Evolution of positive and negative density-dependent dispersal

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Understanding the evolution of density-dependent dispersal strategies has been a major challenge for evolutionary ecologists. Some existing models suggest that selection should favour positive and others negative density-dependence in dispersal. Here, we develop a general model that shows how and why selection may shift from positive to negative density-dependence in response to key ecological factors, in particular the temporal stability of the environment. We find that in temporally stable environments, particularly with low dispersal costs and large group sizes, habitat heterogeneity selects for negative density-dependent dispersal, whereas in temporally variable environments, particularly with high dispersal costs and small group sizes, habitat heterogeneity selects for positive density-dependent dispersal. This shift reflects the changing balance between the greater competition for breeding opportunities in more productive patches, versus the greater long-term value of offspring that establish themselves there, the latter being very sensitive to the temporal stability of the environment. In general, dispersal of individuals out of low-density patches is much more sensitive to habitat heterogeneity than is dispersal out of high-density patches.

1. Introduction

In recent years, evidence has accumulated that dispersal is a highly plastic trait [1–3]. To give just a few, illustrative examples, in family groups of carrion crows (Corvus corone corone) juveniles dispersed less when territories were food-supplemented [4], whereas in the butterfly Boloria eunomia, dispersal rates were raised when patch quality was experimentally decreased but remained lower in untreated patches [5]. Similarly, in the common lizard Lacerta vivipara, local high density promoted higher levels of dispersal [6]. There is, however, much variation between species in the way that dispersal responds to factors such as resource availability and population density. In particular, while some studies show positive density-dependent dispersal [7–9], others show negative density-dependent dispersal [10].

A theoretical framework to account for the above variation in density-dependent dispersal strategies is currently lacking. Although some models have explored the evolution of dispersal in complex environments that are both spatially [11–14] and, in some cases, also temporally heterogeneous [15–22], most of these studies have focused on the evolution of unconditional dispersal rates, whereby individuals express the same phenotype independently of their local environment (e.g. local density). Overall, these studies support the idea that spatial heterogeneity favours lower rates of unconditional dispersal [11–14], whereas temporal heterogeneity favours higher rates of unconditional dispersal [15–22]. Far fewer studies have focused on the evolution of conditional dispersal, whereby individuals adjust their dispersal phenotype to their local environment (e.g. local density) [20,23–26]. Of these, most models predict that high local density should lead to higher dispersal rates, i.e. positive density-dependence [23–25], but some at least predict that high local density should lead to lower dispersal rates, i.e. negative density-dependence [26]; no one model can account for the evolution of both types of response under different ecological conditions. These opposing predictions make it difficult to understand what are the key genetic, ecological and demographic variables that may account

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for the different types of density-dependent dispersal often observed in natural populations.

Here, we use an inclusive fitness approach to model the evolution of both conditional (density-dependent) and unconditional dispersal strategies in response to habitat heterogeneity and local competition. Our main goal is to show how and why, within a single, general model, selection can shift from positive to negative density-dependence in response to key ecological factors. We assume two types of patches—high-quality patches with abundant resources that give rise to a high density of juveniles, and low-quality patches with sparser resources that lead to a lower density of juveniles—and we allow patch quality (and the concomitant density of young) to vary both between patches and over time within a patch. We describe how these different types of environmental heterogeneity influence local kinship, and consider the evolution of both unconditional dispersal rates, and also of conditional dispersal strategies, allowing for dispersal decisions that are density-dependent.

2. Model and methodology

(a) Life cycle

We assume an infinite island model [27,28] with patch heterogeneity in resource availability [28]. Each patch contains \( n \) haploid, asexual breeding individuals. Generations are non-overlapping. We assume that there are two patch types: a fraction \( p \) of patches are high quality with abundant resources, whereas a fraction \( (1 - p) \) are low quality with more limited resources (note that if patch quality may change from one generation to the next, then the equilibrium fraction \( p \) of high-quality patches depends upon the rates with which patches switch in state, as described below). In every generation, individuals in high-quality patches each produce a large number \( F_H \) of young, whereas individuals in low-quality patches each produce a smaller (though still large) number \( F_L = (1 - \sigma)F_H \) of young, where \( 0 \leq \sigma < 1 \) specifies the fecundity difference between individuals in high- and low-quality patches (we assume that fecundity is independent of an individual’s genotype). High-quality patches are thus characterized by a high density of juveniles prior to dispersal, and low-quality patches by a lower density. After reproduction, breeding individuals die.

With probability 1 – \( z_H \) (or 1 – \( z_L \)), a juvenile remains in her high-quality and high-density (or low-quality and low-density) natal patch, whereas with probability \( z_H \) (or \( z_L \)) she disperses away from this natal patch, reaching a random patch in the population (i.e. an island mode of dispersal) with probability 1 – \( c \), where \( c \) is the cost of dispersal. After dispersal, juveniles on a patch (both native and immigrant) compete for the \( n \) available breeding sites. Finally, patches may undergo changes in their quality state: with probability \( \alpha \), a high-quality patch remains high quality, whereas with probability 1 – \( \alpha \) it becomes low quality; with probability \( \beta \), a low-quality patch remains low quality, whereas with probability 1 – \( \beta \) it becomes high quality (so that the equilibrium fraction of high-quality patches is given by \( p = (1 - \beta)/(2 - \alpha - \beta) \) (electronic supplementary material, appendix A). These demographic assumptions are the same as those of Rodrigues & Gardner [28], but while that study assumed a fixed (extrinsically specified) dispersal rate, and focused on the evolution of helping or harming behaviour, we are here concerned with the evolution of the dispersal rate itself.

(b) Methodology

We are interested in the evolution of dispersal rates, chiefly when individuals are free to adopt a conditional, density-dependent strategy for which \( z_H \neq z_L \), but also when they are constrained to adopt an unconditional strategy, such that \( z_H = z_L = z \). In the electronic supplementary material (appendices A–E), we derive convergently stable conditional and unconditional dispersal rates, using the Taylor–Frank ‘direct fitness’ approach to capture the effects of local kin competition [29]. Our analysis involves the derivation of patch-state frequencies at equilibrium (electronic supplementary material, appendix A), followed by expressions for the individual reproductive values \((v_{H,L,A} \text{ and } v_{L,A})\) and stable-class frequencies \((n_{H,L,A} \text{ and } n_{L,A})\) of adults on high- and low-quality patches (electronic supplementary material, appendices B and C), where reproductive value denotes the expected genetic contribution of an individual to the future gene pool of the population [30].

We calculate the mean fitness \( W_H \) (or \( W_L \)) of an adult mother in a high- (or low-) quality patch by determining her expected number of successful offspring weighted by their reproductive value (electronic supplementary material, appendix B). We can then construct expressions for the selection gradients acting on dispersal out of high- and low-quality patches \((S_H \text{ and } S_L \text{ respectively})\). These are given by

\[
S_H = \frac{dW_H}{dx_H} = \frac{\partial W_H}{\partial x_H} + \frac{\partial W_H}{\partial y_H} \eta_H \tag{2.1}
\]

and

\[
S_L = \frac{dW_L}{dx_L} = \frac{\partial W_L}{\partial x_L} + \frac{\partial W_L}{\partial y_L} \eta_L \tag{2.2}
\]

where \( g_H \) and \( g_L \) are the genetic values of actors; \( x_H \) and \( x_L \) are the phenotypes of the focal individual and \( \partial W_H/\partial x_H \) and \( \partial W_L/\partial x_L \), the marginal direct fitness effects on the focal (i.e. the effects on the reproductive success of the focal) of a change in its own phenotype; \( y_H \) and \( y_L \) are the average phenotype in the focal patch and \( \partial W_H/\partial y_H \) and \( \partial W_L/\partial y_L \), the marginal indirect fitness effects on the focal (i.e. the effects on the reproductive success of the focal’s group mates) of a change in the local average phenotype; \( n_{H,L,A} \text{ and } n_{L,A} \) are the relatedness coefficients between the actor and other local adults on high- and low-quality patches (electronic supplementary material, appendix D). When analysing unconditional dispersal rates, we need to consider the mean fitness of an adult, breeding female across both patch types, which is given by \( W = n_{H,L,A}n_{H,L}W_H + n_{L,A}n_{L,L}W_L \). The selection gradient acting on unconditional dispersal is then a weighted average of the selection acting on each type of patch, given by \( S_U = n_{H,L,A}n_{H,L}S_H + n_{L,A}n_{L,L}S_L \) (electronic supplementary material, appendix D).

Expressions for the relatedness among adults on high- and low-quality patches are derived from a system of recursion equations, which assume a neutral population, given by

\[
\begin{align*}
\eta'_{H,A} &= \eta_H \phi_H \left( \frac{1}{n} + \frac{(1 - \eta_H) \eta_{L,A}}{n} \right) + (1 - \eta_H) \phi_L \left( \frac{1}{n} + \frac{(1 - \eta_H) \eta_{L,A}}{n} \right) \\
\eta'_{L,A} &= (1 - \eta_H) \phi_H \left( \frac{1}{n} + \frac{(1 - \eta_H) \eta_{L,A}}{n} \right) + \eta_L \phi_L \left( \frac{1}{n} + \frac{(1 - \eta_H) \eta_{L,A}}{n} \right)
\end{align*}
\]

\[
(2.3)
\]

where \( \eta_H = \alpha \) (or \( 1 - \eta_H = 1 - \alpha \)) is the probability that a
high-quality patch in the current generation was a high- (or low-) quality patch in the previous generation; \(\eta_L = \beta\) (or \(1 - \eta_L = 1 - \beta\)) is the probability that a low-quality patch in the current generation was a low- (or high-) quality patch in the previous generation; \(\phi_H\) (or \(\phi_L\)) is the probability that two juveniles sampled at random after dispersal in a high- (or low-) quality patch are both philopatric; \(1/n\) is the probability that these two juveniles are siblings and \(1 - 1/n\) is the probability that they are not siblings, in which case they are related by \(r_{H,A}\) (or \(r_{L,A}\)) in high- (or low-) quality patches. To determine the coefficients of relatedness at equilibrium, we solve the system of equations (2.3) setting \(r_{H,A} = r_{H,A}' = r_{L,A}' = r_{L,A}\) (electronic supplementary material, appendix E).

Substituting the relatedness coefficients derived above into the expressions given in equations (2.1) and (2.2) for the selection gradients on \(z_H\) and \(z_L\), we can identify candidate evolutionarily stable (ES) dispersal strategies \((z_H', z_L')\) at which the selection gradients on both dispersal rates are equal to zero, i.e. at which \(dW(z_H', z_L')/dz_H = dW(z_L')/dz_L = 0\) (electronic supplementary material, appendix D). These candidate ES strategies are then checked for convergence stability. This implies that natural selection, assuming vanishingly small variation in the population, drives a population towards the equilibrium strategy. Evolutionary stability further implies that such an equilibrium, once established, cannot be invaded by a mutant that disperses at a slightly different rate. The analysis of evolutionary stability of social traits in patch-structured populations is not an easy task. In the electronic supplementary material, appendix F, however, we use the approach developed by Metz & Gyllenberg [31] and Ajar [32] to confirm that the convergently stable equilibria we have identified are also evolutionarily stable. The method involves computing the total number of emigrants that are descendants of a single successful immigrant ([31,32]; electronic supplementary material, appendix F). In addition, we perform individual-based simulations to check our analytically derived results. We find a good agreement between our analytical derivations and the results of the simulations (electronic supplementary material, appendix G).

Below, we explore the impact of the model’s parameters on the evolutionarily stable rates of conditional and unconditional dispersal, derived as described above.

3. Results and analysis

Our results can be explained in terms of two key quantities (figure 1). First, the relative reproductive value of a juvenile that survives dispersal compared with the reproductive value of a philopatric juvenile, denoted \(v\) (and derived in the electronic supplementary material, appendix C),
Figure 2. The ES unconditional dispersal rates (dotted-dashed lines, $z_H^*$), the ES reference dispersal rates (solid lines, $z_R^*$), and the ES conditional dispersal rates (dotted lines, $z_R^*$), and from low-density patches (dashed lines, $z_L^*$) as a function of the temporal correlation ($\tau$) for small group size ($n = 2$) and for large group size ($n = 32$). Temporal variation favours more dispersal from high-density patches, than from low-density patches (i.e. $z_H^* > z_L^*$). This relationship is reversed when the environment is more stable (i.e. $z_H^* < z_L^*$). Parameter values: $c = 0.25$, $p = 0.5$.

determines the direct benefits of dispersal. Because these benefits may vary between patch types, we will write $v_H$ or $v_L$ for this value contingent on the quality of the patch, and $v_U$ for the average benefit across both patch types when we are concerned with the evolution of unconditional dispersal rates. The second key quantity is the relatedness among juveniles, denoted $r$ (and again subscripted $r_H$, $r_L$, or $r_U$), which determines the indirect fitness benefits of dispersal. We can express the condition for the evolution of dispersal as $-1 + (1 - c)v + r \geq 0$ (i.e. as a form of Hamilton’s rule), where the left-hand side of this inequality is given by the selection gradients derived above (electronic supplementary material, appendix D). When $\sigma = 0$, patches do not vary in resource availability, and the environment is homogeneous in that case $v_H = v_L = v_U = 1$ and $r_H = r_L = r_U$, and $z^*_R = (r_H - c)/(r_H - c^2)$ (as given in [29]). Our approach is to use this reference model as a baseline case against which we can compare later results for spatially and temporally heterogeneous populations.

**a) Conditional dispersal**

As figures 2 and 3 show, when the environment is temporally stable, i.e. when the correlation $\tau$ between the quality of a patch in successive generations (derived in the electronic supplementary material, appendix A) is high, the cost of dispersal $c$ is low, and groups are small, selection favours lower rates of dispersal from high-quality patches ($z_H^* < z_L^*$). Conversely, when the environment is unstable, i.e. when $\tau$ is low, the cost of dispersal is high, and groups are big, selection favours higher rates of dispersal from high-quality patches ($z_H^* > z_L^*$).

Let us first focus on how temporal stability drives this reversal. In a temporally stable environment (high $\tau$), offspring born in a high-quality patch are likely to enjoy a high-quality environment as adults if they remain; conversely, offspring born in a low-quality patch are likely to suffer a low-quality environment as adults if they remain. Consequently, the relative reproductive value of offspring that disperse away from a high-quality patch (compared with those that stay) is lower than in a homogeneous population ($v_H < v_L = 1$; figure 1), whereas the relative reproductive value of offspring that disperse away from a low-quality patch is greater than in a homogeneous population ($v_H > v_L = 1$; figure 1). This tends to favour lower rates of dispersal from high-quality patches. The effect is partially offset because the greater fecundity of breeders in high-quality patches leads to more intense competition for local breeding spots, and to greater local relatedness, both of which tend to weaken selection for philopatry, as shown in figure 1. Nevertheless, if $\tau$ is large enough, the differences in reproductive value between high- and low-quality patches outweigh the differences in relatedness, so that the outcome is lower rates of dispersal from higher-quality patches ($z_H^* < z_L^*$; figures 2 and 3).
If the environment is temporally unstable (low \( \tau \)), by contrast, then the quality of a patch in the current generation is a poor predictor of its quality in the next. Consequently, the advantage of remaining in a high-quality patch (or the cost of remaining in a low-quality patch) is reduced (figure 1). Instead, the effects of more intense local competition and greater local relatedness described above predominate. The result is that selection favours higher rates of dispersal from higher-quality patches (\( z_\text{H} > z_\text{L} \); figures 2 and 3).

Intuitively, in a stable environment, a high-quality patch represents an enduring resource that it is worth staying to compete over. By contrast, in an unstable environment, a high-quality patch offers no long-term benefit; rather, it is associated with a short-term increase in local kin competition that it is worth dispersing to escape from.

We now turn to consider the cost of dispersal. As described above, local competition for breeding spots is greater in high-quality patches, where more young are produced, and lower in low-quality patches, where fewer young are produced. This effect tends to favour greater dispersal from high-quality patches (especially when the environment is unstable). As the costs of dispersal decrease, however, greater numbers of surviving immigrants tend to mask local differences in productivity, and equalize the intensity of competition between the two patch types (such that \( n_\text{H} \) decreases relative to \( n_\text{L} \), as shown in figure 1d). Consequently, when the cost of dispersal \( c \) is low, selection is more likely to favour lower rates of dispersal from high-quality patches.

Lastly, we consider how group size influences conditional dispersal strategies. Small group size increases relatedness, especially in the more productive high-quality patches (see the electronic supplementary material, figures S1 and S2). This selects for higher dispersal rates from high-quality patches (figure 2). As more individuals disperse from high-quality patches, competition in these patches decreases, and therefore the direct benefits of dispersing to these patches increase (see the electronic supplementary material, figure S1). As a result, dispersal from low-quality patches increases. The net result is that small group sizes favour the evolution of more negative (or less positive) density-dependence in dispersal, even when patches have some tendency to change in quality (i.e. \( \tau < 1 \); figures 2 and 3).

(b) Unconditional dispersal

The evolution of unconditional dispersal rates reflects average selection gradients across both patch types. Because more offspring are born on high-quality patches, however, stable unconditional rates of dispersal tend to more closely approximate high-quality optima in the conditional case. As figures 2 and 3 show, when the environment is temporally stable, the cost of dispersal is low, and groups are small, conditions that favour negative density-dependence in the
conditional case (see above), heterogeneity among patches favours lower rates of unconditional dispersal ($z_U^* < z_h^*$). Conversely, when the environment is temporally unstable, the cost of dispersal is high, and groups are big (conditions that favour positive density-dependence in the conditional case), heterogeneity among patches favours higher rates of unconditional dispersal ($z_U^* > z_h^*$).

In general, the impact of temporal stability, dispersal cost and group size on the evolution of unconditional dispersal, is very similar to the impact of these variables on the evolution of conditional dispersal from high-density patches (summarized in §3e). For instance, if we compare figure 1a (or 1c) with figure 1b (or 1d), we see that the benefits (both direct and indirect) of unconditional dispersal closely follow the benefits of conditional dispersal from high-density patches, i.e. $v_{1c} \approx v_{1b}$ and $r_{1} \approx r_{2}$ as one varies either temporal stability of the environment or the cost of dispersal.

4. Discussion

Our analysis shows that environmental heterogeneity can exert a strong influence on the evolution dispersal strategies, whether these are unconditional or conditional. At the same time, the way in which individuals respond to such heterogeneity depends critically on the temporal stability of the environment. When the environment is temporally stable (i.e. when local differences in patch quality persist over multiple generations), selection favours negative density-dependent dispersal (i.e. less dispersal from high-quality, high-density patches) and, in the unconditional case, rates of dispersal that are lower than in a homogeneous environment. By contrast, when the environment is temporally unstable, unpredictable or seasonal (i.e. when local differences in patch quality may disappear or even be reversed from one generation to the next), selection favours positive density-dependent dispersal (i.e. more dispersal from high-quality, high-density patches) and, in the unconditional case, rates of dispersal that are higher than in a homogeneous environment.

Temporal stability affects the evolution of dispersal strategies because it influences the relative long-term value of offspring that establish themselves in a patch that is currently high quality versus one that is currently low quality. In a stable environment (where $0 < \tau < 1$), high-quality patches are likely to remain high quality (and low-quality patches to remain low quality) over many generations. Consequently, offspring that establish themselves in a high-quality patch are of relatively high value. If one allows for conditional dispersal, this favours lower rates of dispersal from high-quality, high-density patches in the conditional case. In the unconditional case, the fact that the majority of offspring are born on high-quality patches means that selection favours lower dispersal rates overall for the same reason.

Suppose, by contrast, that the environment is less temporally stable (so that $\tau < 1$). Then, the current quality of a patch is a poor predictor of its future quality, so that the long-term value of offspring is largely unaffected by the quality of the patch in which they establish themselves. At the same time, the high density of juveniles on a high-quality patch means that an individual is less likely to claim a breeding spot there. Under these circumstances, selection favours higher rates of dispersal from high-quality, high-density patches in the conditional case, and in the unconditional case, higher rates of dispersal overall.

The two other main factors (apart from temporal stability) that determine the response to habitat heterogeneity are the cost of dispersal and the group size. Low costs tend to favour more negative (or less positive) density-dependent dispersal, whereas high costs favour more positive (or less negative) density-dependent dispersal. Because lower costs lead to higher dispersal rates overall, we would therefore expect to see (all other things being equal) more negative density-dependent dispersal in populations with higher dispersal rates, and more positive density-dependent dispersal in populations with lower dispersal rates. Similarly, small group size increases kin competition, and this also tends to favour more negative (or less positive) density-dependent dispersal.

So far, we have focused on whether selection favours positive or negative density-dependence in dispersal. However, our analysis also yields predictions about the strength of density-dependence, i.e. the extent to which dispersal rates should vary with density. This depends in a more complex way upon habitat heterogeneity, the cost of dispersal and local group size. When group size is large, and kin competition is negligible, more stable habitats and higher costs of dispersal favour relatively weaker density-dependence (while less stable habitats and lower costs of dispersal favour stronger density-dependence). By contrast, if group size is small and kin competition effects are relatively important, the picture becomes slightly more complicated. For example, in unstable habitats, we may have: strong positive density-dependence when the cost of dispersal is high; no density-dependence when the cost of dispersal is intermediate; and strong negative density-dependence when the cost of dispersal is low. Overall, we expect stronger density-dependence (whether positive or negative) when kin competition effects are present.

How does our model compare with previous analyses of the evolution of conditional (i.e. density-dependent) dispersal? Not many studies have addressed this issue explicitly; of those that have, most predict higher rates of dispersal from high-density patches [20,23–25], whereas fewer predict the opposite trend [26]. None, however, account for both patterns as we do, by invoking varying levels of temporal stability in environmental heterogeneity, and varying levels of kin competition. While our analysis provides, to our knowledge, the first systematic exploration of how and why selection shifts from positive to negative density-dependence in response to key ecological factors, previous models address many complexities of the dispersal process that we have not considered here. To highlight a few interesting possibilities for future analysis, one might extend the present model to allow for patch selection by dispersing individuals, leading to equilibration of reproductive value between patches [33]. In addition, one might consider the impact of variation in individual body condition on dispersal strategies [34], or the interaction between quality, fecundity and group size [35]. Lastly, one might also consider the influence of parent–offspring conflict on dispersal.

Turning to the implications of our model for empirical studies of dispersal, our results suggest that spatial heterogeneity alone is likely to be a poor predictor of conditional dispersal tactics. The cost of dispersal and, to an even greater extent, the temporal stability of the habitat greatly affect the
expected unconditional and conditional dispersal rates. In line with this general prediction, empirical studies focusing on spatial heterogeneity have observed contradictory patterns of density-dependent dispersal under natural conditions, with some studies reporting a positive correlation between density and dispersal [7–9], and others a negative correlation [10]. Experimental manipulations of patch quality have yielded equally confusing results, with some studies reporting an increase in dispersal from patches of reduced quality together with a decrease in dispersal from patches of elevated quality [5], whereas others found that conditional dispersal remained unchanged when patches were elevated in quality [36]. Our results can potentially help to account for this diversity of results, and suggest a need for empirical studies that follow individuals over their entire life cycle while also tracking environmental changes over several generations, in order to assess temporal stability.

Finally, our model also provides some insights into the cues that individuals should use when deciding whether to disperse or not. Several studies suggest that individuals may respond to local densities of individuals [7–9,37,38], resource availability [4,5] and/or the presence of kin [6]. In accordance with this diversity, our analysis indicates that, depending on the stability of the environment, local density may exhibit very different correlations with local relatedness and/or relative reproductive value of dispersing young, ranging from positive to negative. Therefore, density alone may not be a sufficient basis on which to make dispersal decisions, and individuals may instead need to combine multiple sources of information, as anticipated by Clobert et al. [1]. Our model thus suggests a need to integrate proximate and ultimate analyses of dispersal behaviour.

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