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## Toward an ecological synthesis: a case for habitat selection

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**Abstract** Habitat selection, and its associated density and frequency-dependent evolution, has a profound influence on such vital phenomena as population regulation, species interactions, the assembly of ecological communities, and the origin and maintenance of biodiversity. Different strategies of habitat selection, and their importance in ecology and evolution, can often be revealed simply by plots of density in adjacent habitats. For individual species, the strategies are closely intertwined with mechanisms of population regulation, and with the persistence of populations through time. For interacting species, strategies of habitat selection are not only responsible for species coexistence, but provide one of the most convenient mechanisms for measuring competition, and the various community structures caused by competitive interactions. Other kinds of interactions, such as those between predators and prey, demonstrate that an understanding of the coevolution of habitat-selection strategies among strongly interacting species is essential to properly interpret their spatial and temporal dynamics. At the evolutionary scale, the frequency dependence associated with habitat selection may often allow populations to diverge and diversify into separate species. Habitat selection thereby demonstrates how we can map microevolutionary strategies in behavior onto their population and community consequences, and from there, onto macroevolutionary patterns of speciation and adaptive radiation. We can anticipate that future studies of habitat selection will not only help us complete those maps, but that they will also continue to enrich the panoply of ideas that shape evolutionary ecology.

**Keywords** Competition · Evolutionary strategies · Isodar · Ghost of competition · Speciation

### Introduction

Ecologists frequently lament that our discipline lacks generality. Yet many of the theories we have produced, and the questions we ask as ecologists, reduce to five fundamental principles: (1) all organisms consume resources (foraging ecology, consumer-resource dynamics, predator-prey and plant-animal interactions, patterns and processes in food webs); (2) all organisms require space in which to live (habitat, habitat selection, spatial population dynamics, landscape ecology); (3) all organisms interact, at some scale in space and time, with individuals of the same, and other, species (population dynamics and regulation, species interactions, community assembly); (4) all organisms live in dynamic environments that vary across scales in space and time (dispersal, migration, metapopulation dynamics, macroecology); and (5) all organisms strive to copy their genes (life-history evolution, mate choice, foraging and other evolutionary strategies).

Organisms do not forage in patches independent of the risks of predation (e.g., Brown 1988, 1992; Abrahams and Dill 1989; Lima and Dill 1990; Kotler and Blaustein 1995; Brown et al. 1999; 2001); they do not select habitat independent of the kinds and quality of resources in different places, or the demands on those resources from conspecific and interspecific individuals (Fretwell and Lucas 1970; Rosenzweig 1981; Morris 1988), and their life histories certainly do not evolve independent of the habitats that they occupy (McNamara and Houston 1992; Morris 1998). It should be possible, therefore, to link these various processes together, and by so doing, to gain new insights into the pattern and structure of ecological systems. Theories of habitat selection offer special promise because they incorporate a variety of explicit and implicit ecological and evolutionary mechanisms including density-dependence (Fretwell and Lucas 1970;

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Fretwell 1972), interspecific interactions (Rosenzweig 1974, 1979, 1981; Morris 1988, 1989, 1999a; Danielson 1992), resource distributions (Pulliam and Caraco 1974; Sutherland 1983; Fagen 1987; Morris 1994; Morris and Knight 1996; Morris and Davidson 2000), spatial scale (Pulliam 1988; Pulliam and Danielson 1991; Morris 1987a, 1992, 1995), and differences among individuals (Sutherland and Parker 1985; Łomnicki 1988; McNamara and Houston 1990; Milinski and Parker 1991; Kacelnik et al. 1992; Tregenza 1995; Rodenhouse et al. 1997; Houston and McNamara 1999).

My necessarily selective “review” and synthesis concentrates on four themes related to habitat selection and its evolution. First, I try to clean up confusion around concepts and definitions of habitat and habitat selection. Next, I illustrate how habitat selection, and most specifically the ideal-free distribution (and its descendants), represents a stable evolutionary strategy. I discuss some of the roles that habitat selection plays in population regulation at different spatial and temporal scales, and extend the analysis to both competitive and predator-prey interactions. I evaluate habitat selection’s role in creating and maintaining biodiversity, and conclude with a look to the future.

### What is habitat and habitat selection?

Habitat is one of the most widely used and ambiguous terms in ecology. Depending on context, habitat is used interchangeably to represent biome, ecosystem, community, spatial mosaic, and foraging patch. Regardless of context, populations of the same species often live in quite different environments, and vary in their habitat preferences.

Clearly, then, habitat must be defined by the species and populations of interest, and in a manner that reflects underlying processes operating at appropriate spatial and temporal scales. Relevant processes will include population dynamics and the intra- and interspecific mechanisms that influence the local abundance and distribution of individuals. With these points in mind, let us define habitats as spatially bounded subsets of physical and

biotic conditions among which population density (and thus at least one of the parameters of population growth) of a focal species varies from other adjacent subsets. The emphasis on population density connects habitat choice with population regulation (below). It also separates population-level phenomena from changes in individual behavior (and in many cases morphology and physiology) at smaller patch-scales of heterogeneity. Armed with consistent definitions (Table 1), we can begin to explore how habitat and habitat selection interface with other ecological and evolutionary concepts.

### Habitat selection as an evolutionary strategy

One way to assess the relevance of a behavior to ecological patterns and processes is to evaluate its adaptive significance as an evolutionarily stable strategy (ESS, e.g., Maynard Smith and Price 1973). Though various techniques exist to define such strategies, none is likely to be clearer than a graph of the adaptive landscape (Wright 1931) that, for any density-dependent process, will vary with population size (Brown 2001b). We can plot such a landscape by imagining a population occupying two different habitats within which the density-dependent dynamics are given by

$$\frac{dN_A}{dt} = r_A N_A \left(1 - \frac{N_A}{K_A}\right) \quad (1)$$

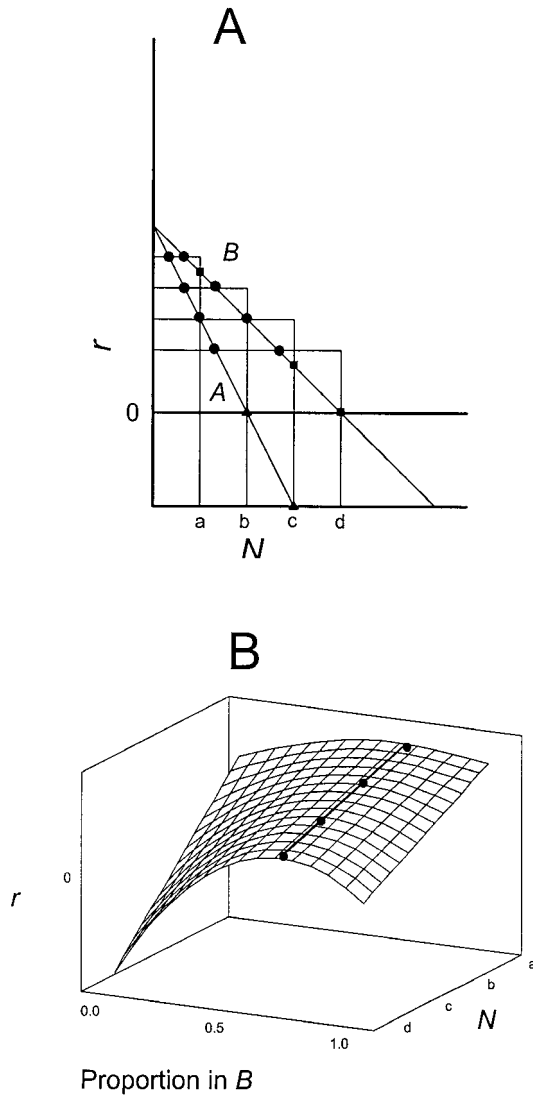
and

$$\frac{dN_B}{dt} = r_B N_B \left(1 - \frac{N_B}{K_B}\right) \quad (2)$$

for habitats *A* and *B* respectively (*N* is population density, *r* is the intrinsic growth rate, and *K* is carrying capacity). Dividing both sides by *N*, we obtain the familiar assumption of a linear decline in fitness with increasing population density. We can then assess the best global strategy of habitat distribution by examining the adaptive landscapes for all possible distributions of individuals between the two habitats at different population densities (Fig. 1).

**Table 1** Some definitions related to habitat and habitat selection

Habitat	A spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets
Habitat distribution	The abundance of individuals among habitats, described in the case of ideal habitat selection, by the habitat isodar
Habitat gradient	A cline of physical and biotic conditions along which the fitness of phenotypes varies either continuously or discontinuously
Habitat selection	The process whereby individuals preferentially use, or occupy, a non-random set of available habitats
Isocline	A line in the state-space of species densities along which the <i>per capita</i> , and population, growth rate (e.g., $\frac{1}{N} \frac{dN}{dt}$ ) is constant
Isodar	A line in the state-space of habitat (usually) densities where fitness (e.g., $\frac{1}{N} \frac{dN}{dt}$ ) is equal in each habitat, but along which fitness varies
Isoleg	A line in the state-space of species densities along which the choice of habitat is equal
Patch	A spatial subset of habitat that is treated as a single homogeneous unit by the behavior of an individual



**Fig. 1A, B** An illustration of how changes in population size of a habitat-selecting species alter the relative abundances of individuals in a pair of habitats. A single phenotype is displayed. **A** Fitness declines with increased density in habitats A and B. Intersections with horizontal lines (solid circles) correspond to those densities that represent optimal habitat selection (an ideal free distribution, Fretwell and Lucas 1970). Filled diamonds represent examples of the fitness expected if the entire population (lower-case letters) occupied habitat A, filled squares represent examples of the fitness expected if all individuals occupied habitat B. The two habitats yield equal fitness at low density, but possess different relationships between fitness and density. **B** A plot of mean fitness against the possible distributions of individuals occurring in the two habitats (proportion of individuals occupying habitat B) at different population sizes. Solid circles represent the optimum distribution of individuals at the four different population sizes illustrated in **A**. The bold line connecting the solid circles corresponds to the optimum across the range of population sizes. Fitness declines with increased population size, but mean fitness is always highest for the same ideal distribution of individuals between habitats (density-dependent selection)

To generate an adaptive landscape for habitat choice, we allow population size to vary  $0 \leq \Sigma N_m \leq \Sigma K_m$  and plot the mean fitness

$$\bar{r} = \frac{\sum r'_m N'_m}{\sum N_m}$$

where  $r'_m$  = the rate of increase in habitat  $m$  at density  $N'_m$  ( $0 \leq N'_m \leq \Sigma N_m$ ;  $\Sigma N'_m = \Sigma N_m$ ) in both habitats for all possible combinations of density in each habitat at every population size. First, imagine that the habitats differ only in the slope of fitness with density  $r_A = r_B$ ;  $K_A < K_B$ . The resulting adaptive landscape sinks with increasing density (Brown 2001b), but there is a single best global strategy of habitat distribution where the proportion of individuals occupying both habitats is constant at all densities (Fig. 1).

Now, consider the case where one habitat has higher fitness at low density than does the other ( $r_A < r_B$ ; Fig. 2). Again, the adaptive landscape sinks with increasing density, but now there is no single best strategy of habitat distribution. The proportion of individuals occupying each habitat (when both are occupied) varies with population size.

If we assume that individuals are free to occupy the habitat of their choice, the optimal strategy in both examples corresponds to those densities where the mean fitness in each habitat is equal (the ideal-free distribution, Fretwell and Lucas 1970). Clearly it would be valuable if we could document, using only the pattern of population densities, whether there is but a single strategy of habitat distribution, or whether the strategy varies with each change in population size. To do this, we imagine ideal habitat selection where the fitness is equivalent in both habitats, that is where

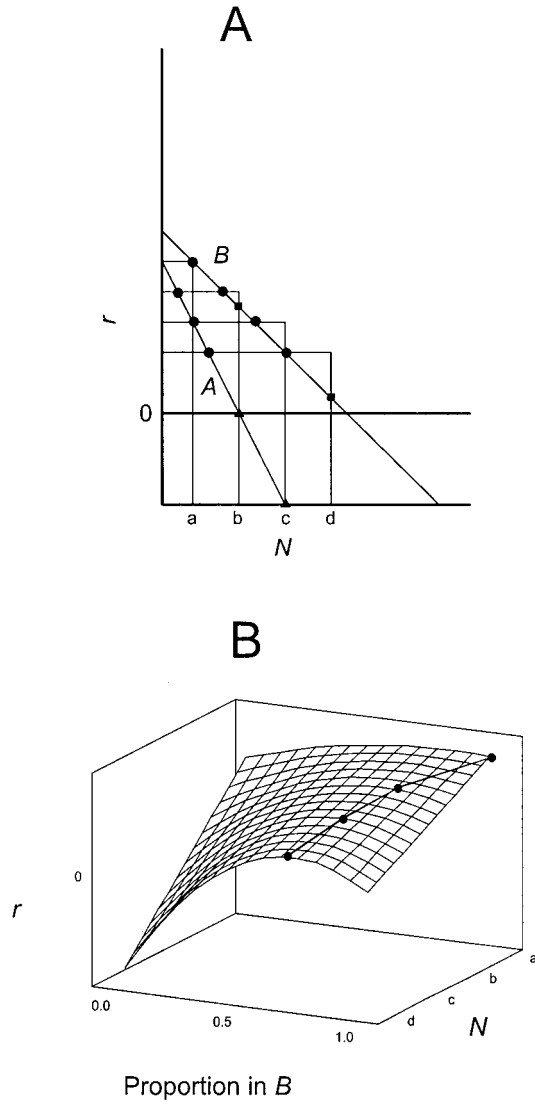
$$\frac{1}{N_A} \frac{dN_A}{dt} = \frac{1}{N_B} \frac{dN_B}{dt}.$$

Following substitution from Eqs. 1 and 2 we obtain the habitat isodar (named after Darwin)

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

the set of densities in the two habitats such that the expected fitness is the same in each (Morris 1987b, 1988). From Eq. 3 we can readily see that the isodar for a pair of habitats with equal  $r$  will be a straight line through the origin (one global strategy, Fig. 3A), whereas for habitats with  $r_A < r_B$ , the linear isodar will have a positive intercept (the habitat-distribution strategy depends on population size, Fig. 3B). Isodars corresponding to both alternatives are well represented in natural systems (e.g., see Morris (1996a) for a linear isodar through the origin, and Morris (1996b) for examples of linear isodars with positive intercepts).

Isodars need not be linear. Interference, for example, can result in curved fitness functions. One way to deal with such effects is to substitute Eqs. 1 and 2 with the general logistic model

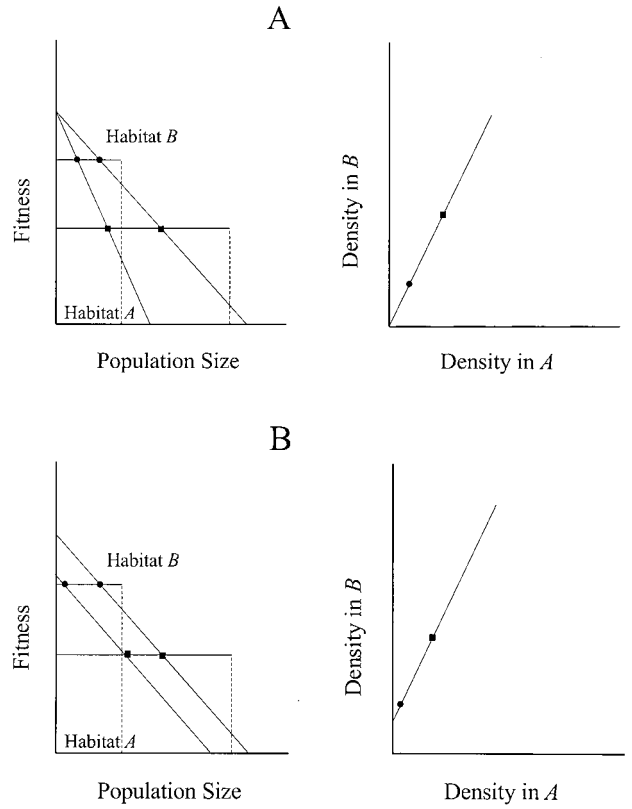


**Fig. 2** An illustration of how changes in population size of a habitat-selecting species alter the relative abundances of individuals in a pair of habitats when the two habitats yield different fitnesses at low density, and fitness declines with increased population density (A). B A plot of mean fitness against the possible distributions of individuals occurring in the two habitats (proportion of individuals occupying habitat B). Symbols correspond to those in Fig. 1. The optimum distribution (solid circles and bold line) switches from occupying habitat B only at low population size to increased occupation of habitat A as population size increases (density and frequency-dependent selection)

$$\frac{dN}{dt} = r_m N_m \left( 1 - \left( \frac{N_m}{K_m} \right)^{\theta_m} \right) \quad (4)$$

(Gilpin and Ayala 1973) where  $\theta$  is the coefficient of curvature of fitness with population density. For the special case of two habitats where  $r_B = r_A$ , the resulting isodar is linear on a logarithmic scale,

$$\log N_B = \left( \log K_B - \frac{\theta_A}{\theta_B} \log K_A \right) + \frac{\theta_A}{\theta_B} \log N_A \quad (5)$$



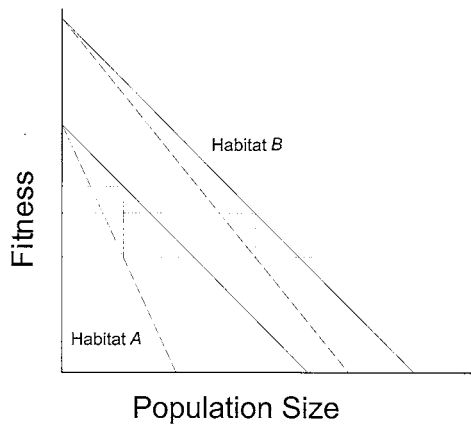
**Fig. 3A, B** An illustration of how the strategy of density-dependent habitat selection yields the habitat isodar. Fitness declines linearly with population density in each habitat. Intersections with horizontal lines correspond to an ideal distribution where the expected fitness is identical in both habitats. A graph of the densities in each habitat assuming that the expected fitness is equal yields the linear isodar. A The two habitats yield similar fitness values at low density but possess different carrying capacities. The isodar passes through the origin and there is a single global strategy of habitat selection. B The two habitats yield different fitnesses at low density, and they possess different carrying capacities. The isodar has a positive intercept, and the strategy of habitat selection varies with population size

but there is no easy solution of the Gilpin/Ayala model for habitats that differ in their intrinsic growth rates. Curved and non-linear isodars also emerge when habitat selection follows Pulliam's (1988) ideal pre-emptive distribution (Morris 1994, below). The main points are that (1) multiple strategies of habitat distribution will exist whenever isodars are curved, or when they are linear with non-zero intercepts, but (2) the habitat distribution follows the single behavioral strategy of selecting habitat in a way that maximizes fitness.

### Habitat selection as a mechanism of population regulation

Differences among habitats in their relationships between fitness and density, and differences in the degree to which individuals have free choice of habitat, play important roles in the spatial and temporal dynamics of populations





**Fig. 4** An illustration of ideal-despotic habitat selection when the effects of competitively dominant individuals are greatest in low-density habitat. Interference by territorial dominants reduces the perceived fitness of each habitat (*dashed lines*). Individuals without a territory select habitat in a way that equalizes each habitat's perceived fitness, but mean fitness differs between habitats (given by the intercepts of vertical lines with the fitness functions). Note that, in this example and contrary to common opinion (e.g., Van Horne 1983), the low-density habitat acts as a high-fitness source of individuals moving toward the higher-density sink

(Fretwell and Lucas 1970; Fretwell 1972; Holt 1985; Morris 1988; Pulliam 1988). Consider the effects of ideal-free distributions in landscapes with variable mosaics of two habitats that differ in their respective intrinsic growth rates at low density (e.g., as in Fig. 3B). A general principle of population dynamics is that populations possessing a high  $r$  are less stable than those with lower  $r$ . Thus, assuming that time lags and stochastic effects are similar in both habitats, populations occupying a landscape dominated by the high- $r$  habitat would be more variable than would populations occupying a landscape with a greater amount of the low- $r$  habitat. Management protocols aimed at increasing the abundance of "highly-suitable" habitats might, therefore, actually destabilize population dynamics. The probability of extinction might also be increased if high- $r$  habitats possess relatively low carrying capacities. Thus, habitat selection can have a direct bearing on larger-scale processes, such as the dynamics of metapopulations, that operate within heterogeneous landscapes [see Doncaster (2000) for a general ideal-free model that integrates across scales ranging from foraging patches to communities].

The effects of habitat selection on population regulation are even more acute for other types of ideal distributions. Consider, first, the situation in which dominant individuals interfere with the habitat choices of subordinates (Fretwell and Lucas 1970; Fretwell 1972). An individual contemplating its habitat choices will perceive that the value of each habitat is reduced by interference from dominant occupants. Individuals optimizing their habitat selection should thereby occupy habitats such that the perceived (mean) value in each habitat is identical (Fig. 4). The resulting ideal-despotic distribution (Fretwell and Lucas 1970) is described by its

isodar, which in this case corresponds to the densities where the expected fitness is the same in each habitat, but where the actual fitness values differ. At equilibrium, despotic distributions describe source-sink dynamics where surplus reproduction in source habitats is exported to nearby sinks [or pseudo-sinks, Watkinson and Sutherland (1995)].

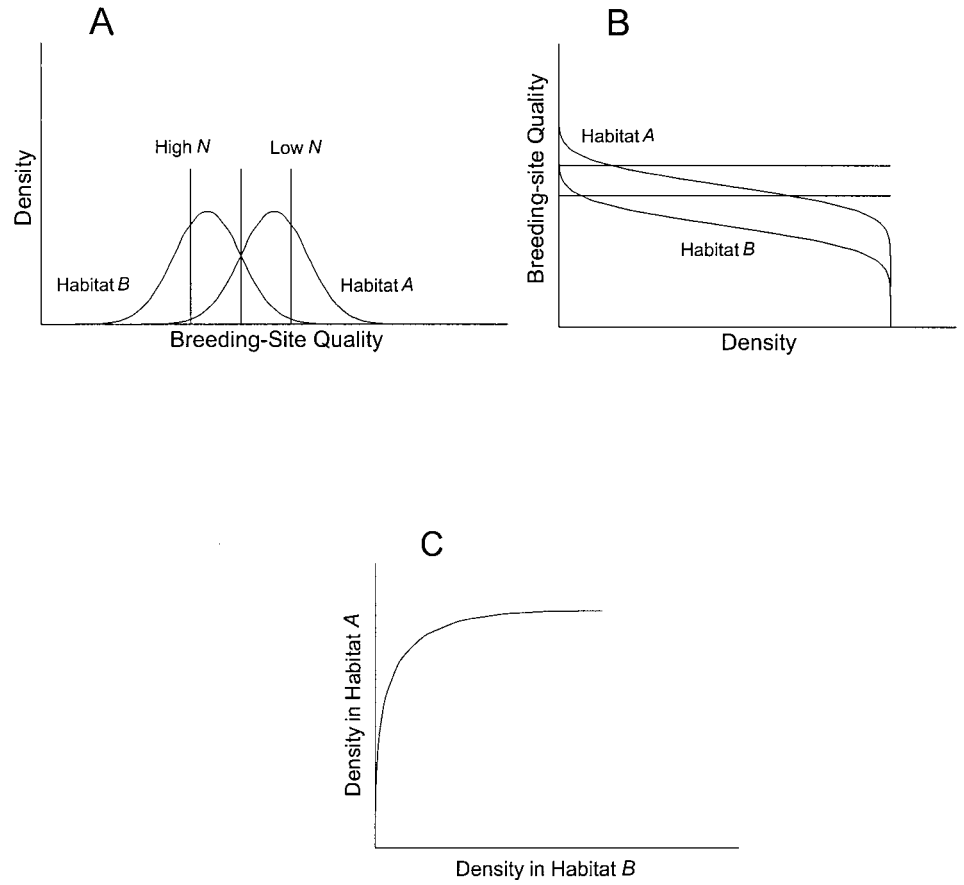
Source-sink dynamics have profound implications to conservation. Elimination of either habitat can destabilize population dynamics. Removal of source habitat can cause local extinction. Removal of sink habitat frustrates dispersal, and magnifies population fluctuations. Regardless, ecologists would benefit from the ability to readily identify each type of habitat. The problem is complicated because, depending on the role of dominants in reducing the fitness of subordinates, high-density habitats may not act as sources (Fig. 4).

Rather than interfere with one another, individuals of many species may simply select the highest-quality site available [site-dependent habitat selection (originally called ideal pre-emptive habitat selection), Pulliam 1988; Pulliam and Danielson 1991; Rodenhouse et al. 1997; McPeck et al. 2001]. Once occupied, a site is pre-empted, and is thus unavailable for other potential colonists. Average reproductive success of the population declines as sites of ever reducing quality are added with increased population size, but the success of every individual depends only on the quality of site it occupies, not on any direct interactions with other individuals (McPeck et al. 2001).

Habitats that differ in the relative abundances of high- and low-quality sites will also differ in mean reproductive success, and habitats with many high-quality sites will act as sources of immigrants to habitats with many low-quality sites (Pulliam 1988). When the total population growth rate is at equilibrium, the occupation of high-quality sites whose residents have high fitness is balanced by individuals occupying low-quality sites within which they cannot replace themselves. The set of conditions occupied (the realized niche) is thus less than the set of conditions within which individuals can live and replace themselves (the fundamental niche).

We can use site-dependent regulation to demonstrate the versatility of isodar analysis. Imagine two habitats where the distribution of site quality in each obeys a different normal distribution of values (I assume equal variances and different means, but readers can substitute any distribution, and modify any set of its descriptive parameters, that they prefer). The relationship between fitness and density can be visualized easily by plotting the cumulative decline in site quality with increasing density (Fig. 5). Ideal site-dependent selection, and its typically curved or non-linear isodar, emerges when we solve the set of cumulative site-quality distributions to equalize fitness across habitats (Fig. 5). The shape of the isodar can thus take us at least part way toward the goal of specifying functional relationships between realized fitness and density (Turchin 1999, later, I make a similar point regarding interspecific competition). The value of

**Fig. 5** An illustration of ideal site-dependent habitat selection. Panel **A** illustrates the distributions of site quality in two hypothetical habitats. Individuals obeying a site-dependent strategy should, with increasing density, occupy sites of ever decreasing quality (site selection moves from right to left with increasing density). Panel **B** illustrates the resulting cumulative distributions. Site quality is reduced as more individuals are added to each habitat. The ideal site-dependent distribution at different population sizes is illustrated by intercepts of the cumulative distributions with horizontal lines of equal fitness. The resulting isodar's curved or non-linear shape (panel **C**) will vary with the distribution of site quality in each habitat (Morris 1994, redrawn from Morris (1995))



isodar theory as part of a synthetic research program on population regulation (Turchin 1999) is illustrated nicely by Tom Knight's (2000) observations and experiments on habitat selection in brook trout (*Salvelinus fontinalis*). In brook trout, body-size is a reliable indicator of the ability to pre-empt other individuals from high-quality sites (Knight 2000). Non-linear isodars mimicked cumulative body-size distributions (Knight 2000).

### Habitat selection and species interactions

Danielson (1991, 1992) extended site pre-emption to examine its effects on the net interaction between competing species. The models examined otherwise competing species with distinct habitat preferences (Pimm and Rosenzweig 1981) where each species preferentially occupied the other's sink habitat. Danielson's models demonstrated that a competitor, by removing sink habitat from the repertoire of available sites, can convert the direct competitive relationship into a variety of indirect interactions including reversals of the superior competitor, and even mutualistic coexistence. The net effect depends on the mix of habitats in the landscape. Despite these complications, isodar theory suggests that we should be able to use the pattern of habitat selection to infer species interactions. I provide solutions for two

common interactions, competition and predator-prey dynamics between pairs of species in two habitats.

### Competition

Imagine two habitat-selecting species whose interactions can be modeled by Lotka-Volterra-Gause competition. The respective dynamics for species 1 competing with 2 in habitats *A* and *B* are given by

$$\frac{dN_{1A}}{dt} = r_{1A}N_{1A} \left( \frac{K_{1A} - N_{1A} - \alpha_{12A}N_{2A}}{K_{1A}} \right) \quad (6)$$

and

$$\frac{dN_{1B}}{dt} = r_{1B}N_{1B} \left( \frac{K_{1B} - N_{1B} - \alpha_{12B}N_{2B}}{K_{1B}} \right) \quad (7)$$

where  $\alpha_{12m}$  is the competitive effect of species 2 on species 1 in habitat *m*. Setting per capita growth rates equal in the two habitats as before

$$\frac{1}{N_{1A}} \frac{dN_{1A}}{dt} = \frac{1}{N_{1B}} \frac{dN_{1B}}{dt},$$

we obtain, following substitution (from Eqs. 6 and 7), and letting

$$C = \frac{(r_{1B} - r_{1A})}{r_{1B}} K_{1B}$$

$$b = \frac{r_{1A} K_{1B}}{r_{1B} K_{1A}}$$

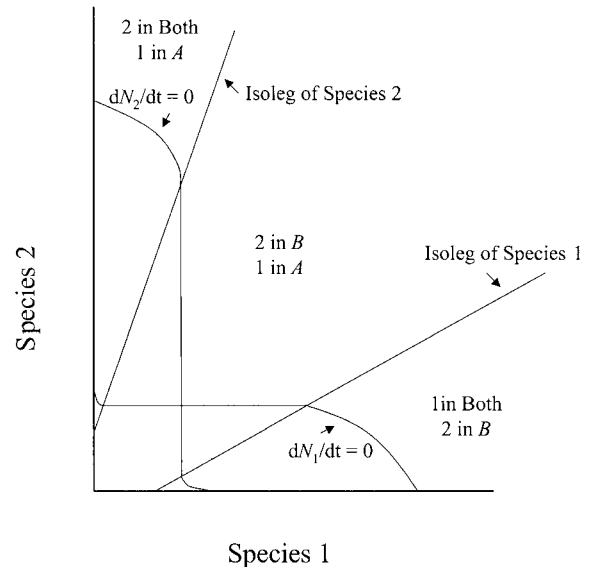
$$N_{1B} = C + bN_{1A} + b\alpha_{12A}N_{2A} - \alpha_{12B}N_{2B} \quad (8)$$

where Eq. 8 represents the isodar for species 1 in competition with species 2 in habitats A and B. A comparable isodar describes competitive habitat selection by species 2. Four important points emerge from Eq. 8, (1) we can use the pattern of density-dependent habitat selection to measure interspecific competition, (2) the effects of competition may often vary between habitats, (3) the single species isodar is unchanged as long as the appropriate competitive effects with other species are included in the isodar equation, and (4) the multi-species isodar can be solved simply by using multiple linear regression (Morris 1989; Rodríguez 1995; Morris et al. 2000a, 2000b).

Isodars are crucially important in our attempts to understand the role of habitat in the competitive coexistence of species (Morris 1999a, 1999b). So too, is Mike Rosenzweig's invention of isoleg theory (Rosenzweig 1974, 1979, 1981, 1991). An isoleg is the set of joint densities of two species that defines a boundary in habitat choice by one of the species (Table 1). Most often, isolegs portray absolute habitat preferences that separate regions of species densities where the target species restricts itself to a single habitat on one side of its isoleg, and opportunistically uses that habitat and at least one more on the other (Fig. 6). Thus, a graph of an absolute isoleg is also a graph of the intercepts of competition isodars (when scaled for density; isodars plot densities in each habitat, isolegs plot densities in all occupied habitats of interest).

Isolegs imply that competition between species may often exist as a ghost (Rosenzweig 1974). In cases of distinct habitat preferences, for example, each species occupies a separate habitat at equilibrium. By occupying separate habitats the species are incapable of competing with one another, even though their competition is responsible for the habitat segregation (Fig. 6). The ghostly paradox is resolved by isodars that incorporate explicit estimates of competition within each habitat (Morris 1999a).

Preliminary tests of isodars between putative competitors highlight both the value, and challenges, of the approach. Analyses of two species of stream-dwelling salmonid fishes (*Salmo salar*, *Salvelinus fontinalis*) revealed their competitive dynamics as well as their habitat preferences (Rodríguez 1995), but the competitive dynamics were confounded by density-dependent switches in behavior (schooling). Tests on brown and collared lemmings (*Lemmus trimucronatus*, *Dicrostonyx groenlandicus*) confirmed distinct preferences for moist versus dry tundra, as well as asymmetric habitat-dependent competition. But the asymmetry also produced a new kind



**Fig. 6** An example of the ghost of competition for a pair of species with distinct habitat preferences for two different habitats, A and B. Species 1 prefers habitat A, species 2 prefers B. The positively sloped lines represent each species' isoleg, the set of densities separating regions of equal habitat choice. Each species occupies only its preferred habitat in the region between the isolegs. Negatively sloped curves represent the isoclines of the system. The isoclines are warped by habitat selection. As the population of species 2 approaches its isoleg from the northwest, for example, the proportion of individuals of species 2 using habitat A declines, and so too does the average competition with species 1 (that is restricted to its preferred habitat A in this region of state space). The ghost can be revealed by isodars that measure the intensity of competition in each habitat (redrawn from Morris 1999a; Morris et al. 2000a; Rosenzweig 1981)

of kinked isoleg for collared lemmings that switches from positive to negative slope where it crosses the non-competitive isoleg of *Lemmus* (Morris et al. 2000a). A ghost region exists at a low density that allows whichever species is most abundant to "break-out" and dominate local lemming "cycles".

Peculiar horizontal isolegs were revealed in isodar tests of competition between large swamp rats (*Rattus lutreolus*) and smaller chestnut mice (*Pseudomys gracilicaudatus*) in Australian heathlands (Morris et al. 2000b). The magnitude of competition estimated from isodars mimicked estimates obtained from earlier removal experiments where *Rattus* was shown to be a superior competitor to *Pseudomys*. The habitat-dependent competition revealed by isodars is also consistent with varying competitive dynamics as heath habitat changes with pyric succession. Thus, in both the lemming and heathland-rodent systems, we have been able to measure isodars, to draw their associated (and novel) isolegs, and to infer the shapes of their equally novel non-linear isoclines. By using isodars, we have revealed the functional forms of species interactions required by contemporary theories (Abrams 2001). More to the point, isodars reveal that nonlinear interactions may often be associated with habitat selection.

Isodar analyses do not always yield competitive dynamics, but even when they “fail”, they can provide original insights into species coexistence. Deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*) provide an example. Isodar analysis of their joint densities in moist north-facing forests and adjacent dry south-facing slopes in the Rocky Mountains did not detect any evidence of competition that could account for their habitat-dependent coexistence. Deer mice preferentially exploit the xeric habitat, and voles, the moist one. Generalized predators that also exhibit habitat selection should preferentially exploit the moist north-facing slopes when voles are abundant (reduces predation on mice), and concentrate on drier habitats when deer mice are abundant (reduces predation on voles). Adaptive habitat selection by predators can thereby lead to stable “apparently competitive” coexistence of their prey. The predator-mediated and habitat-dependent coexistence of voles and mice suggests that we need to explore habitat selection in predator-prey systems.

### Predator-prey dynamics

I begin with the simple Lotka-Volterra predator-prey model where a single species of predator controls the density of its prey and vice versa. Thus, the dynamics in habitat  $m$  can be given by

$$\frac{dN_m}{dt} = b_m - P_m a_m \quad (9)$$

and

$$\frac{dP_m}{dt} = e_m(P_m a_m N_m) - s_m P_m \quad (10)$$

for prey ( $N$ ) and predators ( $P$ ) respectively (e.g., Morin 1999) where  $b$  is the per capita birth rate of prey,  $a$  is the predator’s per capita attack rate,  $e$  is the efficiency of conversion of prey into predators, and  $s$  is the death rate of predators in the absence of prey. Ideal habitat selection by prey in habitats  $A$  and  $B$  occurs when

$$\frac{1}{N_A} \frac{dN_A}{dt} = \frac{1}{N_B} \frac{dN_B}{dt}$$

which, following substitution from Eq. 9 yields the predator’s distribution when the prey is on its isodar

$$P_B = \left( \frac{b_B}{a_B} - \frac{N_B b_A}{N_A a_B} \right) + \left( \frac{N_B a_A}{N_A a_B} \right) P_A. \quad (11)$$

The distribution of predators depends on the distribution of prey. Changes in the ratio of prey in the two habitats modify both the intercept (first RH term in brackets) and slope of the predator’s isodar. The intercept and slope of the predator’s isodar will be constant only when prey are at a stable equilibrium, or when the ratio of prey in the two habitats is also constant (implies a linear prey isodar with zero intercept). If we now repeat the process by allowing ideal habitat selection by predators

(the predator is on its isodar), the prey’s (linear) distribution is given by

$$N_B = \left( \frac{e_A a_A}{e_B a_B} \right) N_A - \frac{s_A + s_B}{e_B a_B}. \quad (12)$$

Equation 12 demonstrates that a zero prey intercept can occur only if the habitat-selecting predator faces similar mortality in both habitats. Though such “simple” models may appear limited in their utility, they have profound implications to our understanding of distribution because they specify, clearly, that the habitat choices of each species depend on those of the other. This point contrasts with other models where adaptive habitat choice by predators alone often fails to reach an ideal-free distribution and destabilizes predator-prey dynamics (Abrams 1999). But predator and prey traits, including habitat selection, coevolve and must be examined simultaneously (Abrams 2000).

One recipe to solve predator-prey games in two habitats begins by defining both the predator’s and the prey’s fitness generating functions (Vincent and Brown 1984; Brown and Vincent 1987; Brown 1992). Follow this by fixing population size and solve, for each species, and for all possible distributions of the interacting species, the distribution of individuals of the target species under which fitness is equal in both habitats (the best-response curves; Grand and Dill 1999; Heithaus 2001). Points of intersection of the best-response curves for predators and prey represent equilibrium distributions (that can be either stable or unstable) in the two habitats. The connection to isodar theory can be made by recognizing that the intersections of the best-response curves represent points on the respective predator-prey isodars.

Predator-prey models of habitat-selection have crucially important lessons for empirical ecologists. Field experiments that add supplemental food to natural populations often yield unanticipated results (Boutin 1990). The predator-prey game may tell us one reason why. Imagine that predator and prey populations are at an ideal-free equilibrium along their respective isodars (note that my use of the term equilibrium refers to the intersection of the best-response curves that may, or may not, also correspond to equilibrium population sizes). A supplementation experiment manipulates, in effect, the predator’s distribution of prey. The optimal response for individual predators is to alter their habitat use according to the predator’s best-response curve. The new distribution of predators will trigger adaptive movement by prey. Two of the many interesting and confounding possibilities are (1) that a predator census conducted with different habitat biases may detect a positive, neutral, or negative density response and, (2) that subsequent movement by prey will alter the intended treatment effect of the experiment. This example ups the ante on the optimization research program. Not only can we use the program to understand population dynamics, more importantly, we cannot possibly hope to understand the dynamics of populations unless we first understand the adaptive



behaviors underlying habitat selection (e.g., Ranta and Kaitala 2000).

### Multiple species in many habitats

The dynamics of whole communities, whether in space or time, can be far more difficult to predict and understand than the two-species two-habitat models I discuss here. Four problems are likely to dominate any analysis evaluating the dynamics of a community inhabiting many different habitats.

1. The complexity of the field or experimental design increases rapidly with the number of species and habitats included in the analysis. An experiment on two species that manipulates density of each species sequentially across four levels in one habitat at a time has 16 treatments. A design adding just one more species has 24. Complexity increases dramatically when multiple comparisons are made.
2. As the number of possible habitat choices increases, habitat selection is likely to become more and more susceptible to changes in the relative abundances of habitats in the landscape, and to their spatial context. Preference for any single habitat may also depend on spatially dependent interactions between pairs, or groups, of habitats. One way to search for such effects is to contrast pairs of isodars calculated by substitution (e.g., calculate the isodar between habitats *B* and *C*, from the isodars for habitats *A* and *B*, and for habitats *A* and *C*). If landscape has no influence at the scales of habitat selection, the density in each habitat will be determined uniquely by the density in its neighboring habitat (Morris and Brown 1992; Morris 1997). Isodars calculated by substitution will be identical to those calculated separately for each pair of habitats.
3. As the number of species in a community increases, habitat selection of any one species is likely to vary. Interactions between and among species may depend on the identity and abundance of other species within the community. Multiple species and their indirect and higher-order effects can be included in isodars (e.g., Morris 1989; Morris et al. 2000a, 2000b; see also Shenbrot and Krasnov 2000) as long as sample sizes are sufficient for their analysis. Such an analysis may be appropriate to assess the dynamics of a target species in any specific pair of habitats, but it is unlikely, by itself, to explain the coexistence of all members of the community.
4. As the complexity of the community increases, it will become ever more difficult to measure habitat choices for all species at similar scales. The abundance of individuals in different habitats (and thus, the isodar) changes with the scale of habitat selection (above). Our estimates of density, of habitat preference, and of interactions among species are likely to vary unless we can be certain that all species are measured at the same scale of their habitat preference.

### Habitat selection as an engine and source for biodiversity

#### Competitive speciation

Michael Rosenzweig's (1978, 1995) theories of competitive speciation and incumbent replacement (Rosenzweig and McCord 1991; Brown 2001a) stand as prime examples that illustrate how habitat selection can influence macroevolution. Imagine a population of a habitat-selecting species living along a habitat gradient. Imagine further that we can map the location along the gradient where each phenotype maximizes its fitness (this map would, in the absence of density and frequency dependence, represent the preferred habitat of every individual in the population). But habitats, and the phenotypes that exploit them, will not fit a uniform distribution. Some parts of the gradient will be more abundant than other parts, and so too will be the phenotypes living in those places. Moreover, the fitness landscape may also possess a rugose, rather than uniform, profile.

How should phenotypes distribute themselves along the "bumpy" landscape? Presumably, they should optimize their relative aptitudes to the different conditions along the habitat gradient. Evolutionary, physiological, and behavioral tradeoffs (e.g., Levins 1962, 1968) guarantee that increased aptitude to one set of conditions comes at the cost of reduced aptitude in others (Brown 1998, phenotypes will vary in their abilities to exploit any given habitat). But the conditions themselves may often change rather abruptly. Gradients of precipitation, for example, may not correspond with gradients of essential nutrients. Either gradient may change slowly or rapidly depending on such things as local topography, regional meteorology, geology, or history.

The fitness landscape will also vary with the density and frequency of phenotypes in the environment (Rosenzweig 1995; Brown 1998). Mean fitness declines with increased density, and so too, does the ecological opportunity of the most abundant phenotypes that compete intensely for what was originally the highest peak along the fitness distribution. Extreme phenotypes, rewarded by their rarity and their divergent location on the landscape, will escape competition. Not only do the deviants experience high ecological opportunity in their habitat, their fitness will be enhanced if they mate with similar phenotypes in that habitat. The resulting environmentally-induced disruptive selection and character displacement will, in time, lead to the evolution of a different specialist species in each habitat (Rosenzweig 1978, 1995; Rice 1987).

Specialists may also evolve if the fitness landscape is relatively homogeneous (or unimodal), if the phenotypic frequencies are more or less unimodal, and if the variance in competition among different phenotypes is less than the variance in resources. The phenotypic character first evolves toward the maximum of the resource distribution and leads, again, to intense competition as population size increases [the character, under these conditions, evolves

to an evolutionary minimum (Dieckmann and Doebeli 1998)]. The equilibrium is unstable, however, because extreme phenotypes will possess relatively high fitness. Assortative mating is thereby increasingly advantageous, and the original population will branch into divergent specialists (Geritz et al. 1998; Doebeli and Dieckmann 2000). Each daughter species' specialization favors a different segment of the original resource distribution. If resources are distributed non-randomly in space we can anticipate a correlated habitat preference that, through Rosenzweig's mechanism, will speed the processes of disruptive selection and evolutionary reinforcement.

The "one habitat, one species" rule breaks down in environments containing multiple habitats. Exposure to a habitat increases the probability of evolving aptitude and preferences to that habitat (Rosenzweig 1981; Holt 1985, 1987, 1996; Holt and Gaines 1992). If the environment is extremely fine-grained (MacArthur and Levins 1964; Levins 1968) and thereby fragmented, the encounter rates of individuals with patches of a given habitat will be low. Low encounter rates create a high cost of selecting just one habitat because individuals must move through unexploited patches, and a single generalist strategy will emerge (Brown and Pavlovic 1992; Brown 1996). If, on the other hand, the environment is coarse-grained, encounter rates with any single habitat will be high, and costs of selecting that habitat (or a subset of habitats) will be low. Different specialist strategies will evolve to exploit separate habitats. Varying degrees of specialization can evolve in intermediate grain sizes as long as each coexisting species possesses at least one habitat in which it is the superior competitor. In three habitats, Brown's model predicts ten different possible evolutionarily stable strategies.

Competitive speciation is not without critics (Rosenzweig 1995), and may be difficult to distinguish from models of evolutionary branching (e.g., Geritz et al. 1998; Doebeli and Dieckmann 2000) that, as we have seen, also invoke disruptive selection at evolutionary minima. Regardless of mechanism, character displacement and the eventual diversification of species will often be mediated via habitat (e.g., Boughman 2001; Schluter 2000, 2001; Via 2001). The coexistence and diversity of species will depend similarly on habitat, and we should be able to detect its influence, and Brown's predicted patterns (Brown 1996), in the assembly of diverse ecological communities.

### Species assembly

Habitat's influence on species assembly is revealed in Barry Fox's detailed studies of several mammalian communities. When regionally co-occurring species belong to two or more functional groups, their assembly within a particular community represents a pronounced non-random component of the overall set of possible residents (Fox 1987, 1989; Fox and Kirkland 1992, Fox and Brown 1993, 1995). Coexisting mammals often obey

the probabilistic rule that community assembly fills "each functional group with an equal number of species before adding an additional species of any other group" (Brown et al. 2000).

Though the statistical assumptions of Fox's rule have been highly contentious (e.g., Wilson 1995; Stone et al. 1996, 2000; Fox 1999; Simberloff et al. 1999; Brown et al. 2000) the mechanism, at least at a small scale, appears tightly linked to the efficient use of habitat by competing consumers. Consumer-resource models (and our general understanding of tradeoffs) predict, for example, that the intensity of resource competition should be greater among ecologically similar consumers than among dissimilar species (Tilman 1982). The conditions allowing coexistence of similar species will be less common than those enabling coexistence of dissimilar competitors. Thus, a pair of consumers that are very similar to one another in resource use will be able to coexist across a relatively small range of habitats that allow both species to forage with profit. Dissimilar competitors whose complementary ecological requirements are quite different can coexist across a much broader range of habitats. When we make similar arguments about guilds, we produce Fox's rule (Morris and Knight 1996). Species belonging to separate guilds are more likely to coexist than are species belonging to the same guild.

Two predictions of the "guild assembly" model yield tests based on habitat. (1) A "non-Fox" assembly with members drawn from *i* guilds should occupy a larger range of habitats than Fox assemblies drawn from fewer guilds, and (2) different guilds should be biased toward different habitats. Morris and Knight (1996) tested the theory on a boreal-forest rodent community comprised of eight species belonging to four guilds (microtine, sciurid, zapodid, cricetine) at a spatial scale where each species had the opportunity to enter any assembly. Both predictions were confirmed. Non-Fox assemblies representing three guilds occupied a greater range of habitat variation than did Fox assemblies representing only two guilds. Cutovers supported different combinations of rodent guilds than did residual forest.

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### The future of habitat selection

Though studies of habitat selection have produced rather substantive insights into a variety of ecological and evolutionary phenomena, we understand relatively few of habitat's myriad effects on individuals, populations, communities and landscapes. Several questions cry out for answers. At one level we still have much to learn about the interactions between habitat and dispersal. What rate, and distance, of dispersal should evolve simply from processes of habitat selection in persistent populations? What proportion of dispersal can be attributed directly to density-dependent habitat selection compared to the proportion caused by a fixed or conditional propensity to disperse [e.g., "balanced" habitat-contingent strategies (McPeck and Holt 1992)]? How do the answers to these

two questions modify our understanding of dispersal's role in the evolution of specialized versus generalized species (e.g., Holt and Gaines 1992; Holt 1996; Ronce and Kirkpatrick 2001)?

At a more basic level, we do not know which conditions lead to alternative ideal strategies of habitat selection. Does habitat heterogeneity interact with costs of dispersal to determine whether individuals select habitats based on mean quality (ideal-free and ideal-despotic distributions), or whether they select sites of different quality (site-dependent selection)? Does the evolution of agonistic versus cooperative behavior dictate the habitat selection strategy, or does cooperation emerge because of it (e.g., Morris et al. 2001)?

The apparent existence of multiple strategies in predator-prey systems is especially interesting. Though the isodars are undoubtedly complex and respond in complicated ways to the risk of predation (Brown 1998), we need to know whether studies of habitat selection are tractable in such systems. Do more "realistic" community models yield the same sets of strategies revealed by Brown's analysis (Brown and Pavlovic 1992; Brown 1996), or even more, alternative strategies? If more, how can we simplify our models without losing sight of the essential mechanisms in habitat selection? Do we work at different organizational, spatial and temporal scales so that we can subsume the complications in our analyses of habitat selection (as we might do, for example, by including predation and its risk as components of the many influences modifying the relationship between fitness and density)? Or do we need to begin thinking of new state spaces in which we can map the spatial and temporal dynamics of isodars themselves (in much the same way that they map the derivatives of population growth between habitats)?

Many current theories either do not incorporate costs of habitat selection, or are most easily interpreted in the absence of costs. Dispersal costs, for example, can be expected to increase with distance and set an upper limit to the scale of habitat selection (Morris 1987a, 1992). An individual should choose to disperse only if increased fitness in its new home range can compensate for the risks, time lost from reproduction, and other associated costs of dispersal. The farther an individual disperses, the greater must be the potential fitness benefit. If fitness declines with density, individuals that disperse a long distance will need to disperse farther down a density gradient than "short-distance" dispersers. The example leads to a wonderful prediction (the isodar intercept increases with distance) confirmed with deer mice (Morris 1992), but it also demonstrates that estimates of habitat quality are susceptible to the design of field experiments and what we measure.

We need to explore, in much more detail, the kinds of community organizations that emerge from different strategies of habitat selection. Can we predict, for example, the relative frequencies of alternative structures based on the perceptual scale of species and the characteristics of the landscapes they exploit? Do those

frequencies correspond to probabilistic rules of species assembly? Can we estimate the expected time course over which one type of community changes to another? How do the temporal and spatial scales of community structures interact and influence the dynamics and persistence of their collective and individual members?

The future of habitat selection is not restricted to animals. Indeed, we are already beginning to see impressive applications of both habitat selection and foraging theory to plants (and by inference to other "sessile" organisms). Gersani et al. (1998) have led the way with extraordinarily imaginative experiments that allow "fence-sitter" plants to harvest resources from different habitats containing variable resource concentrations and densities of competitors. When given a choice, plants match their investment in roots to the availability of resources. Theories that explain and apply habitat selection by plants (including very important lessons for plant breeders and agronomists) are already in the literature (Brown 1998, 2001b; Gersani et al. 2001; Morris et al. 2001).

Many of the questions I pose will not yield their solutions easily, and some of the answers may not please us. But pleasant or perplexing answers, whether they confirm our ideas or blur our understanding, are but a small part of our quest. Progress in science is made not only by getting answers to unsolved problems, but also by developing ideas that cause us to ask bold, original questions. The success of studies on habitat selection, and of the optimization research program on which they rest (Mitchell and Valone 1990; Brown 2001b), lies in their consistent and future ability to meet those challenges.

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