

Dispersal among habitats varying in fitness: reciprocating migration through ideal habitat selection

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Current evolutionary models of dispersal set the ends of a continuum where the number of individuals emigrating from a habitat either equals the number of individuals immigrating (balanced dispersal) or where emigrants flow from a source habitat to a corresponding sink. Theories of habitat selection suggest a more sophisticated conditional strategy where individuals disperse from habitats where they have the greatest impact on fitness to habitats where their per capita impact is lower. Asymmetries between periods of population growth and decline result in a reciprocating dispersal strategy where the direction of migration is reversed as populations wax and wane. Thus, for example, if net migration of individuals flows from high- to low-density habitats during periods of population growth, net migration will flow in the opposite direction during population decline. Stochastic simulations and analytical models of reciprocating dispersal demonstrate that fitness, carrying capacity, stochastic dynamics, and interference from dominants interact to determine whether dispersal is balanced between habitats, or whether one habitat or the other acts as a net donor of dispersing individuals. While the pattern of dispersal may vary, each is consistent with an underlying strategy of density-dependent habitat selection.

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All organisms live in environments that are heterogeneous in both space and time. Dispersal among patches, habitats, and populations is thus favored by natural selection and represents a major component of each species' life history. Dispersal is crucial for the persistence of any species and has major ramifications on population and community dynamics.

The burgeoning literature on dispersal emphasizes three dominant inter-dependent themes: 1) Theoretical studies evaluating evolutionarily stable dispersal strategies in heterogeneous environments (some recent examples include Travis et al. 1999, Lebreton et al. 2000, Metz and Gyllenberg 2000, Ferrière and Le Galliard 2001 and Leturque and Rousset 2002). 2) Studies keying on the

cues that animals may use to guide dispersal decisions (Danchin et al. 2001, Doligez et al. 2002). 3) Research on the role that dispersal plays in the temporal dynamics and spatial dispersion of populations (our emphasis in this contribution).

The spatial and temporal consequences of dispersal are often evaluated in the context of two extremes, each of which represents a different evolutionarily stable strategy (ESS, Doncaster et al. 1997, Diffendorfer 1998). In one view, populations in source habitat produce a surplus of emigrants that disperse to nearby sinks (Anderson 1970, Holt 1984, 1985, Shmida and Ellner 1984, Pulliam 1988, Pulliam and Danielson 1991). In the second perspective, the ESS yields an equivalent

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number of individuals moving between patches; dispersal is “balanced” and inversely proportional to carrying capacity (McPeck and Holt 1992, Doncaster et al. 1997, Rousset 1999, Holt and Barfield 2001).

Both source–sink and balanced models of dispersal are based on the underlying assumptions that habitats differ in carrying capacity and that fitness depends on population density. In the case of balanced dispersal, density-dependent dispersal equalizes fitness between habitats varying in carrying capacity (McPeck and Holt 1992). In source–sink systems, habitat selection regulates the overall population even though fitness is negative in one habitat (Pulliam 1988). It is prudent, therefore, to explore theories of habitat selection for yet other kinds of dispersal strategies.

We begin by describing a theory based on ideal-free habitat selection (Fretwell and Lucas 1970) in persistent populations fluctuating through time (Royama 1992). The theory predicts a dispersal strategy where individuals flow from one habitat to another during population increase, and flow in the reverse direction during population decline. We present results from simulation models demonstrating that differences in fitness, carrying capacity, levels of stochastic variation, and competitive dominance can all determine whether net dispersal is balanced between habitats or directed toward one or the other. We then demonstrate why the predictions of the habitat-selection model differ from those of balanced dispersal. We provide an analytical proof of reciprocating dispersal, and highlight some of its additional implications, in the appendix.

A companion paper (Morris and Diffendorfer 2004) tests which of the three theories is compatible with dispersal by white-footed mice. Though elements of each theory are supported, the data are most consistent with dispersal based on density-dependent habitat selection. Emigration is biased away from high-fitness habitats during periods of population increase, and similarly biased against low-fitness habitats during population decline.

We classify habitats as either “donor” or “receiver” to denote the net flow of individuals between them. We use these new terms in place of the more narrowly established “source” (net exporter of individuals because $r > 0$), “sink” (net importer of individuals because $r < 0$), and “pseudosink” (receives immigrants even though $r > 0$) habitats (Pulliam 1988, Watkinson and Sutherland 1995).

Reciprocating dispersal by ideal habitat selectors

Theory for two habitats

Our analysis of dispersal by density-dependent habitat selectors takes place in an environment composed of

only two habitats. Imagine a density-dependent habitat-selecting species where individuals (1) choose between the two equal-sized habitats to maximize individual fitness, (2) are free to occupy either habitat that they choose, and (3) where population growth in each habitat i can be described by the discrete logistic equation (Gotelli 2001, p. 35). If so, then for each habitat (i),

$$N_{i(t+1)} = N_{i(t)} + r_i N_{i(t)} \left(1 - \frac{N_{i(t)}}{K_i} \right) \quad (1)$$

where N is population size, r is the maximum discrete rate of population increase, and K is carrying capacity. Rearranging Eq. 1 for two habitats, A and B, we obtain

$$\frac{N_{A(t+1)} - N_{A(t)}}{N_{A(t)}} = r_A - \frac{r_A N_{A(t)}}{K_A}$$

and

$$\frac{N_{B(t+1)} - N_{B(t)}}{N_{B(t)}} = r_B - \frac{r_B N_{B(t)}}{K_B} \quad (2)$$

that define the per capita population growth rates in each habitat where population size, N , is conveniently also equal to population density in the equal-sized habitats. If individuals perform perfect density-dependent habitat selection by moving between habitats in a way that maximizes mean fitness, and if there are no costs or constraints on dispersal, the density in each habitat will be adjusted until the expected fitness (measured here as the per capita population growth rate) in each occupied habitat is equal (ideal-free habitat selection, Fretwell and Lucas 1970). Thus

$$\frac{N_{B(t+1)} - N_{B(t)}}{N_{B(t)}} = \frac{N_{A(t+1)} - N_{A(t)}}{N_{A(t)}}$$

and following substitution from Eq. 2,

$$N_B = K_B \left(1 - \frac{r_A}{r_B} \right) + \frac{r_A}{r_B} \frac{K_B}{K_A} N_A \quad (3)$$

defines the linear habitat isodar (Morris 1988). The isodar represents the set of densities, assuming ideal habitat selection, that produces equal expectations of fitness across both habitats. The isodar is the solution, in density space, to the evolutionarily stable strategy of habitat selection when organisms maximize individual fitness (Morris et al. 2001). Isodars have been used successfully to reveal habitat distributions of mammals (Morris 1992a, 1996, Ovidia and Abramsky 1995, Hansson 1996, Knight and Morris 1996, Abramsky et al. 1997, Morris et al. 2000a, b, Edwards et al. 2002, Lin and Batzli 2002, Ramp and Coulson 2002), birds (Fernández-Juricic 2001, Shochat et al. 2002), salmonid fishes (Rodríguez 1995), and ectoparasites (Krasnov et al. 2003).

The isodar predicts the number of individuals in each habitat and can also predict dispersal across heteroge-

nous landscapes. As populations grow and decline, individuals will disperse between habitats to equalize fitness until the respective densities satisfy the isodar solution. The optimum dispersal strategy will be zero only if the relative densities in the two habitats remain constant as the population in each habitat waxes and wanes to exactly the same degree. This will occur only if population size is perfectly matched with carrying capacity,

$$\frac{K_B}{N_B} = \frac{K_A}{N_A} \quad (4)$$

(the habitat matching rule, Parker 1978, Sutherland 1983, Pulliam and Caraco 1984, Morris 1994) which one can show from the isodar Eq. 3 to occur if $r_B = r_A$. It follows that whenever $r_B \neq r_A$, habitat-selecting individuals will disperse to equalize fitness between habitats with every episode of population increase or decline (Appendix 1).

We investigate the patterns of dispersal that this classical “discrete-logistic” model generates in two ways. First, we use graphs to illustrate changes in fitness, density, and dispersal as populations increase and decrease through time. Second, we supplement the heuristic graphs with explicit simulations to determine the conditions that generate donor and receiver habitats. We confirm the robustness and generality of our predictions by simulating dispersal using a generic logistic model (Hutchinson 1978) that has slightly different assumptions than the classical version (Appendix 1).

We also explore, briefly, the effects of interference on dispersal. When dominant individuals restrict the habitat choices of sub-ordinates, fitness is no longer equal between habitats. Rather, sub-ordinates base their habitat choice on their perception of how the presence and abundance of dominants reduce each habitat’s quality (ideal-despotic habitat selection, Fretwell and Lucas 1970, Fretwell 1972). The despotic effect can be visualized most easily as a reduction in carrying capacity that alters the fitness-density relations used by sub-ordinate individuals to select one habitat over another. Accordingly, we simulated this scenario of ideal-despotic dispersal with models that reduce the habitats’ perceived carrying capacity.

Methods

Simulating ideal-free dispersal in stochastic environments

Our simulations contrasted pairs of habitats within which populations grew according to stochastic versions of the discrete logistic equation. The models varied the carrying capacity in Eq. 1 so that populations would either increase or decrease in size. Each model included

separate demographic (population growth) and dispersal phases (Fig. 1). A population first grew or declined, then animals dispersed between habitats assuming perfect density-dependent habitat selection that equalized individual fitness (we provide a justification for our fitness measure in Appendix 1). Following population growth, the models summed the total number of individuals in both habitats. Then, during the dispersal phase, they redistributed animals in the two habitats with new densities matching those predicted by the isodar (Eq. 3). We initiated the simulations with densities equal to the carrying capacities in each habitat (these densities always lie on the isodar). We censused the population between each phase so that we could “count” the number and direction of dispersing individuals.

We ran each simulation for 50 time intervals (each composed of one demographic and dispersal episode) so that we could plot the output at a reasonable scale. In some simulations we allowed the population to grow and decline in random order. In the majority of simulations, however, the population alternated between periods of increase and decline. Such a pattern is common in many temperate-zone species, including the mouse population we used to test the model (increase during the spring and summer and decline in the fall and winter, Morris and Diffendorfer 2004).

Varying habitat quality

We simulated changes in habitat quality in two ways. First, within a single run of the simulation, we allowed

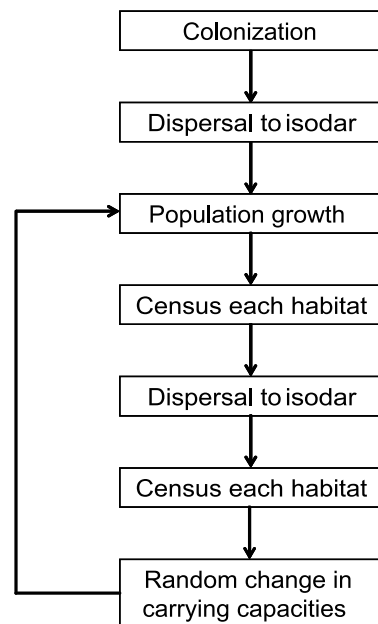


Fig. 1. A schematic illustration of the algorithm used to simulate ideal habitat selection.

the population to vary either randomly or seasonally at time j by multiplying the carrying capacity of each habitat times one plus a normally distributed random variate, (x_{ij}) with a mean = 0, and a fixed standard deviation ≤ 0.2 . Separate variates with the same sign (either positive or negative) were drawn for each habitat. We assumed, implicitly, that environmental variance modifies carrying capacity rather than maximum fitness (r) at low density (Hutchinson 1978). Thus, the net population change relative to carrying capacity, (right-hand term from Eq. 1) was

$$r_i K_i \left(1 - \frac{K_i}{K_i(1 + x_{ij})} \right) = r_i K_i \left(1 - \frac{1}{(1 + x_{ij})} \right) \quad (5)$$

During each demographic phase the model drew random values of x_i within a single standard deviation. For completely random dynamics, the population then grew (or declined) according to Eq. (5). For seasonal dynamics, the randomly-drawn variates were assessed to determine whether they were of the same sign as those used in the preceding demographic phase. If they were of the same sign, the values were rejected and each subsequent random draw was assessed similarly until a pair of values (one for each habitat) were obtained such that each one differed in sign from the previous demographic phase. The population was thus forced into alternating periods of growth and decline. Second, in other simulations, we investigated how fitness altered dispersal by parameterizing habitats so that they possessed different values of r ($1.1 \leq r \leq 2.75$). Our simulations did not modify r within a run. Each simulation maintained a constant 'pattern' of dynamics that avoided complications with changes in the stability of populations other than those associated with habitat.

Measuring dispersal

It is relatively straightforward to count the number of animals moving between the habitats under conditions of perfect density-dependent habitat selection. Beginning with the isodar representing the set of densities in each habitat (Eq. 3), and assuming that individuals select between habitats to equalize population growth rates, total population size, N_{tot} , can be calculated from Eq. 3 as

$$N_{tot} = N_B + N_A = \left(\frac{K_B(r_B - r_A)}{r_B} \right) + \left(\frac{r_A}{r_B} \frac{K_B}{K_A} \right) N_A + N_A \quad (6)$$

The number existing in habitat A, assuming perfect habitat selection, must therefore be

$$N_A = \frac{N_{tot} - \alpha}{\beta + 1} \quad (7)$$

where α and β correspond to the 1st and 2nd parenthetical terms in Eq. 6 respectively. We measured the number of dispersing individuals in our simulations by the difference between the density predicted by density-dependent growth in each habitat (Eq. 1, demographic phase of the simulations) and the density in the habitat after the population had been redistributed by habitat selection (Eq. 7, dispersal phase in the simulations). Examining those equations, we note that the number of dispersing individuals is large when r_A/K_A is small (negative term in Eq. 1 is small) and when K_B/r_B is large (Eq. 7 is small).

We generated frequency distributions of the net flow of emigrants (the total number leaving habitat i minus the total number entering it) by replicating each 50 time-step simulation with identical parameters 100 times (a total of 5000 demographic and dispersal phases). Donor habitats were identified as those where the mean net flow of emigrants in the entire set of simulations was at least twice the value of its standard error. The second habitat was a receiver. Balanced dispersal occurred whenever the 95% confidence interval about the mean included zero emigrants.

We provide an analytical proof that density-dependent habitat selection produces reciprocating dispersal in Appendix 1. The appendix also demonstrates that a habitat-selecting species living in temporally variable environments will have a lower density of individuals living in the preferred habitat than would occur in an environment with no temporal variation (undermatching).

Ideal-despotic dispersal

We completed our analysis of reciprocating dispersal by simulating ideal-despotic distributions (Fretwell and Lucas 1970, Fretwell 1972) where dominant or despotic individuals alter the "perception" of a habitat's quality. We imagine situations where dominant territory holders exclude sub-ordinate individuals from settling in an area that could in fact, support both individuals. We calculated a habitat's "perceived" fitness distribution by reducing its seasonally varying carrying capacity from $K_i(1 + x_{ij})$ to $(K_i(1 + x_{ij}))d_{ij}$ (where d_{ij} is a fixed proportion representing the reduction in carrying capacity in habitat i during season j caused by despotic interactions).

The 'despotic' simulations were identical to those for the discrete logistic except during the dispersal phase. Individuals moved between habitats on the basis of the perceived fitness distribution (ideal-despotic habitat selection) instead of the unfettered, cost-free distribution (ideal-free habitat selection). Thus, populations grew stochastically according to the actual fitness distribution in each habitat, but individuals dispersed according to

the perceived fitness difference between habitats (ideal despotic). This process accentuated the already existing asymmetry in population growth and decline between habitats with different growth rates.

Our final set of simulations assessed whether balanced or reciprocating dispersal yields the greatest long-term return. We compared simulations where dispersal was balanced (equivalent to no habitat selection; the segment of the population in each habitat grew and declined with no dispersal), with concurrent simulations of dispersal that equalized fitness. Each pair of competing simulations ran for 100 discrete time intervals with identical parameter values and stochastic effects. We defined the best strategy as the one that yielded the greatest mean population size (both habitats combined). Mean population size in these simulations is a short-hand measure of the expected number of descendants produced by individuals obeying each strategy.

All of our simulations assume that fitness declines linearly with increasing density. We have not modelled the curved functions that occur, for example, with ideal-pre-emptive distributions (Pulliam 1988, Pulliam and Danielson 1991, Morris 1994). While models of pre-emptive distributions may reveal intriguing dynamics, the basics of the reciprocating-dispersal model will necessarily be retained because dispersal is linked to differences between habitats in relative growth rates and changes in fitness through time.

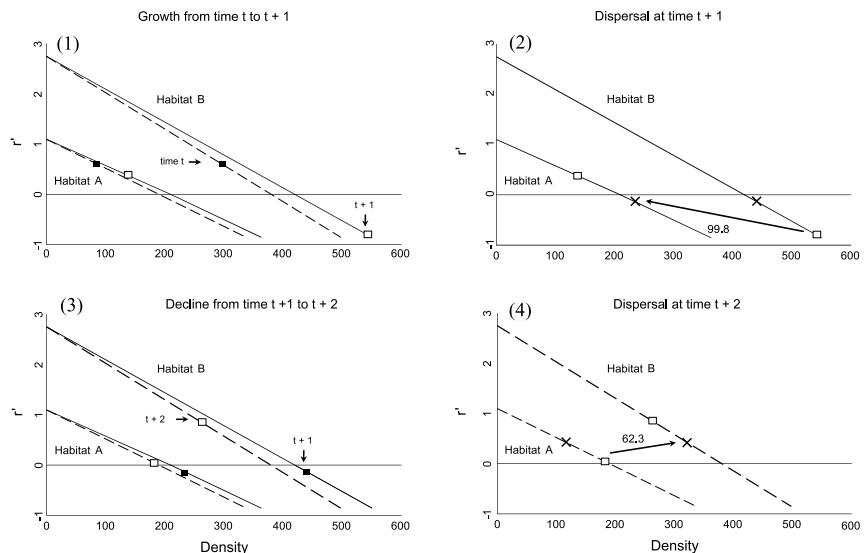
Results

An illustration of dispersal caused by ideal habitat selection

We graphed an example of dispersal emerging from the discrete logistic model to illustrate the main consequences of density-dependent habitat selection when populations fluctuate in size (Fig. 2). Three effects dominate the habitat-dependent dynamics. (1) The habitat with the higher density will, even when fitnesses are identical in both habitats, add more individuals during population increase than will the low-density habitat. It will also lose more during population decline. The consequences of this fundamental asymmetry for the direction of dispersal depend on (2) the differences among habitats in their maximum fitness (i.e. the differences in the per capita population growth rate), and (3) the rate of decline in fitness with density.

Figure 2 illustrates how dispersal interacts with maximum fitness, density and stochastic effects. The four panels trace population growth from time t to $t+1$ (panel 1), subsequent dispersal (panel 2), then population decline from $t+1$ to $t+2$, followed by a second opportunity for dispersal (panel 4). In this example, fitness declines more rapidly with increasing density in the habitat with the higher growth rate (B). Population growth occurs in response to increased carrying capacity

Fig. 2. An illustration of how ideal-free habitat selection leads to reciprocating dispersal. The four numbered panels follow population dynamics through a cycle of growth followed by ideal-free habitat selection, then subsequent decline followed by another episode of habitat selection. Realized fitness (r') declines linearly with density in two habitats, A and B. The predicted number of dispersing individuals (and their direction) is printed on panels 2 and 4. The dashed line represents the original population at time t (and again at $t+2$), while the solid line represents the population after growth at $t+1$. The curves correspond to increases and declines in each habitat's carrying capacity by a constant proportion ($x = \pm 0.05$). In panel 1, K increases and the population, with equal fitness in both habitats (filled squares), grows asymmetrically because more individuals occupy habitat B than A. The asymmetrical growth causes fitness to become unequal in the two habitats (open symbols). Since fitnesses are no longer equal in both habitats, 99.8 individuals disperse from habitat B to regain an ideal-free distribution (crosses in panel 2; partial individuals reflect parameter values used in the simulation). After this peak, K is reduced in each habitat by the same proportion (panel 3, dashed line), and following population decline, fitness is greater in habitat B than in A. Note that fewer individuals disperse from habitat A to B (62.3) following decline (panel 4), than flowed from B to A following the increase in population size. Habitat B is a net donor of emigrants and habitat A is a net receiver of immigrants. Parameter values as follows: $K_A = 200$, $K_B = 400$, stochastic variation $x = \pm 0.05$; $r_A = 1.1$, $r_B = 2.75$.



(solid fitness line, panel 1), decline is associated with reduced carrying capacity (dashed line, panel 3). During periods of population growth (demographic phase of our model, t to $t+1$, panel 1), the density in habitat B increases more than in A. After population increase, but before dispersal, individuals in habitat A have higher fitness than those in habitat B. Indeed, in panel 1 of our example, the density in habitat A following population growth is actually less than that habitat's carrying capacity, whereas the density in B exceeds K_B . Thus, an individual in habitat B can achieve greater fitness by emigrating than by philopatry, and we expect individuals to move to A in the dispersal phase (panel 2) until the fitness in both habitats is equal (in this case, the 99.8 emigrants from B push the density in A beyond K_A). Relative to carrying capacity, a smaller proportion of individuals leave habitat B than enter A (emigrants from B = immigrants to A but emigrants/ K_B < immigrants/ K_A).

In the subsequent demographic phase ($t+1$ to $t+2$, panel 3), the population declines because densities in both habitats exceed their carrying capacities. During the decline, habitat B loses more individuals than habitat A. The decline is, however, less than it otherwise would have been without emigration in the previous dispersal phase. The consequence of this asymmetry is that only 62.3 individuals should emigrate from habitat A to equalize fitness (panel 4, a large proportion, relative to habitat A's carrying capacity, enter B). A key result is that the buffering effect of perfect density-dependent habitat selection on the magnitude of population fluctuations (dispersal results in smaller changes in N_A and N_B than would occur without dispersal) is insufficient to reverse the asymmetries in growth rates between the habitats. Habitat B, with its higher growth rate, is a net donor of individuals, while habitat A is the receiver. Other examples (not illustrated) with small differences in r (and a higher rate of decline in fitness in the low r habitat [A]) demonstrate that habitat A, can become the donor.

The simple graphical model illustrates how density-dependent habitat selection produces a pronounced pattern of reciprocating dispersal where individuals flow between habitats in one direction during periods of population increase, and in the opposite direction during periods of population decline (Fig. 2). The relative differences in each habitat's maximum rate of population growth, and the decline in that rate with density, will determine which habitat acts as a net donor of emigrants. So too will differences in stochastic effects on carrying capacity.

To visualize the role of stochasticity, imagine that the density in each habitat is at its respective carrying capacity (and therefore, on the isodar). Imagine that stochastic influences increase (or decrease) carrying capacity in habitat i during season j by some fraction x_{ij} . The net population change, relative to carrying

capacity, is modified by the stochastic effect (Eq. 5). Thus, in addition to the effect of density on the number of recruits or deaths, the density-dependent increase and decline in population size between habitats is proportional to their respective density-dependent population growth rates, and to differences in stochasticity. If stochastic effects are greater in one habitat than in another, they will accentuate already existing differences in population growth and dispersal (by increasing maximum divergence of the fitness curves) and similarly help to determine whether the habitat is a net donor or receiver of dispersing individuals.

To summarize, when the rate of decline in fitness is relatively rapid in the high- r -high- K habitat, it receives fewer immigrants from the low- r -low- K habitat following population decline than it exports following population increase; the high- r -high- K habitat is a net donor of emigrants. When the rate of decline in fitness is relatively rapid in the low- r -low- K habitat, it exports more emigrants following population decline than the number of immigrants it receives following increase; the low- r -low- K habitat is a net donor of emigrants. Stochastic dynamics influence the total number of dispersing individuals, and differences in the degree of stochasticity between habitats help to determine the net balance between immigrants and emigrants.

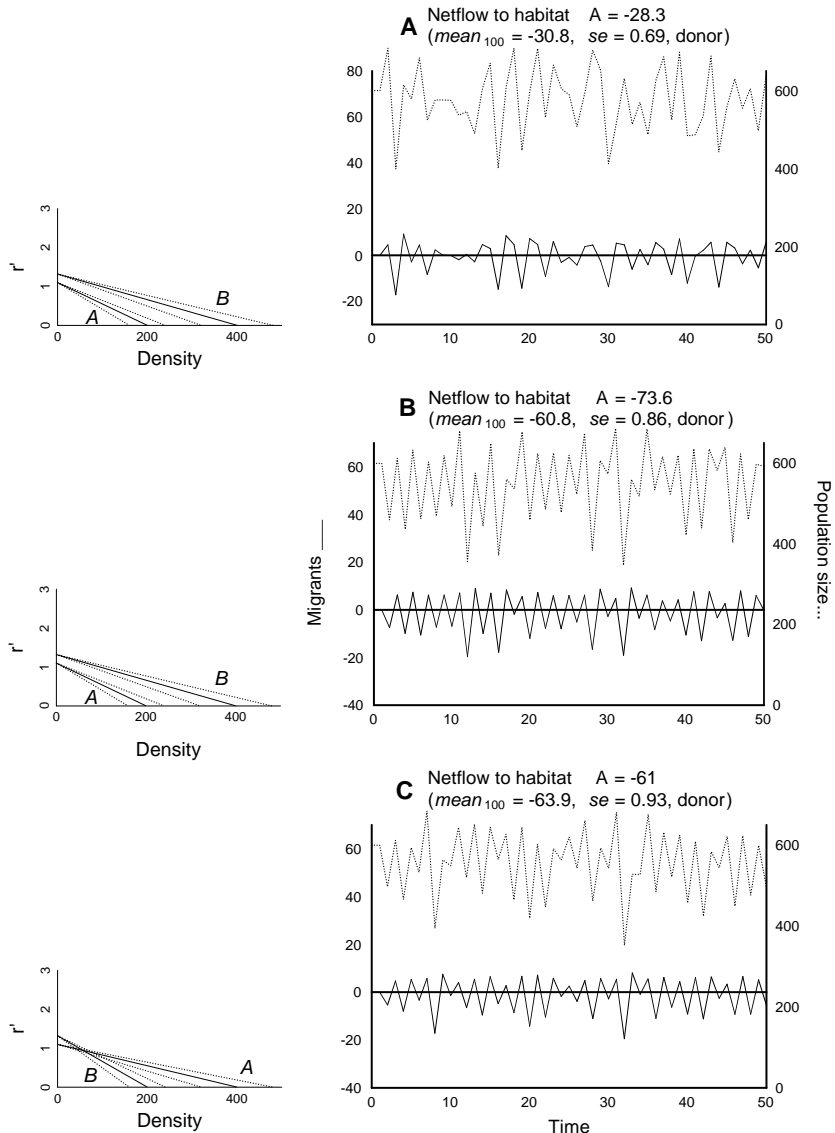
Simulations of ideal habitat selection

Ideal-free habitat selection produces reciprocating dispersal

Our first set of simulations compared ideal-free habitat selection between habitats differing in both maximum fitness (r) and carrying capacity. We allowed carrying capacity to vary either at random (Fig. 3A) or seasonally (Fig. 3B, C). In each case dispersal reciprocated between habitats, and the low- r habitat (A) acted as a net donor of dispersing individuals. Habitat A was also a net donor of emigrants even when its carrying capacity was twice as large as that in habitat B (Fig. 3C). The pattern was reversed (A became a net receiver) when we increased the carrying capacity in A to six times that in B (not illustrated). The simulations confirm the point, made above, that whether a habitat functions as a donor or receiver of emigrants depends not only on the magnitude of differences in growth rates, but also on the rate of decline in fitness with density. Despite having a lower r , habitat A acted as a donor because the dispersal strategy depends on the interplay between per capita population growth, carrying capacity and stochastic variation.

We repeated the simulations with different values for growth rates and stochasticity to explore more fully the conditions causing a habitat to function as either donor or receiver. When population growth rates are low and differ by a small amount between habitats, the dynamics

Fig. 3. Examples of how ideal-free habitat selection in stochastic environments with quantitatively different habitats ($r_A \neq r_B$) can produce donor-receiver dynamics with reciprocating dispersal. Large graphs represent population dynamics and dispersal, small graphs summarize parameter values. Solid lines on small graphs represent the decline in fitness with density, dashed lines represent the range of stochastic effects. Solid lines on large graphs represent dispersal of individuals to (+ve) or from (-ve) habitat A, dotted lines represent total population size, time is measured in simulation intervals. Note that all large plots are drawn to the same scale, but that the actual values on the ordinate vary. Stochastic effects are random in A, and seasonal in B and C. Parameter values as follows: $r_A = 1.1$, $r_B = 1.32$, stochastic variation $x = \pm 0.2$ of K_i for all scenarios; A and B, $K_A = 200$, $K_B = 400$, C, $K_A = 400$, $K_B = 200$. Initial densities correspond to carrying capacities.



in each habitat are similar, but of different magnitudes. The low- r , rapid-decline-in-fitness habitat (A) is the donor (Fig. 4A). When population growth rates are dissimilar, the high- r , rapid-decline-in-fitness habitat (B) dominates the dynamics and acts as the donor (Fig. 4B). In each case, the flux of individuals also helps to dampen the fluctuating population dynamics that would otherwise exist in the donor habitat.

Reciprocating dispersal is retained, but net dispersal can be reversed, when stochastic effects vary between habitats
Our simulations demonstrate that the pattern of dispersal depends on underlying differences between habi-

tats in stochastic population dynamics. We provide an example in Fig. 4 and 5. Dispersal that otherwise flows directionally away from the habitat with the steeper fitness function (Fig. 4A) is reversed when that habitat (A) has the greatest stochastic variation in carrying capacity (Fig. 4C). But habitat A's ability to function as a donor is enhanced when stochastic dynamics in habitat B are increased (compare Fig. 4A with Fig. 5).

The rate and net flow of emigrants can be altered by dominance

Though we simulated several scenarios of ideal-despotic habitat selection, one illustrates, vividly, the effects of

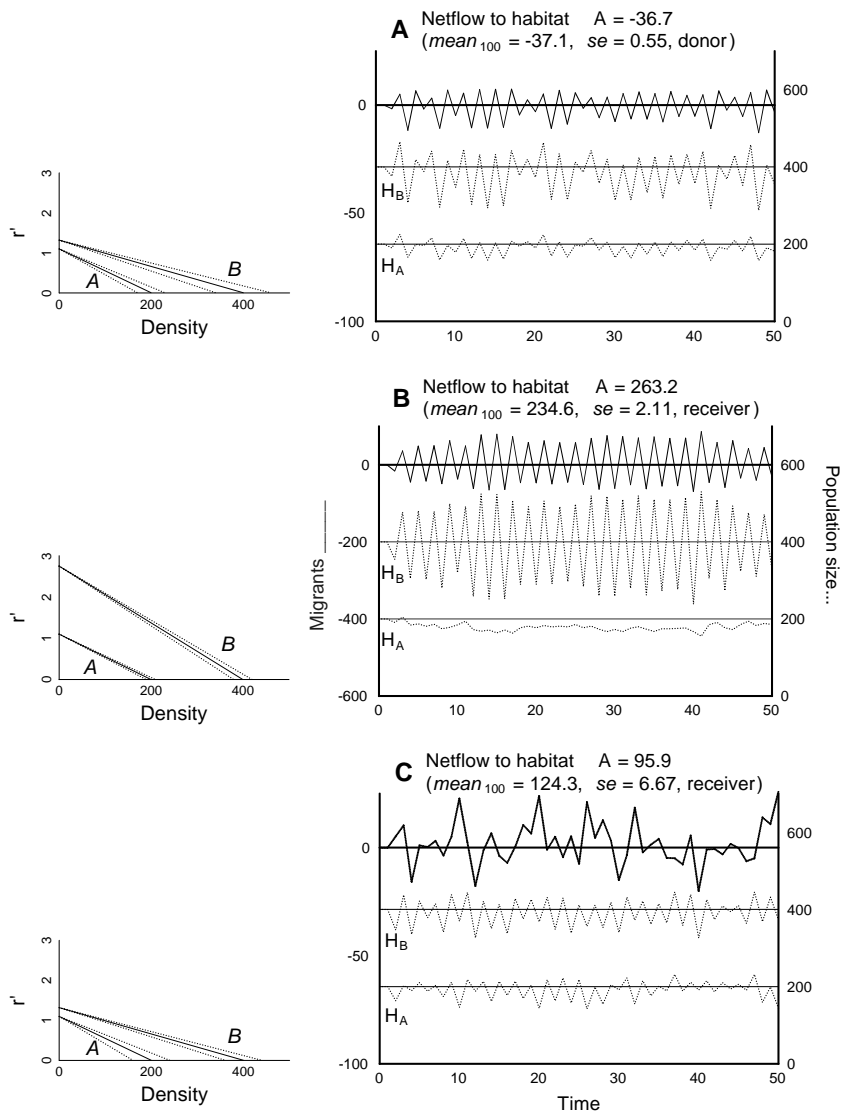


Fig. 4. Examples of how ideal-free habitat selection in stochastic environments with quantitatively different habitats produces different donor and receiver habitats with reciprocating dispersal. Large graphs represent population dynamics and dispersal, small graphs summarize parameter values. Solid lines on small graphs represent the decline in fitness with density, dashed lines represent the range of stochastic effects. The top solid line in the large graphs in each panel plots the number of individuals either migrating from (-ve) or into (+ve) habitat A (note that the scale of migrants is different in panel B than in panels A and C). The middle dotted line in each panel is a plot of the population dynamics in habitat B, while the lower dotted line is a plot of the dynamics in habitat A. In panel A, population growth rates in the two habitats are similar, and A is a net donor habitat. In B, population growth rate is much greater in habitat B, and it is a donor habitat. In C, the growth rates are the same as in panel A, but the stochastic effect in habitat A is greater than that in B, and A is a receiver habitat. This is a particularly interesting scenario because the density in the low-r habitat (A) is maintained below its average carrying capacity. The component of the population in habitat A retains potential for population increase even though it is a net receiver for immigrants. Large increases in density in habitat B result in high immigration into habitat A following periods of population growth. The inflated density in A accelerates its decline when

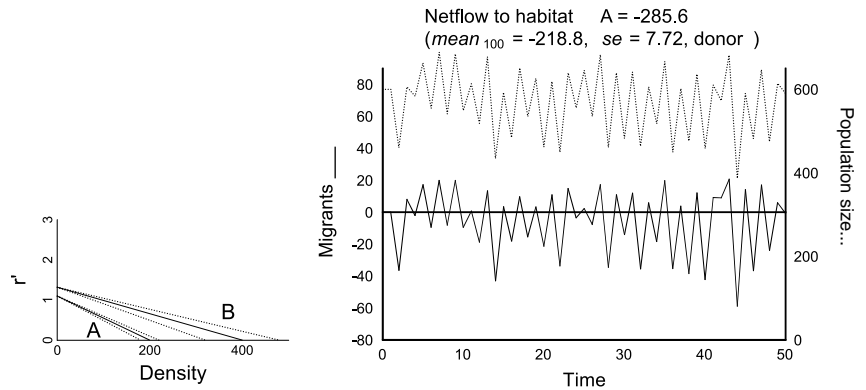
population growth is negative. Habitat A's growth rate is not large enough, however, to cause it to exceed its carrying capacity. Parameter values as follows: $K_A = 200$, $K_B = 400$ for all scenarios; A, $r_A = 1.1$, $r_B = 1.32$, stochastic variation $x = \pm .15$ of K_i ; B, $r_A = 1.1$, $r_B = 2.75$, $x = \pm .05$; C, $r_A = 1.1$, $r_B = 1.32$, $x = \pm .2$ of K_A and ± 0.1 of K_B . Initial densities correspond to carrying capacities.

despotism on dispersal. Compare the number and direction of migrants in Fig. 6 with those in Fig. 3. Other than competitive dominance, the parameter values are identical for the scenarios of habitat selection illustrated in panel B of the two figures. Relative to ideal-free habitat selection, there is a striking increase in the number of dispersing individuals when dominants interfere with the habitat choices of sub-ordinates. Note, too, that dominance, even when equivalent between habitats, can reverse donor and receiver habitats relative to ideal-free habitat selection (contrast Fig. 6C with Fig. 3B).

Multiple patterns from reciprocating dispersal are retained with ideal-despotic habitat selection

The net influence of dominance on dispersal depends on habitat differences in population growth rate and whether dominant individuals have equal or divergent effects in different habitats. If competitive dominance is greatest in the high-r, low-decline-in-fitness habitat (B), for example, that habitat can be a constant donor of emigrants (Fig. 6A). Population size in the high-r habitat (B) is maintained at relatively low levels by dominants that force dispersal of sub-ordinate individuals. The directional movement of excess individuals away from B

Fig. 5. An example of ideal-free habitat selection in a stochastic environment with quantitatively different habitats where the magnitude of variation in stochastic dynamics is greater in habitat B than it is in habitat A. The large graph represents population dynamics and dispersal, the small graph summarizes parameter values. The solid line on the small graph represents the decline in fitness with density, dashed lines represent the range of stochastic effects. Habitat A is a donor. Compare with the opposite scenario in Fig. 4C when stochastic dynamics are greater in habitat A (A is a receiver). Parameter values as follows: $r_A = 1.1$, $r_B = 1.32$, $K_A = 200$, $K_B = 400$, $x = \pm 0.1$ of K_A and ± 0.2 of K_B . Initial densities correspond to carrying capacities.



ensures that its rate of population increase remains high. Directly opposite of the previous predictions, the high- r habitat (B) can become a consistent receiver when the effect of dominance is greatest in the low- r habitat (habitat A, Fig. 6B). When the effects of dominance are equal in both habitats (Fig. 6C), the number of migrants is reduced, and rather than all migrants originating from a single habitat (Fig. 6A, B), the flow of migrants reciprocates between them. Thus, when dominance is asymmetrical between habitats, directional migration may occur that would typically be associated with source-sink models of dispersal (a consistent flow of individuals from one habitat to another). In the present case, however, neither habitat is a sink.

Other simulations (not illustrated) confirmed our suspicion that, depending on parameter values, it is even possible to create scenarios where reciprocating dispersal can produce a net balance of migrants between habitats. These simulations demonstrate that the number of individuals moving between habitats is clearly an insufficient metric to test among competing models of dispersal.

Reciprocating dispersal produced larger mean population sizes than did balanced dispersal

Our simulations contrasted balanced (no habitat selection) versus reciprocating dispersal (ideal habitat selection) under otherwise identical conditions. Population size was unequivocally greater with habitat selection than without it. Only one of the 200 possible comparisons between growth and dispersal intervals in the two different scenarios yielded a greater population size for the balanced dispersal model than for reciprocating dispersal. Using the parameter values in Fig. 3B, the mean population size with reciprocating dispersal contained 78.08 ($se = 3.69$) more individuals than when dispersal was balanced. We obtained similar results

using the parameter values in Fig. 4C (mean population size with reciprocating dispersal contained 50.46 [$se = 1.82$] more individuals than with balanced dispersal). The strategy of density-dependent habitat selection was superior to that of balanced dispersal.

Discussion

We have explored only a small subset of factors (Stamps 2001) that weave previously unexpected patterns in the exquisite tapestry of habitat selection, dispersal and population dynamics. Even so, it is obvious that theories of density-dependent habitat selection in spatially and temporally variable environments produce a highly consistent pattern of reciprocating dispersal where the source of emigrants varies through time. The pattern is retained whether populations fluctuate seasonally or at random. And it occurs whether individuals are free to occupy the habitat of their choice, or whether dominants interfere with habitat selection. Though population density in stochastic environments is undermatched (too few individuals in the better habitat) with respect to habitat quality in a purely deterministic environment, reciprocating dispersal buffers variation in fitness that would otherwise occur between habitats, and modulates both temporal and spatial patterns in population dynamics. Habitat selection can thus serve as an appropriate null model for landscape ecology (Morris and Brown 1992), and for spatially-variable population dynamics. Many of the spatial patterns in abundance and movement that we observe may be explained simply by habitat selection, and not require additional complexities associated with spatial characteristics of the landscape.

The net flow of individuals from one habitat to another depends on differences in basic habitat suit-

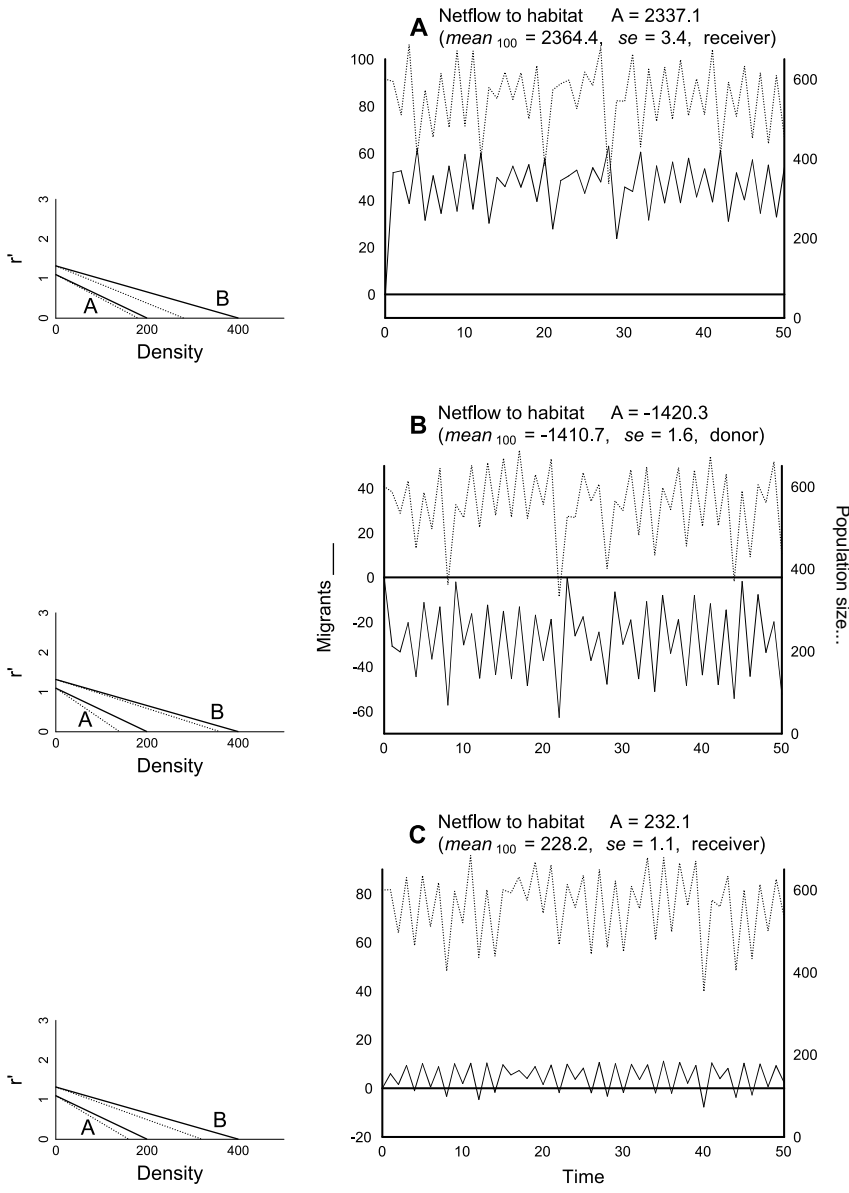


Fig. 6. Examples of how quantitative differences in habitat in stochastic seasonal environments with habitat variation in dominance can lead to either uni-directional (all migrants leave only one habitat, A and B) or bi-directional (migrants leave from both habitats) dispersal (C). Large graphs represent population dynamics and dispersal, small graphs summarize parameter values. Solid lines on small graphs represent the decline in fitness with density, dashed lines represent the effect of dominance (stochastic effects are not illustrated). Solid lines on large graphs represent seasonal dispersal of individuals to (+ve) or from (-ve) habitat A, dotted lines represent total population size, time is measured in simulation intervals. Note that all large plots are drawn to the same scale, but that the actual values on the ordinate vary. Parameter values as follows: $K_A = 200$, $K_B = 400$, $r_A = 1.1$, $r_B = 1.32$, $x = \pm 0.2$ of K_i for all scenarios; despotic effects: A, $d_A = 0.9$, $d_B = 0.7$; B, $d_A = 0.7$, $d_B = 0.9$; C, $d_A = 0.8$, $d_B = 0.8$. Initial densities correspond to carrying capacities.

ability, differences between habitats in population regulation (the rate of decline in fitness with density), and differences in how stochastic events modify the pattern of population regulation (changes in carrying capacity or the slope of fitness with density). But it is critical to remember that the outcome, in each case, depends on the ability of organisms to choose one habitat over another by accurately assessing fitness (or a close correlate), and on the continual optimization of emergent dispersal strategies by natural selection.

The theory also warns us, for organisms capable of density-dependent habitat selection, that the dichotomy

between balanced dispersal and source-sink dynamics is by-and-large artificial. Organisms with adaptive habitat selection will occupy whichever habitat offers a fitness advantage. As density and population growth co-vary, the identity of favored habitats changes, and so too does the direction of dispersing individuals. While there are, no doubt, several evolutionary routes that can influence the degree to which dispersal is either fixed or contingent on local densities (Morris 1991a), we cannot ignore the ubiquitous pattern of reciprocating dispersal that emerges from strategies of density-dependent habitat selection.

The model of dispersal we present here corresponds most closely to McPeck and Holt's (1992) simulation of dispersal in spatially varying but temporally constant environments (reciprocating dispersal is a consequence of populations that fluctuate in synchrony). Their balanced dispersal hypothesis predicts an ESS composed of genotypes with low per capita dispersal from high-density patches, and high per capita dispersal from low-density patches. Our alternative model based on density-dependent habitat selection predicts that dispersal, at least in populations with fluxes in abundance, may yield either balanced dispersal or patterns identical to source-sink dynamics. Why do two theories, both based on evolutionarily stable strategies of habitat selection, yield different predictions about dispersal?

The simulation conducted by McPeck and Holt (1992) first allowed the population to reach an evolutionarily stable strategy of near-zero unconditional dispersal (per capita dispersal rate is constant). Next, the simulation allowed pairs of conditional dispersal strategies (per capita dispersal rate varies between habitats) to compete with one another, and to replace any previous strategy. Thus, if one of the conditional strategies was based on a high dispersal propensity from the habitat with low mean density, it could be balanced by a second conditional strategy of a somewhat lower dispersal rate from a habitat with high mean density (balanced dispersal, dispersal propensity inversely proportional to carrying capacity). The simulation demonstrated the "Newtonian" rule that if the dynamics of a system are to remain constant, then any action in one part must be balanced by an equal reaction in another.

The alternative reciprocating dispersal model is supported by the few studies that have examined dispersal patterns between alternative habitats. Grant (1978), in a characteristically seminal experiment, documented seasonal colonization of woodland habitat by meadow voles (*Microtus pennsylvanicus*) dispersing from grasslands in southern Quebec, a pattern also apparent in a related experiment in Saskatchewan (Morris and Grant 1972). Indeed, seasonal dispersal is common among several species of *Microtus* (Lidicker 1985). Many small mammal species appear to have two classes of dispersing individuals, depending on whether dispersal occurs while populations are growing (pre-saturation) or are at their maximum size (saturation; Lidicker 1975; Anderson 1989 proposed an alternative view). The seasonal and population-dynamic patterns of dispersal are both consistent with density-dependent habitat selection.

Lin and Batzli's (2001) experiments are especially revealing. Emigration and immigration of meadow and prairie voles (*M. pennsylvanicus*, *M. ochrogaster*) were tallied in four kinds of habitats representing all combinations of low and high cover (mowed and unmowed grassland) and high and low food concentration (supplemental rabbit chow or none). Though many animals

moved from one habitat to another, there was no net flow of individuals from one habitat to another for meadow voles. Prairie voles, on the other hand, moved from low-quality habitat where their fitness was also low to high-quality habitat that yielded higher fitness. Thus, the pattern of dispersal appeared to be balanced for meadow voles, and unbalanced for prairie voles (Lin and Batzli 2001). The relative qualities of the different treatments vary for the two species, however, (prairie voles are much more tolerant of low cover) and there is no reason to suppose that the results are necessarily inconsistent with reciprocating dispersal driven by density-dependent habitat selection. Indeed, an intriguing interaction of emigration rates with habitats and seasons occurred in both species. The interaction is a necessary but insufficient condition for reciprocating dispersal.

A similar study by Andreassen and Ims (2001) on root voles dispersing among patches of different sizes and connectivity appears, at first reading, inconsistent with dispersal driven by density-dependent habitat selection. Voles tended to move from low-density patches to even lower density patches (density dependent), but simultaneously exhibited a reduced probability of dispersal in the highest-density patches. But differences in the rates of dispersal are completely consistent with density-dependent habitat selection. Habitats with high density often possess a built-in asymmetry in the rate of dispersal relative to patches of lower density. One version of this asymmetry is illustrated in Fig. 2 for a "cycle" of population growth and decline. Though a large number of individuals emigrated from the high-density habitat following population growth, they nevertheless represented a relatively small proportion of the population (0.19). Emigration from the habitat with lower density following population decline was less, but the rate was greater (0.35, Fig. 2). Similar asymmetries will often exist amongst multiple habitats during any one phase of population growth or decline. The actual pattern will depend on the relationships between fitness and density in the different habitats.

Diffendorfer et al. (1995, Diffendorfer 1998) documented balanced dispersal in an experimental study in northeast Kansas. The net number of animals moving between blocks of unmowed habitats was balanced for three different species of small mammals (cotton rats *Sigmodon hispidus*, prairie voles *Microtus ochrogaster*, and deer mice *Peromyscus maniculatus*). Yet each species expressed strong seasonal changes in rates of movement, and in some cases, a pronounced bias in the direction of movement within a season. In cotton rats, most dispersal occurred in autumn, and proportional movements (number of animals moving/number of animals present in a block) were biased with ~26% of individuals moving to larger blocks from smaller ones. Only ~2% of the rats moved in the opposite

direction. Smaller blocks supported much lower numbers of cotton rats. In prairie voles, most movements again occurred in the fall, a period of general population decline. During this time, the three largest blocks (supporting on average 23 individuals each), gained animals, while the three smallest blocks (supporting on average only 9.6 individuals each) lost animals. Finally, Diffendorfer et al. (1995) found no differences in survivorship or reproduction across the blocks, indicating that animals might be equalizing fitness through habitat selection.

The directionally and seasonally reciprocating biases in movement, as well as similar values for fitness-related demographic variables across blocks, suggests strongly that density-dependent habitat selection drives dispersal by small mammals in northeast Kansas. We cannot be certain whether the example truly represents reciprocating dispersal because the three species compete with one another and use the mowed areas between blocks differentially (Schweiger et al. 2000). An in-depth analysis of both intra- and inter-specific densities will be necessary to evaluate fully whether dispersal in the Kansas system emerges from density-dependent habitat selection.

Reciprocating dispersal is demonstrated clearly in our accompanying analysis of 19 years of habitat-selection data by white-footed mice (Morris and Diffendorfer 2004). White-footed mice select habitats according to an ideal-despotic distribution (Morris 1989, 1991b, Halama and Dueser 1994). High-fitness forest habitat acted as a donor of emigrants as the population increased during the spring and summer, and as a receiver of immigrants while the population declined over winter. Had we analyzed our white-footed mouse data in ignorance of the seasonal flux of individuals, we could have confirmed either balanced dispersal or source-sink models of population regulation (Morris and Diffendorfer 2004). Both would have been incorrect.

We hope that our demonstration of marvellously rich and novel consequences from a simple rule, 'optimize fitness by dispersal', will lead others to explore the intriguing dynamics hidden so deceptively by density-dependent habitat selection. Ecologists must consider strategies of habitat selection if they are to understand, thoroughly, the evolution of dispersal and its effects on populations and communities.

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Appendix 1

Ideal-free dispersal (a generic logistic model)

Some might question whether the form of parameterization in Eq. 1, and our choice to allow stochastic variation in carrying capacity, might unduly influence patterns and interpretations of reciprocating dispersal. We assessed this question, as well as the dependence of dispersal on both the magnitude of habitat differences in fitness and its decline with density, by mimicking population growth with paired generic difference equations

$$N_{B(t+1)} = r_B N_{B(t)} - b_B (N_{B(t)}^2) \quad (A1)$$

and

$$N_{A(t+1)} = r_A N_{A(t)} - b_A (N_{A(t)}^2) \quad (A2)$$

for habitats B and A respectively. Letting per capita fitness equal $(N_{(t+1)} - N_{(t)})/N_{(t)}$ as above, the resulting isodar is given by

$$N_B = \frac{(r_B - r_A)}{b_B} + \frac{b_A}{b_B} N_A \quad (A3)$$

We substituted equation (A3) for the “discrete logistic” isodar in Eq. 3, converted it into the form of Eq. 7, and repeated the simulations by multiplying b times one plus a normally distributed random variate. Comparison of the growth equations (A1 and A2 with 1) reveals that stochastic changes in K (Eq. 1) must be mirrored by stochastic changes in b . It is not quite as obvious, however, that stochasticity in the different models will have identical effects on their two isodars (compare Eq. A3 with Eq. 3). Our simulation methods and runs of the generic model mirrored those we used to simulate discrete logistic dynamics.

Reciprocating dispersal is a generic property of ideal-free habitat selection

Reciprocating dispersal was retained in our simulations using the generic logistic model (A1). Though our choice of parameter values resulted in relatively low dispersal, the pattern is reciprocal and yields a variety of possible

outcomes. The net flow of individuals from one habitat to another depended, again, on the magnitude of differences between habitats in maximum fitness (r), and in the rate of decline of fitness with population density. When maximum fitness was substantially greater in habitat B than in A, and when the decline in fitness was also greatest in the high-fitness habitat (B), B acted as the donor of emigrating individuals (Fig. A1A). The opposite occurred if fitness declined more rapidly with density in A, and if maximum fitness was similar between the two habitats. Habitat A was the donor (Fig. A1B).

Fitness in variable environments: the conquistador effect

Our measures of an individual’s fitness might appear to ignore the difficulties that arise when populations fluctuate through time. Individuals living in temporally varying environments may maximize geometric-mean fitness rather than the arithmetic average that we use here (Levins 1968, Boyce and Perrins 1987, Morris 1992b, Holt and Barfield 2001). Identifying a suitable fitness measure is even more problematic when environments vary simultaneously in space and time, and when individuals are free to move among habitats (Kokko and Sutherland 1998, Brommer et al. 2000, Holt and Barfield 2001, Kokko and Lundberg 2001).

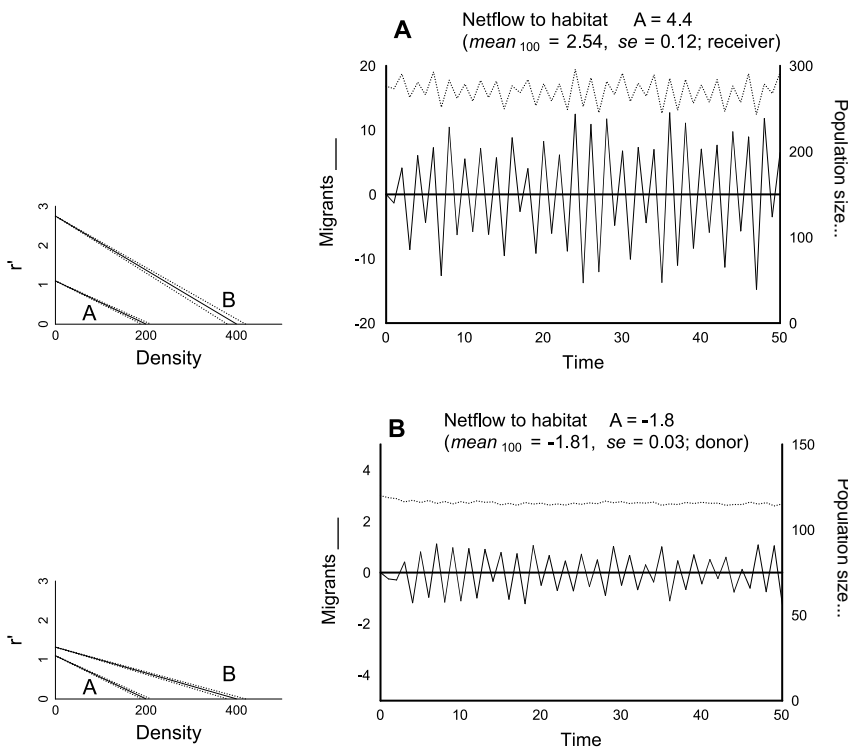


Fig. A1. Examples of reciprocating dispersal that emerge from generic models of ideal-free habitat selection in stochastic environments. Large graphs represent population dynamics and dispersal, small graphs summarize parameter values. Solid lines on small graphs represent the decline in fitness with density, dashed lines represent the range of stochastic effects. Note that the two large graphs are drawn at different scales. Parameter values as follows: $r_A = 1.1$, $b_A = 0.0055$, and $x = \pm 0.05$ for both scenarios, in A, $r_B = 2.75$, $b_B = 0.006875$, in B, $r_B = 1.32$, $b_B = 0.0033$. Initial densities were 20 in habitat A in both scenarios, and 256 in habitat B in scenario A, and 100 in habitat B in scenario B.

Why should we suspect that individuals move to habitats with higher mean fitness? Might it not be advantageous for an individual living in a declining population to stay in its current habitat until fitness recovers during the next favorable period? Would individuals that base their dispersal decisions on the multiplicative fitness benefits accrued through their descendants living in different habitats have higher fitness than those individuals obeying ideal habitat selection? We can answer each question by returning to scenario 1 in Fig. 2. Imagine that, at time $t+1$, the carrying capacities in each habitat increase, followed by corresponding increases in each habitat's population density (Fig. 2, panel 2). Fitness is negative in habitat B and positive in habitat A. Now imagine that, at time $t+2$, carrying capacities return to their original values. If there is no dispersal, or if dispersal is balanced, density in habitat B will be greatly reduced because the fitness there is negative, while that in habitat A would increase (fitness is positive). The few surviving individuals in habitat B that stayed home are now ready to reap their fitness bonus during the next increase in K_B at time $t+3$, but so too are individuals immigrating from habitat A. The immigrants, already profiting from their own bonus at $t+2$, can now steal that in habitat B.

Dispersal could be frustrated if habitat residents completely restrict immigration, or if other dispersal costs (e.g. mortality, time lost from reproduction) exceed any possible fitness benefit. If residents can only reduce the rate of immigration, the general pattern of reciprocating dispersal remains (below). But surely the residents would capitalize on their cumulative numbers and native advantage to repel the relatively small number of immigrants. A short historical interlude might help to resolve the debate. In the 16th century, a handful of greedy and audacious Spanish conquistadors raced across Mexico and Peru. Powerful and opulent civilizations, their treasuries and temples bursting with gold, crumbled before them. In turn, huge galleons, laden with the plundered riches, fell prey to brash, marauding privateers. The lesson: no matter how superior your numbers, no matter how great your strength, someone will always scheme to steal your wealth. The greater the reward, the more acceptable the risk. As in so many other areas in evolutionary ecology, you can't bank your fitness because the world is filled with (clever) thieves.

Reciprocating dispersal: a formal theory

Consider the dynamics of a population occupying two habitats, A and B in which the dynamics in habitat i are given by

$$N_{i(t+1)} = N_{i(t)} + r_i N_{i(t)} - b_i N_{i(t)}^2 \quad (A4)$$

We note for future use that the equilibrium population density in each habitat is

$$N_i^* = \frac{r_i}{b_i} \quad (A5)$$

If we plot N_B against N_A , the slope of the resulting isodar is b_A/b_B . Now, place the densities in each habitat on the isodar, and let the population grow from time t to $t+1$. The population densities will move in state space from the point $(N_{A(t)}, N_{B(t)})$ to $(N_{A(t+1)}, N_{B(t+1)})$. We can determine whether this new point lies on the isodar (no dispersal) by calculating the joint growth trajectory in both habitats, and contrasting that slope with the slope of the isodar.

The slope of the growth trajectory, S_G , is given by

$$S_G = \frac{N_{B(t+1)} - N_{B(t)}}{N_{A(t+1)} - N_{A(t)}} = \frac{r_B N_{B(t)} - b_B N_{B(t)}^2}{r_A N_{A(t)} - b_A N_{A(t)}^2} \quad (A6)$$

Knowing that the joint densities started on the isodar, we also know that

$$N_{A(t)} = \frac{r_A - r_B}{b_A} + \frac{b_B}{b_A} N_{B(t)} \quad (A7)$$

Using (A7) in (A6), we have

$$S_G = \frac{r_B N_{B(t)} - b_B N_{B(t)}^2}{r_A \left(\frac{r_A - r_B}{b_A} + \frac{b_B}{b_A} N_{B(t)} \right) - b_A \left(\frac{r_A - r_B}{b_A} + \frac{b_B}{b_A} N_{B(t)} \right)^2} \quad (A8)$$

If $S_G = b_A/b_B$ (the isodar slope), population growth tracks along the isodar and there is no adjusting dispersal between habitats. But whenever $S_G < b_A/b_B$, habitat A is overpopulated following population increase (and habitat B underpopulated in relation to the IFD), and individuals should disperse from habitat A to habitat B to equalize fitness in both habitats. Inspection of Eq. (A8) shows that whenever $r_A > r_B$, the growth trajectory can never exceed the isodar slope. That is, as long as habitat A is the better habitat in terms of maximum population growth rate, S_G will always be more shallow than the isodar, and IFD-adjusting dispersal flows from habitat A to habitat B following population growth. Whenever a population is increasing, the "better" habitat will always be the donor (Fig. A2). The opposite will occur during population decline (reciprocating dispersal). Corresponding logic applies when habitat B is the superior habitat. Here, if $S_G > b_A/b_B$, IFD-adjusting dispersal flows from habitat B to habitat A during population growth, and in the opposite direction during population decline. We reach the same conclusion: the "better" habitat is the donor. It is also rather straightforward to show that Eq. A8 can never = b_A/b_B for $N_B > 0$ and $r_A > r_B$.

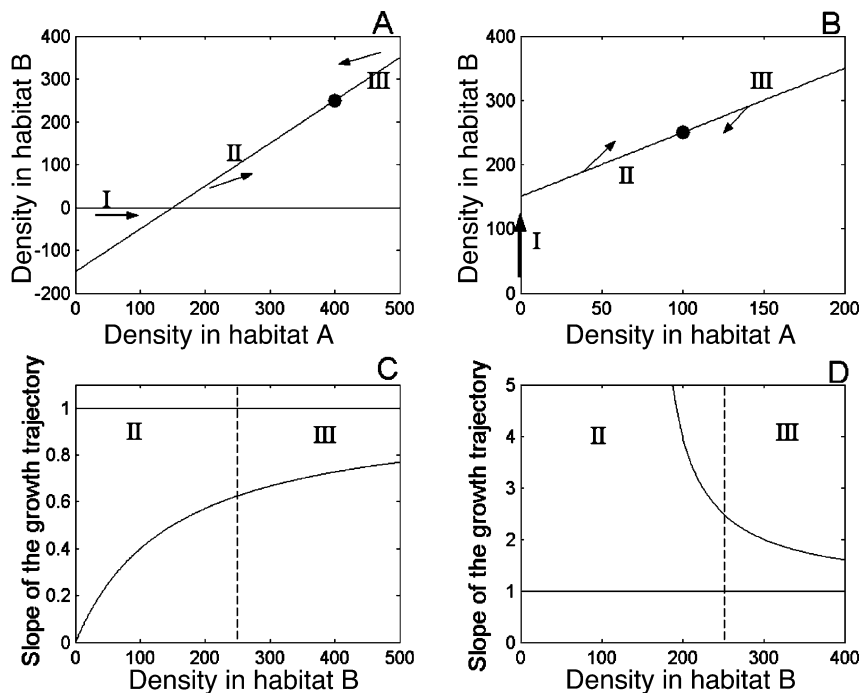


Fig. A2. An illustration of the isodars and population-growth trajectories under two different scenarios. In A, habitat A is the better habitat ($r_A > r_B$). In B, habitat B is the better habitat ($r_A < r_B$). In A, three regions of the isodar are illustrated, I-the region when the population occupies habitat A only, II-the region when both habitats are occupied but densities are below the respective habitat carrying capacities (filled circle), III-both habitats occupied above their carrying capacities. In B, region I corresponds to exclusive occupation of habitat B. The arrows in A and B represent the slope and direction of the population-growth trajectories. In C, the slope of the growth trajectory is plotted as a function of the density in habitat B for regions II and III from panel A. The slope of the growth trajectory is always more

shallow than the isodar (in this example the isodar has slope = 1 [horizontal line]). Note that the direction of the growth trajectory changes above carrying capacity (the vertical dashed line in C). Below carrying capacity dispersal is from habitat A to B. Above carrying capacity dispersal is from habitat B to A. The corresponding growth trajectory slopes for the isodar illustrated in B are plotted in D. The proportional difference in density between habitats declines as population size increases along the isodar (assuming a non-zero intercept), and the slope of the growth trajectory approaches the isodar. Note when densities in habitat B are less than the isodar intercept, that the growth trajectory is vertical (and similarly, it is horizontal for the corresponding region in A). The slope asymptotically approaches infinity as the density in habitat B decreases toward the isodar intercept. Thus, when both habitats are occupied, the number of dispersing individuals increases as the population departs from carrying capacity. Fluctuations above and below carrying capacity will determine whether net dispersal is balanced, or whether one habitat acts as a donor of emigrating individuals. Parameter values as follows: $r_B = 0.25$, $b_A = b_B = 0.001$ for both scenarios; A and C, $r_A = 0.4$; B and D, $r_A = 0.1$.

Quantifying dispersal

It is also possible to calculate the IFD-adjusting dispersal after population growth. After growth, the joint densities will move from the point $(N_{A(t+1)}, N_{B(t+1)})$ to the isodar on a perpendicular trajectory (overall density remains constant). That trajectory has the slope $-b_B/b_A$ given that the isodar has slope b_A/b_B . It is then relatively easy to show that the line that goes through the point $(N_{A(t+1)}, N_{B(t+1)})$ and that is orthogonal to the isodar is given by the equation

$$N_B = N_{B(t+1)} - \frac{b_B}{b_A} N_{A(t+1)} - \frac{b_B}{b_A} N_A \quad (A9)$$

The IFD on the isodar where the system comes to rest after dispersal is given by the intersection of the "orthodar" and the isodar, i.e. when

$$N_{B(t+1)} - \frac{b_B}{b_A} N_{A(t+1)} - \frac{b_B}{b_A} N_A = \frac{r_B - r_A}{b_B} + \frac{b_A}{b_B} N_B \quad (A10)$$

Solving for N_A , we have

$$N_A = \frac{1}{\frac{b_A}{b_B} + \frac{b_B}{b_A}} \left(N_{B(t+1)} - \frac{b_B}{b_A} N_{A(t+1)} - \frac{r_B - r_A}{b_B} \right) = N'_{A(t+1)} \quad (A11)$$

where the prime indicates that equation (A11) is the new ESS density in habitat A. The values for $N_{i(t+1)}$ are given by the growth equations (Eq. A4). The corresponding value for $N'_{B(t+1)}$ is given by the isodar.

Stochastic isodar

Suppose the carrying capacity of the two habitats is changing randomly from t to $t+1$. That is, following population growth and adjusting dispersal to move densities back onto the isodar, subsequent population growth is dictated by new values of b_i . The above procedure can easily accommodate this form of stochas-

ticity by changing the values for b_i at the appropriate time step. We also note that when b_B varies randomly, then by Jensen's inequality, the expected slope of the isodar will be steeper than the deterministic one. The same would also be true if we used the geometric mean isodar to represent fitness in a temporally variable

environment. Since stochastic variation in carrying capacity results in a steeper isodar than would occur otherwise, population densities will be undermatched. That is, there will be fewer individuals in the better habitat B, and more individuals in habitat A, than expected in a constant environment.