualify as an asset worth protecting (if the individual perceives this accurately enough). Because individuals on poor sites are then expected to show breeding dispersal (Krebs 1971; Mestre and Bonte 2012), spatial habitat quality variation could therefore, as a whole, promote dispersal.

The ME (McNamara and Dall 2011), in turn, refers to the fact that if good habitats lead to better reproduction than poor habitats, then an individual is disproportionately likely to be born in a good habitat (relative to the global availability of such habitat). The interesting corollary is that the simple fact of being born gives an individual implicit knowledge that its local habitat quality is likely to be above the average of the entire landscape—even if no other cues exist (for earlier treatments of this effect, though without use of the term "multiplier effect," see Hastings 1983; Holt 1985). If juveniles stay at "home" and eventually breed there, this knowledge effect could extend to adult life. The ME can thus as a whole select against dispersal if habitats vary in quality (Hastings 1983; Holt 1985; McNamara and Dall 2011).

We therefore have a rather contrasting set of predictions that appear to be based on starkly different assumption structures. If individuals can condition their dispersal on spatial variability (McPeek and Holt 1992; Leturque and Rousset 2002; Rodrigues and Johnstone 2014), we expect a different set of responses than the simple dispersal-reducing effect of spatial variability when explicit habitat assessment is impossible (Hastings 1983; Holt 1985; McNamara and Dall 2011). Real life is unlikely to be black and white with respect to information use, however. In reality, assessment of habitat is a continuum ranging from cases where the only source of information is the demographic effect (disproportionate production of individuals in good sites) that a natal site of a randomly chosen young individual tends to be of above average quality, to cases where individuals can immediately assess their current habitat in an error-free manner.

Thus, we suspect that the evolved dispersal rates of individuals differing in state (especially with respect to their assets) will depend on exactly how well they are informed about their current habitat quality. Past models have tended to assume that all individuals either have this information or that they do not; they also often assume only one dispersal event and discrete generations, which effectively prevents comparing the dispersal behavior of individuals with and without assets. Overlapping generations thus offer intriguing ways to combine the APP with the ME, not least because information provided by the ME can only exist for those individuals who have not yet dispersed. To consider all these processes requires a model where dispersal propensity can depend on life stage, where habitat quality variation ranges from absent to substantial, and where different accuracies of habitat quality assessment, including no perceptual ability, that is, all "knowledge" is evolutionarily acquired.

THE MODEL

Addressing the impact of asset-protection and MEs requires considering spatially varying habitats, and to be able to explicitly contrast natal and breeding dispersal requires overlapping generations. Habitats in our model can therefore be either good or poor, and this impacts the reproductive success of their inhabitants. Habitats consist of breeding sites (territories) that have 3 types of residents: a breeder "owns" the territory, but there can also be nonbreeders who in turn come in 2 flavors: "natals" if they have not yet dispersed, and "floaters" if they have left their place of birth. We differentiate between natals and floaters because if the ME is strong, selection should favor expressing 2 different dispersal rates depending on whether individuals are still in the habitat that produced them. Breeders are expressing yet another dispersal rate.

We assume that individual breeders with a territory (owners, "breeders") cannot be ousted, thus some breeding success is guaranteed for them, but with spatial variation in habitat quality, being an owner (of a potentially poor territory) also means foregoing chances of competing for other (potentially better) territories. Natals and floaters acquire breeding territories at a rate of territories becoming vacant due to mortality and dispersal of breeders. Competition is concentrated on the site they reside in, but with some additional probability of outcompeting others at sites that are not their focal one. To evaluate the role of direct cues of habitat quality, we assume that individuals may have either perfect, imperfect or no knowledge of the quality of their local environment, beyond the evolutionary knowledge offered by the ME.

Our individual-based simulation model assumes s breeding territories, each being potentially occupied by 1 breeding male and 1 breeding female and a number of nonbreeders of both sexes. A proportion z of breeding territories is considered to consist of good habitat and the remainder is considered poor habitat. All individuals are assigned to a territory but only breeders can reproduce. Within each sex, an individual's state is thus characterized by its life-history stage (natal, floater, breeder) and type of habitat (good, poor).

A simulation is initiated by creating N diploid breeders, each a male or a female (50% probability of being either). Every individual has 6 diploid loci that determine its dispersal probability d ($0 \leq d \leq 1$) conditional on its life-history stage (natal, floater, breeder) and its *perceived* current habitat quality (good or poor; note that this may differ from reality if there is perceptual error, see below). The individual disperses with a probability equal to the mean of the 2 alleles at the appropriate locus. Alleles were initiated as uniformly distributed random numbers chosen from the range [0, 1].

In the first generation, the breeding territories are filled in a quality-dependent manner, which also maximizes the number of pairs that form and minimizes the number of cases where a territory is occupied by either a female alone or a male alone: males and females take turns, first choosing good territories until none are available, then choosing poor territories, but always preferring a site with a mate over a site without one. This simple procedure leaves initially approximately $s - N/2$ poor territories empty. The number is approximate because the number of males is not necessarily exactly equal to the number of females. For example, if $s = 700$, $z = 0.5$, and $N = 1000$, we have approximately 500 males and 500 females, which will fill all the 350 (sz) good territories and approximate 150 of the poor ones.

Each generation has the same sequence and timing of events. A generation starts with reproduction within each territory that has both a male and a female breeder; it is followed by mortality, and then 2 steps during which individuals can change their location: a dispersal stage and a stage of competing for breeding sites. During the latter, an individual can acquire the status of a breeder if previous breeders have died or dispersed.

Reproduction occurs in those territories that have at least 1 individual of each sex (only the breeding pair can produce any young; see below for more information on breeding pair formation). The number of offspring produced follows a Poisson distribution with mean λ in poor territories and $\alpha\lambda$ ($\alpha \geq 1$) in good territories, thus good territories have higher reproductive success by a factor α. Offspring sex is randomly determined. In addition to Mendelian inheritance at all loci, each of the dispersal alleles mutate in offspring after birth with probability μ. A mutation changes the allele's value with an amount taken from a normal distribution with range $[-\sigma_d, \sigma_d]$. Allelic values that fall below 0 or exceed 1 are set at 0 or 1, respectively.

Mortality is set to occur after reproduction, with all individuals having the same probability (m) of surviving to the next generation. Survivors then assess their habitat. An individual's perception of a habitat may differ from reality, and we model the error as ε (with $0 \leq \varepsilon \leq 0.5$). Here, $\varepsilon = 0$ represents perfect perception of habitat quality such that an individual residing in good habitat always perceives it as good, and vice versa. At the other extreme, $\varepsilon = 0.5$ implies that there are no effective cues as an individual is just as often wrong as it is right. Individuals that misperceive the quality of their local territory use the dispersal allele for the habitat type they are not in. For example, if a natal individual residing in a good quality territory makes a perception error in assessing the territory (it does so with probability ε), it will disperse based on the "natal in poor habitat" dispersal locus.

The dispersal stage makes dispersing individuals land in a randomly selected territory, thus if $z = 0.5$, there is an equal chance of landing in a good or a poor territory. For simplicity, we do not exclude the possibility of landing in the territory the individual dispersed from; the large number of sites makes this in practice unlikely. Breeders (and natals) that disperse become classified as a floater until they (again) find a breeding territory.

Following dispersal, there is competition for breeding sites, which is shorthand for competing to acquire the status of a breeder at a site. Like dispersal, this can lead to shifts in individuals' location, but these are now movements that directly target vacancies that have been created by mortality or breeder dispersal. Some of the breeding territories have become vacant for potential breeders of a given sex. We assume that nonbreeders (natals and floaters alike) can perceive vacancies in more than one territory, but their competitiveness for a vacancy is elevated by a factor $r > 1$ (which we call the locality factor) if the vacancy occurs in the territory where they currently reside. For example, if $r = 10$ and the former female breeder has died, the local female nonbreeders, if there are any in the focal territory, are each equally likely to acquire the territory, and their probability of doing so is 10-fold that of any nonbreeders that currently reside elsewhere.

Competition for sites occurs in a specific order and this order is designed to maximize the number of breeding pairs. First, males compete for territories without male breeders that have at least one local female (breeding or nonbreeding). Secondly, males compete for the territories that lack a male breeder but have no local females (but at least one local male who is not yet assigned breeder status). Last, males compete for completely empty territories. Nonbreeding females compete after males have taken up breeding territories: first for territories that lack a female breeder but have a breeding male and local nonbreeding females. Secondly, females compete for territories without any type of female but with a breeding male. Thirdly, females compete for territories without a breeding male, and thus also lack nonbreeding males, but with local nonbreeding females. Finally, females compete for territories that have no males or females of any type. Individuals that acquire a breeding position change state to a breeder; the nonbreeders retain their current state (natal or floater) and location as they may compete for a breeding site again in the next year if they survive to compete again. A breeding pair will breed again in the next year unless one or both members of the pair disperse or die.

Because natal philopatry may lead to competition between kin, we ran additional simulations in which we "shuffled" all individuals within their category (natal, floater, or breeder), sex, and territory quality class (Poethke et al. 2007). In this exercise, individuals' current locations are swapped within each class, which keeps the numbers of individuals per site intact but cancels all kin structuring in the population. For example, a female natal individual in a good territory randomly takes the place of another female natal individual in a good territory, meaning that the numbers of individuals in each category, sex, and territory quality class are identical before and after shuffling, while the genetic structure of the population has changed. Comparing the results then allows assessment of the effects of kin competition on the evolution of dispersal rates. The results of these additional simulations can be found in the Supplementary Material.

All simulations were run for 5000 generations, which proved sufficient to yield no further change on average. All simulations led to identical results for both males and females, wherefore only one sex is shown in the figures below (where applicable). We used the following parameter values as a "baseline," that is, unless otherwise stated: $s = 700$, $z = 0.5$, $N = 1000$, $\lambda = 0.3$, $\alpha = 5$, $\varepsilon = 0$, $r = 10$, $\mu = 0.1$, and $\sigma_d = 0.1$. The chosen values ensure the population does not go extinct unless mortality is higher or productivity is lower (smaller α or z) than the baseline. The main results will focus on varying α, z, ε, and m; for results of variation in λ and r, as well as those where kin competition has been removed, see Supplementary Material).

RESULTS

Based on the APP (Clark 1994), one might expect that breeders, being the only type of individual with "assets," should evolve lower dispersal rates than nonbreeders. We found this to be true only in a qualified way: breeders in good territories were always reluctant to disperse (Figures 1–3). In the absence of territory quality variation (Figure 1a at $\alpha = 1$), or when individuals were unable to assess the quality of their territory (Figure 3c), all breeders behaved identically, and breeding dispersal remained low compared with juvenile dispersal. Outside these special conditions, breeders in possession of poor quality territories showed a much wider variety of responses: breeding dispersal rates could either increase or decrease with habitat quality variation (Figure 1) or with the proportion of habitat that is better than their own (Figure 2). The breeding dispersal of such individuals could then either fall below or exceed that of juveniles (Figures 1–3).

The decisive factor explaining these patterns is a demographic one: breeding dispersal from poor territories increased sharply with mortality (m; Figure 3), though less so in the presence of large perceptual error hampering territory quality assessment (ε; as noted above, high ε creates conditions where all breeders behave similarly). These effects did not remain minor. When mortality was high and cues of territory quality were reliable, breeders in poor territories evolved much higher dispersal rates than any other type of individual (Figure 3a,b).

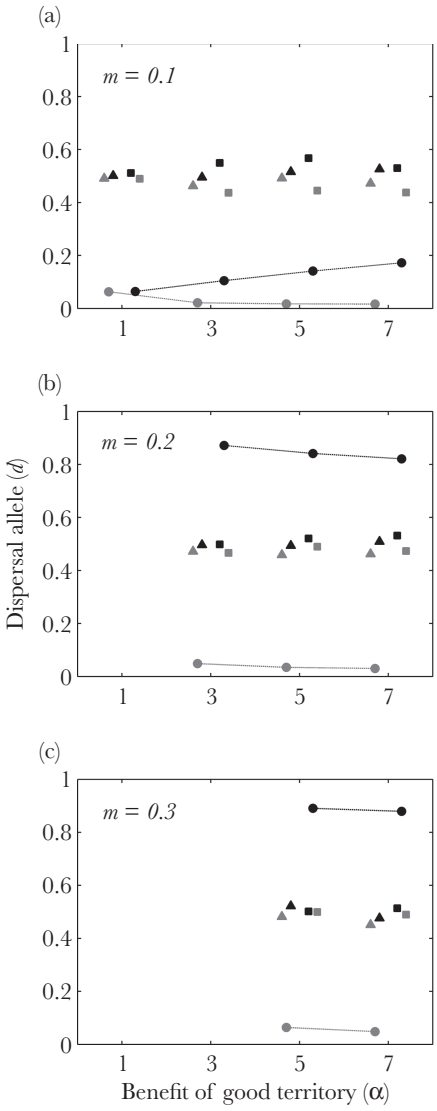

Figure 1
Evolved means of the dispersal allele with different benefits of a good territory (α) for each of the 6 states measured at 5000 generations for mortalities (a) $m = 0.1$, (b) $m = 0.2$, (c) $m = 0.3$. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in gray are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Note that extinctions occur in (b) and (c) with $\alpha < 3$ and $\alpha < 5$, respectively. Standard errors (SEs) not shown as all SE < 0.02. Parameter values: $s = 700$, $z = 0.5$, $N = 1000$, $\lambda = 0.3$, $\varepsilon = 0$, $r = 10$, $\mu = 0.1$, and $\sigma_d = 0.1$.

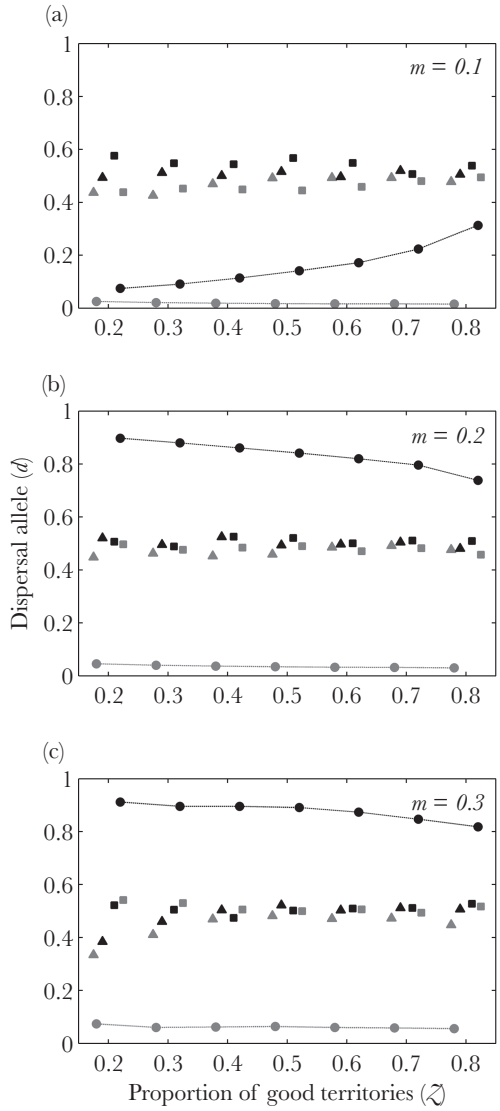

Figure 2
Evolved means of the dispersal allele with different proportions of good territories (z) for each of the 6 states measured at 5000 generations for (a) $m = 0.1$, (b) $m = 0.2$, and (c) $m = 0.3$. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in gray are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Note that extinctions occur in (c) with $z \leq 0.3$. Standard errors (SEs) not shown as all SE < 0.02 (except when extinctions occur). Parameter values: $s = 700$, $N = 1000$, $\lambda = 0.3$, $\alpha = 5$, $\varepsilon = 0$, $r = 10$, $\mu = 0.1$, and $\sigma_d = 0.1$.

The explanation for such high breeding dispersal rates from poor territories highlights the pitfalls of only considering concrete possessions, such as territories, as assets. A nonbreeder in our model has an invisible asset: the ability to compete for a larger number of vacancies than the one territory that a breeder is committed to. Therefore, if territory vacancies created by mortality occur at a sufficiently high rate, a nonbreeder's reproductive value can exceed that of a breeder whose territory is poor. This argument fails, however, under conditions of low mortality: breeders that disperse become nonbreeders and have to compete with a very large accumulated pool of nonbreeders, and the high number of competitors (Figure 4) then makes it much less likely that breeding dispersal pays off at either habitat quality (Figure 3 with low m).

Because of these complexities, it is not obvious whether making outside options more lucrative selects for more dispersal. One way to increase the "lucrativeness" is to increase α, the difference between reproductive success in good versus poor sites. High α means that breeders at poor territories forego potentially much better options elsewhere, but any dispersal-promoting effect of α only occurs at low mortality (Figure 1a). Higher mortality rates negate the effect of α because they make dispersal from poor territories high throughout a large range of habitat quality variation

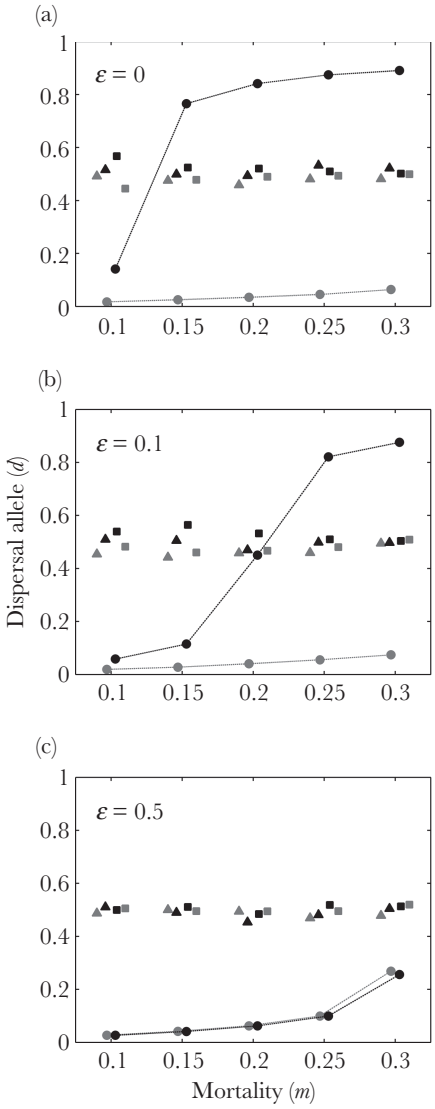

Figure 3
Evolved means of the dispersal allele with different mortality probabilities for each of the 6 states measured at 5000 generations for (a) no perceptual error, ε = 0, (b) ε = 0.1, (c) ε = 0.5. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in gray are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Standard errors (SEs) not shown as all SE < 0.02. Parameter values: $s = 700$, $z = 0.5$, $N = 1000$, $\lambda = 0.3$, $\alpha = 5$, $r = 10$, $\mu = 0.1$, and $\sigma_d = 0.1$.

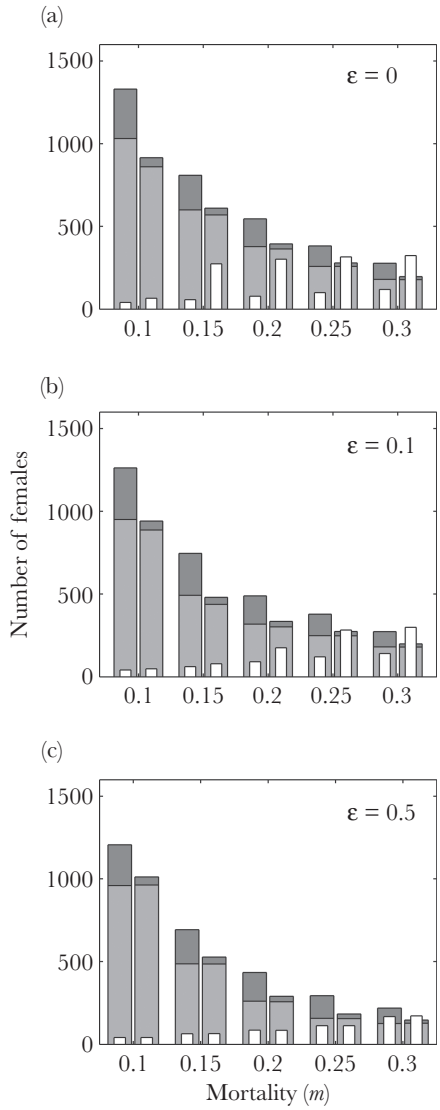

Figure 4
The number of nonbreeding females (paired gray bars, dark gray—natal females, light gray—floater females) competing for available breeding spots (paired white bars), the left bar of each pair denotes good territories and the right bar denotes poor territories, (a) ε = 0, (b) ε = 0.1, (c) ε = 0.5. Each bar gives the mean of 40 simulations at 5000 generations. Parameter values are as in Figure 3. Note that the figure would look identical if we used males instead of females.

(Figure 1b,c). The dispersal-promoting effect of z, the proportion of territories that are of high quality, is likewise not uniform. Therefore, it is not sufficient to only consider the existence of outside options, since the likelihood of acquiring them after leaving the current option depends on the severity of competition. This competition is likely strong if there are many dispersers from other sites, and/or in case of low breeder turnover resulting from low mortality.

For nonbreeders, the expectations are likewise complex. On the one hand, one can extend the APP to the "invisible" assets of likely future prospects in the current habitat. We would then expect nonbreeders in good territories to evolve lower dispersal rates compared with nonbreeders in poor territories. On the other hand, with a strong ME, we would expect individuals that have already moved at least once (floaters) to evolve higher dispersal rates than nonbreeding natals that have remained in their natal site. This is because information from the ME only applies in the natal territory, as we assumed no spatial autocorrelation in territory quality.

Nonbreeders appear to follow the extended form of the APP, as long as relatively accurate information on habitat quality was available (Figure 3); however, differences between different categories of nonbreeders were always slight (Figures 1–3). Still, especially when good territories are scarce, the dispersal rate for nonbreeders from good territories is consistently lower than from poor territories (Figure 2).

It is considerably harder to detect effects of the ME, as natal individuals did not evolve systematically lower dispersal rates than

floaters (Figures 1–3). Additionally, variation in reproductive success between good and poor territories does not consistently select against dispersal as the ME might predict (Figure 1). This is likely to reflect the fact that ME in its purest form assumes no knowledge beyond the emergent information that arises from demography (individuals are disproportionately born in good sites) and evolution (which impacts dispersal rates of competitors); our results show that dispersal strategies can strongly react to individuals differing in their state, particularly of the perceived habitat quality when this is possible to assess. Another fact that makes the effects of the ME harder to detect in our results is density dependence often overriding the habitat quality advantages offered by the ME. Competition for high quality breeding territories intensifies as soon as the numerous natal individuals attempt staying there (Figure 4). This means that their success of acquiring the territory becomes density-dependent: more philopatry means smaller chances of acquiring the local high quality territory. A disperser trades off these prospects for less intense competition in (potentially) poor territories, and dispersal rates evolve to be intermediate where these effects balance.

We ran a series of supplementary simulations to examine the generality of the results. Higher values of breeding success, λ, led to little change from our baseline values for all other dispersal rates than those of breeders in poor sites, which become reduced when λ is high (Supplementary Figure S1). Increasing the importance of local competition (such that nonbreeders compete most efficiently for a vacancy in their current territory; high r) led to little change except for a clearer differentiation between nonbreeders (natals and floaters) in good versus poor sites (Supplementary Figure S2); this makes intuitive sense because being a nonbreeder at a poor site becomes more strongly penalized when most breeding vacancies are filled by a strictly local—as opposed to neighboring—individual. Finally, when we remove kin competition from our model, the results are near identical to our original results (compare Supplementary Figures S3–S5 with Figures 1–3).

DISCUSSION

Our model sheds light on why juveniles of many animals exhibit higher dispersal propensities than adults. The short answer is that the model confirms the importance of the asymmetry that an adult might already own a breeding site, which could be lost when moving; in some cases, this creates situations where breeders at any site evolve low dispersal rates. However, our modeling also reveals that the caveats are important. Individuals who at first sight do not appear to own anything may be in a better position to view for available vacancies than individuals who have settled for a less than ideal option. In the presence of habitat quality variation, we can therefore sometimes expect breeders residing in suboptimal territories to be more prone to disperse than any other type of individual. Although we have not explicitly modeled preferential treatment of individuals that reside among kin or queues of territory inheritance, such processes could further tilt the balance between philopatry and dispersal in favor of the former (see Ekman et al. 2001).

In general, our work highlights that the balance of dispersal-promoting and philopatry-promoting factors can very strongly depend both on how accurately individuals perceive their current options relative to what is available in the population as a whole (Switzer 1993; Boulinier and Danchin 1997; Schjørring 2002; Doligez et al. 2003; Valone 2007). These factors are, in our model at least, stronger than the effects of kin competition (see below). Consider, for example, the situation where accurate information of habitat quality is completely unavailable (ε = 0.5 in Figure 3c); now breeding dispersal remains low regardless of other parameter values. This might appear surprising, as the opposite effect—more dispersal with less information—has been found in models that make differing assumptions about information use (Enfjäll and Leimar 2009). Our result becomes intuitive, however, once one realizes that individuals that dispersed from a territory perceived to be poor would more often than half the time (if $z = 0.5$, more individuals as a whole will be born in good than poor habitat) make the mistake of leaving the state with the best reproductive value of all.

Our results also highlight the capacity of demographic parameters (here mortality) to change the rank order of dispersal propensities. Such a strong effect may appear surprising, given that mortality was identical (set at m) for every individual in the population: at first sight, one might expect less breeding dispersal, not more, if the current breeding attempt is more likely to be an individual's last one, as is the case when m is high (Ronce et al. 1998, 2000). However, high mortality also means that there are few competitors alive to compete for each vacancy that is created, and this greatly improves the likely payoff of the dispersing strategy. This strengthens the view that effects of the disperser's life span cannot be considered in isolation from the rate of territory acquisition (see Kokko and Lundberg 2001).

There is an intriguing possibility not included in our model: the perceptual errors themselves might depend on the experience that individuals have accumulated. If breeders are more knowledgeable than floaters, our results suggest that it is not a priori clear that their site fidelity will increase. That is because knowing that one's own site is poor can select for leaving that site. One simple way to learn is to use one's own breeding success as a cue of habitat quality (Pärt and Gustafsson 1989; Switzer 1993; Haas 1998; Öst et al. 2011), but more detailed knowledge accumulation is obviously possible too. In this context, it is interesting to note that learning has a greater scope to operate in species that are long lived enough to have time to correct their mistakes. In a habitat choice context, each mistake can take up a significant "chunk" of life span (Kokko and Sutherland 2001).

Our model did not consider density-dependent dispersal strategies in the sense of individuals measuring and using local density as a cue. It is known that the consequent rules for dispersal plasticity can depend on whether dispersal is performed at the natal or adult stage (Parvinen et al. 2012); however, in these models, the timing of dispersal is considered as separate scenarios rather than letting them potentially co-occur in a population. The latter type of approach would help understand when we expect either or both to occur in a specific population.

Kin competition is generally known to select for dispersal (Hamilton and May 1977; Ronce et al. 2000; Rodrigues and Johnstone 2014), yet strong effects of kin competition are not necessarily universal: for example, in the model of Poethke et al. (2007), a marked effect of kin competition was restricted to cases where dispersal rates remained low (<0.1). In our model, nonbreeders evolved higher rates than 0.1 based on demographic considerations alone. At least 3 features of our model create conditions where the selective pressure to disperse more, based on reducing the intensity of competition as experienced by related individuals at the natal site, will be relatively low. First, the most likely future breeders at the natal site are always the disperser's own parents: they retain the priority to breed at the site if they themselves do not disperse (or die). This likelihood is independent of the focal offspring's dispersal decisions. Second, high dispersal—which in our model arises

through other factors—implies a continual influx of immigrants to any site, thus one disperser's efforts to reduce competition at the natal site can become relatively insignificant. Third, it should be noted that the relatedness structure in a diploid species with stochastically variable life spans of parents (as in our model) creates less strict kin competition than in some classic models of dispersal (e.g., Hamilton and May 1977), which assumed asexual reproduction such that individuals are bound to compete with their clones.

Numerous models have confirmed that spatial heterogeneity may favor dispersal if it is conditionally expressed (e.g., McPeek and Holt 1992; Leturque and Rousset 2002; Rodrigues and Johnstone 2014). Our model is in line with this work as it, too, highlights that dispersal can be strongly shaped by heterogeneity, but as our modeling of the APP necessitates taking into account conditional (state-dependent) responses, it is probably not surprising that dispersal does not increase uniformly with the degree of heterogeneity. The habitats are at their most diverse in our model when α is high and when $z = 0.5$, but these values do not maximize dispersal. Instead, the results show how strongly demography shapes the outcomes. One might, for example, expect that high z (implying that most sites are good) select for high dispersal from the few remaining poor sites, as randomly landing at a site, is likely to lead to improved site quality. However, high z also means high global productivity, and thus a disperser from a poor (or any) site faces reduced chances of acquiring a territory at all. Whether the balance then favors more or less dispersal from poor sites (Figure 2) is modulated by overall mortality, which has a strong impact on the strength of competition (Figure 4).

Although the results from our model are in many ways in agreement with established empirical knowledge—for instance, natal dispersal is more frequent than breeding dispersal in many species (Greenwood and Harvey 1982; Paradis et al. 1998; Johst and Brandl 1999), and breeding animals in good quality territories have been found to be less prone to disperse or disperse shorter distances than individuals in poorer habitats (Krebs 1971; Stacey and Ligon 1987; Cline et al. 2013)—the details of the fit between model predictions and reality remain unknown. Qualitative support, however, can be found in certain studies, in the sense that previous breeding success has been shown to lead to higher site fidelity (Haas 1998; Danchin and Cam 2002) and breeding failure as a result from, for example, predation has been shown to increase the propensity and distance of dispersal even in relatively site tenacious animals (Öst et al. 2011); some species show evidence of paying attention to both intrinsic site quality and own breeding success (Kokko et al. 2004). Such results imply that breeders can be sensitive to current site quality, and indeed a key qualitative prediction from our model is that conditional dispersal rates can evolve to be much more variable among breeders than among any other class or between classes of individuals. In our model, we did not specify exactly how animals might assess site quality: we simply assumed that they do so either perfectly or with some error. Responses that are at least partly based on own experience (see Switzer 1993) could potentially strengthen the conditionality among breeders even more, as they gather direct experience of local habitats in a manner that can be more difficult for nonbreeders (though cases of public information could make such differences milder again, see Danchin et al. 2004).

Like all models, ours is a simplification of reality and the robustness of its conclusions needs to be evaluated against its assumption structure. For example, we do not necessarily expect kin competition to always play an equally minor role as in our model; above we have outlined the reasons why this is likely to happen in our particular case. We have assumed a strict dominance hierarchy in the sense that a breeder is guaranteed some reproductive output if it survives and does not disperse, whereas competition among nonbreeders is of a much more egalitarian nature: apart from an advantage of being "nearby" (the locality factor r), there is no impact of age or other asymmetries among individuals. We also assumed that the sole determinant of movement-related fitness is success in competing for vacant territories (of varying quality). Obviously, if there are either immediate or delayed survival consequences of spending time as a nonbreeder in different habitats, then the payoff structure will become more complicated.

In conclusion, our model demonstrates that individuals can possess both visible and invisible assets when they differ in their state of territory ownership, the likely quality of the habitat they are in, the proportion of the world that has this quality, and the benefits of being in a good quality site. Demography can have a major influence on whether an individual who is already breeding should commit to its site or whether it should still consider joining the pool of dispersers: high breeder turnover selects for greater dispersal propensities as a whole and can lead to patterns that deviate from the general expectation that natal individuals should disperse more. It is only under low turnover conditions that territories of any quality are an asset worth protecting under all circumstances.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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