5 Habitat selection in mosaic landscapes

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5.1 INTRODUCTION

Landscape ecology, with its emphasis on spatial patterns and processes, articulates a pressing need to consider spatial heterogeneity and spatial dynamics in studies of population dynamics, species interactions and evolution (e.g. Turner and Gardner, 1991). A parallel perspective argues that predictive landscape ecology must incorporate evolutionary principles developed in the more traditional ecological disciplines (Morris and Brown, 1992). This chapter attempts to meet both objectives by integrating evolutionary theories of habitat selection with an empirical and applied framework for landscape ecology.

I begin by reviewing single-species models of habitat selection. I demonstrate how density-dependent models can be tested with data frequently available to landscape ecologists, how the models can be used to infer spatial scale as well as temporal dynamics in habitat quality, and how they can be extended to multiple-species communities. I contrast the utility of new methods with traditional approaches and conclude by posing a series of questions that should be solved as we develop studies of landscape ecology from a habitat selection perspective (Chapters 2, 6 and 9). My intent is not just to discuss the theory, but to demonstrate how it can be applied to solving problems in landscape ecology (Chapter 1).

Most of my examples are drawn from the population and community dynamics of mammals. The bias is more than one of familiarity. Many of the models have not yet been tested with, or applied to, other groups of organisms.

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5.2 DENSITY-DEPENDENT HABITAT SELECTION

5.2.1 SINGLE-SPECIES MODELS

Theories of density-dependent habitat selection assume that, over some range of population densities, reproductive success should decline with increasing population density (Figure 5.1). Increased density can be expected, among other things, to place higher demands on resources in short supply and on the availability of breeding sites, to magnify risks of predation, and to increase susceptibility to pathogens. These effects vary among habitats and each habitat can, for a given population, be represented by a characteristic fitness-density function (Figure 5.1). At low population size, individuals should congregate in the habitat yielding maximum fitness. As density increases individuals should occupy alternative habitats whenever their expected reproductive success in those habitats equals or exceeds that in already occupied habitat (Fretwell and Lucas, 1970).

Several models address different assumptions about how individuals should distribute themselves among habitats (Fretwell and Lucas, 1970; Lomnicki, 1988; Pulliam, 1988; Milinski and Parker, 1991; Kacelnik, Krebs and Bernstein, 1992; Oksanen, Oksanen and Fretwell, 1992). The most familiar of these, the ideal free distribution (Fretwell and Lucas, 1970), predicts that densities should be adjusted such that an individual's average reproductive success is equivalent in each habitat (Figure 5.1). Thus, the population size of a species in any given landscape, and its average density over the landscape, are going to be functions of the quality and distribution of habitats (Holt, 1985).

Experimental tests of the ideal free model have concentrated on the behavioral decisions of individual 'foragers' (references in Milinski and Parker, 1991). Tests at the landscape scale have been elusive because it is frequently impossible to obtain the necessary replicated simultaneous data on reproductive success and population density across a variety of habitats (for exceptions, see Krebs, 1971; Whitham, 1978, 1980; Morris, 1989a, 1991). Yet landscape tests are essential if theories of density-dependent habitat selection are to contribute to the development of landscape ecology, and vice versa. Landscape pattern represents the geographical and evolutionary context within which habitat selection modifies local population densities and community composition. The resulting patterns of relative abundance and species diversity alter the landscape, and highlight the dynamic linkage between landscape and theories of habitat selection. Neither can be understood in ignorance of the other. Can we modify the original theory to enable tests at the landscape scale?

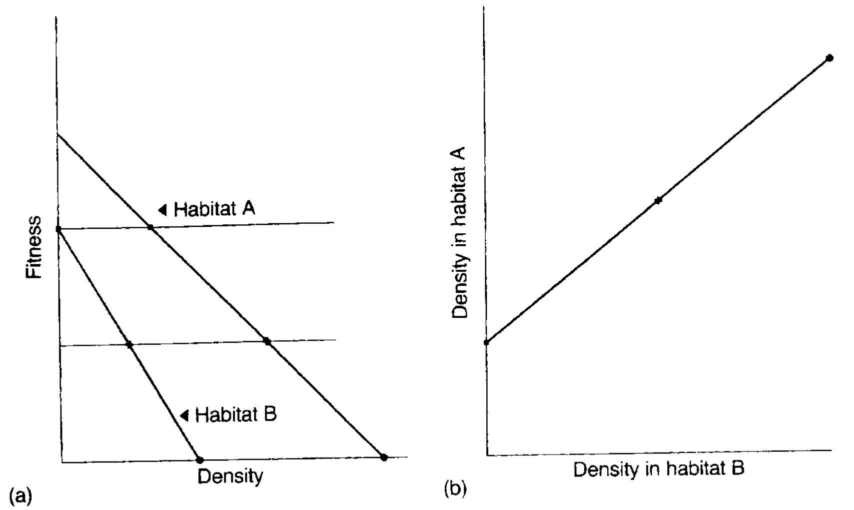


Figure 5.1 (a) A simple representation of the ideal free model of density-dependent habitat selection. Two habitats are shown, each with a characteristic shape and decline in reproductive success with increasing density. At low density, individuals should choose habitat A because their expected fitness is greater than in habitat B. The expected fitness in habitat A will be reduced with increases in density. Individuals should begin to occupy habitat B when the average fitness there is equivalent to that in A. The densities should be adjusted by movement between habitats such that the average reproductive success is equivalent in both (horizontal lines, the pairs of points represented by symbols are replotted in (b)). The pair of habitats depicted here are perceived to differ from one another qualitatively (different slopes) and quantitatively (different intercepts). Discussion of more complicated shapes for fitness-density curves can be found in Fretwell and Lucas (1970), Fretwell (1972), Milinski and Parker (1991), Kacelnik, Krebs and Bernstein (1992), and Morris (1992, 1994).
(b) An isodar generated from the fitness-density curves depicted in (a). The isodar plots the set of densities in habitat A versus those in habitat B such that the expected reproductive success of an individual is the same in both (the intersections of all possible horizontal lines with the fitness–density curves). The fitness–density curves, in this case, diverge from one another, yielding an isodar with slope > 1.0.

5.2.2 ISODAR THEORY

Imagine a density-dependent habitat-selecting species occupying a landscape composed of two habitats as depicted in Figure 5.1(a). According to the ideal free assumption, the respective densities of individuals in the two habitats will be given by the intersection of each habitat's fitness–density function with a set of horizontal lines corresponding to equal reproductive success in both habitats. These densities can be replotted as an isodar (Figure 5.1(b)), a line along which the expected reproductive success of individuals is the same in each habitat (Morris, 1987a, b, 1988). To draw an isodar for the two habitats represented in Figure 5.1(a), plot the density in habitat A against the corresponding density in habitat B such that the fitness is the same in each (examples of these densities are indicated by symbols). The isodar represents the solution to an evolutionarily stable strategy of ideal density-dependent habitat selection. The intercept corresponds to the how far apart the fitness–density curves lie from one another. The slope specifies the relative slopes of the respective fitness–density curves (Morris, 1988). Empirical isodars can be easily generated from estimates of population density in different habitats across any landscape.

Two kinds of habitat differences are likely to have dramatic effects on the slopes and intercepts of fitness–density curves, and on the isodars generated by them. First, imagine a quantitative difference whereby the two habitats differ from one another only in the amount of resource available for consumption. Because the habitats are assumed equivalent in every other respect, individuals should be equally efficient at garnering resources from each. Nevertheless, an individual exploiting the rich habitat at any given population density can expect to have more resources available to convert into reproduction and survival than it can expect by exploiting the poor habitat. The fitness–density curve of the rich habitat will lie above that of the poor one. The isodar will have a non-zero intercept (Figure 5.1).

Now imagine that the two habitats have the same resource renewal, but that they differ in some qualitative respect (e.g. habitat structure or the identity of resources). Individuals can expect to be more efficient at harvesting resources and converting them into descendants in one habitat than in the other. This qualitatively superior habitat can support a greater density if the resource is harvested to the same level in both habitats, but less is spent on non-foraging activities (e.g. foraging costs) than in the inferior habitat. The per capita impact on average fitness will be less than in the inefficiently exploited habitat. Alternatively, efficient consumers may reduce the renewal rate of resource (Holt, 1984). Each individual living in the efficiently exploited habitat would have a larger effect on competing individuals than would those living in the other. The fitness–density curves for each scenario will have different slopes, as will the resulting isodars. Isodars can thus detect not only density-dependent habitat selection, they can also infer the kind of habitat differences involved in habitat choice (Figure 5.1; Morris, 1988).

Preliminary isodars have yielded encouraging results. Studies on insular rodents in the Gulf of Maine (Crowell, 1983), on forest rodents in Ontario (Morris, 1988, 1989b), on prairie rodents in Alberta (Morris, 1992; Figure 5.2) and on desert rodents in Israel (Abramsky, Rosenzweig and Pinshow, 1991; Rosenzweig, 1991) produced significant isodars consistent with the theory's predictions. It appears that estimates of population density can be used to infer relative qualities of habitats in natural landscapes.

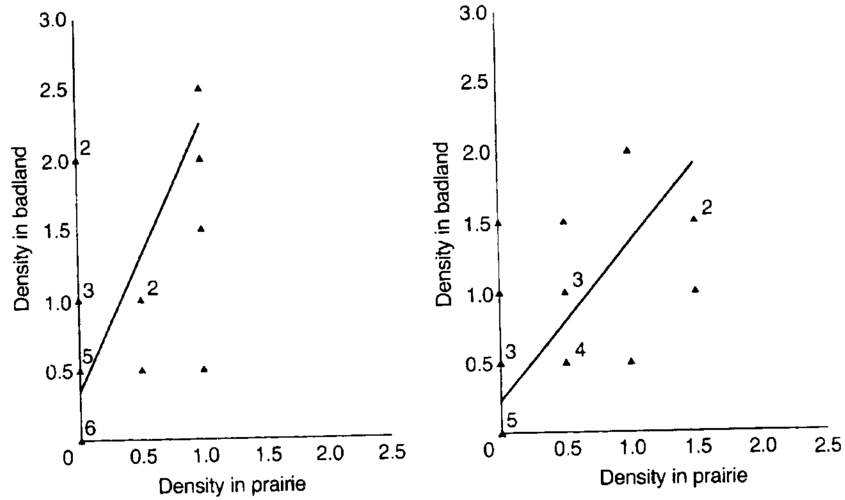


Figure 5.2 Isodars contrasting the density of deer mice (*Peromyscus maniculatus*) occupying prairie and badland habitats in southern Alberta. Badland habitat supports a greater density of deer mice than does prairie. (Geometric mean regression; source: Morris, 1992.)

5.3 PUTTING ISODARS TO WORK IN LANDSCAPE ECOLOGY

5.3.1 INFERENCES OF SPATIAL SCALE

The potential of landscape ecologists to test and apply spatial theories depends upon the investigators' ability to correctly identify the scale(s) at which crucial processes, such as dispersal, occur (Kareiva, 1990; Kotliar and Wiens, 1990; Levin, 1992; Chapter 1). For some species or sets of species, and types of interactions, this may be sufficient to provide insights into patterns of spatial distribution. For many other species and their interactions it will be necessary to integrate purely spatial models with models that specify the quality of patches in heterogeneous landscapes. This is the principal domain of habitat selection theory.

Current theories have identified three scale-dependent processes likely to dominate decisions on habitat choice (Figure 5.3). At some small spatial scale, individuals will be unable to discriminate between habitats and will exploit each equally. This scale should vary with the size and

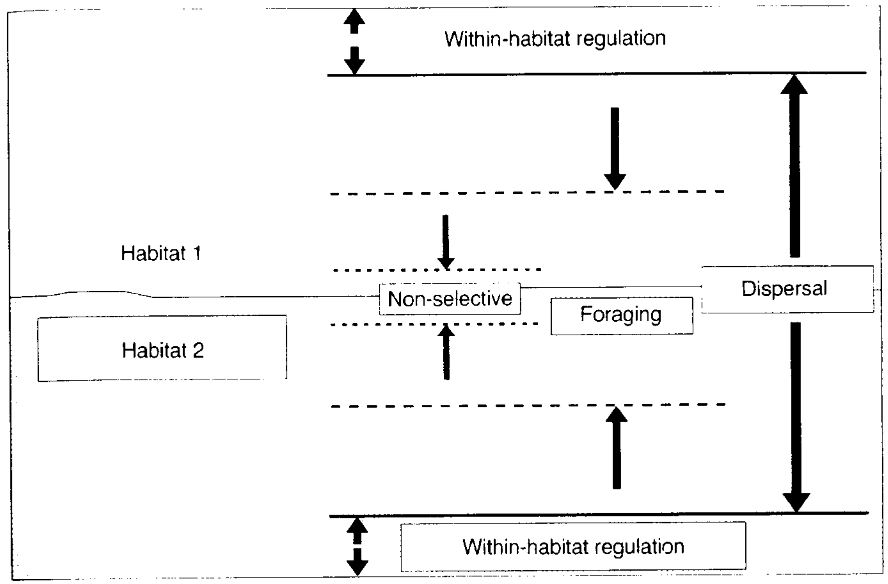


Figure 5.3 The scales of habitat selection between two homogeneous habitats sharing a common border. At some small scale near the boundary, individuals will be unable to discriminate between the habitats and will thus be non-selective in habitat use. At a somewhat larger scale, individuals whose home range spans the boundary will preferentially allocate 'foraging' in one habitat or the other. At a still larger scale, habitat selection can occur only by moving the home range from one habitat to the other (dispersal). Beyond the dispersal scale individuals are incapable of habitat selection, and population dynamics in the two habitats will occur independently of one another. (Source: Morris, 1992.)

perception of the organism, and with the nature of the boundary between habitats.

At the scale of a single home range, individuals can differentially allocate exploitation activities among alternative patches. But differential exploitation carries a cost. The gains that an individual achieves by selecting one patch over another must compensate for the time and energy spent traveling through or around the non-selected patch. An individual that encounters patches in the proportions in which they occur in the environment (a so-called fine-grained forager; MacArthur and Levins, 1964) should become non-selective in habitat use even though the average fitness to be gained in the better habitat exceeds that in the alternative (Rosenzweig, 1974, 1981; Brown and Rosenzweig, 1986).

At a larger scale, individuals can select one habitat over another (or the mix of the habitats in the home range) only by dispersal. Dispersal also carries a cost, but one that is fundamentally different from that of foraging. Individuals attempting to maximize their reproductive success by dispersal should move from one habitat to another only when the increased fitness to be gained there compensates for the lost reproductive potential during dispersal and establishment of the new home range (Morris, 1987a, 1992). Individuals should change habitats only when the expected fitness in the alternative exceeds that of the currently occupied habitat.

The different scales of habitat selection have profound influences on isodars, and on the 'connectedness' of population dynamics among habitats. At the non-selective scale, the two habitats are used indiscriminately. The isodar should pass through the origin with a slope of 1.0. At the foraging scale, exploitation of the 'rich' patch subsidizes exploitation of the 'poor' one. The subsidy, in a home range including both habitats, devalues the apparent quality of the rich habitat, and inflates that of the poor one. Exploitation in a mixed-habitat home range will be reduced relative to what it would be in a home range located entirely within a rich habitat. The opposite occurs in the poor habitat. Home-range size in mixed habitats should thereby be larger (and average density less) than would occur among sets of home ranges located only within the rich habitat. Home-range size in mixed habitats would be smaller (and average density higher) than in only poor habitat. It can thus be seen that foraging cost reduces the difference between the fitness–density curves of the two habitats. The isodar intercept is similarly reduced (Figure 5.4).

The opposite effect occurs at the larger dispersal scale. The 'quality' of the newly colonized habitat must exceed that in the immigrant's previous habitat if dispersal is to result in no loss in reproductive success. This means that the apparent quality of the new habitat must be greater than would occur if there was no dispersal cost. A habitat will be colonized only if its density is lower (and its expected reproductive success thereby greater) than that required for cost-free habitat selection. The isodar intercept will be increased (Figure 5.4). Density-dependent risks of dispersal will increase the isodar slope (Morris, 1992). Beyond the dispersal scale, habitats may be effectively disconnected from the effects of density-dependent habitat selection.

Each scale of habitat selection, as well as the effective limits on the ability of habitat selection to regulate population size, can be evaluated with isodars (Morris, 1992). The basic protocol involves establishing belt transects capable of assessing population density across distinct boundaries between habitats. Transect segments of different lengths, and at varying distances from the habitat boundary, are contrasted with one another by regression to look for the tell-tale differences in isodar intercepts and slopes that identify the shift from non-selective, through foraging, to dispersal scales of density-dependent habitat selection (Figure 5.5).

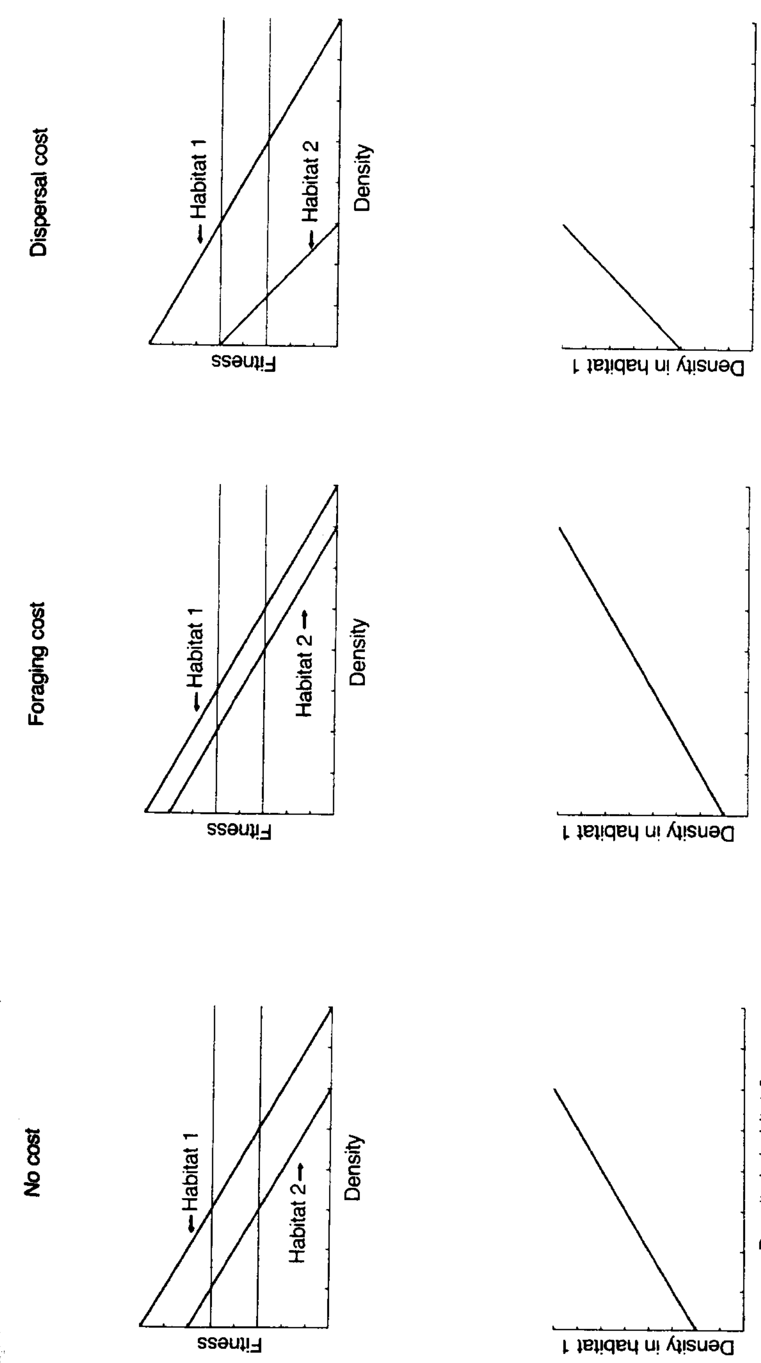


Figure 5.4 The effects of foraging and dispersal costs on the slopes and intercepts of isodars. Fitness–density curves are plotted, with the resulting isodars given below. (Source: Morris, 1992.)

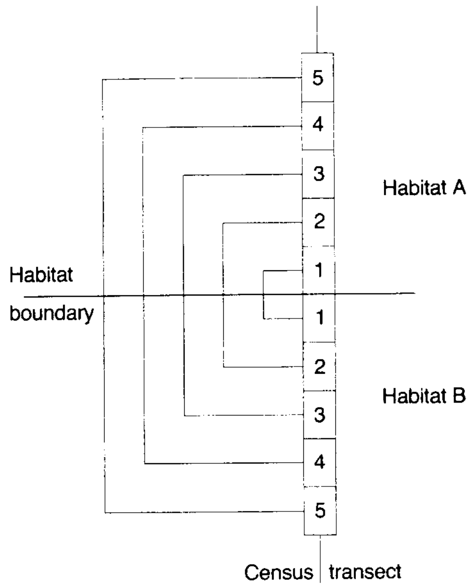


Figure 5.5 A protocol to assess foraging and dispersal scales of density-dependent habitat selection. Replicated census transects bisect two habitats occupied by the species of interest. Each set of 'connecting lines' represents a separate regression comparing densities in segments located at different distances from the boundary. The regressions assess predicted shifts in isodar intercepts and slopes that document the limits of foraging and dispersal scales of habitat selection (thorough analyses would evaluate densities in segments of increasing length). (Source: Morris, 1992.)

I tested the theory's ability to detect foraging and dispersal scales by contrasting deer mouse (*Peromyscus maniculatus*) densities along replicated live-trap transects bisecting prairie and badland habitats in southern Alberta (Morris, 1992; Figure 5.2). The isodar shown on the right of Figure 5.2 was generated along a transect from segments close to the boundary between the two habitats; the one on the left was generated from more distant segments. The slope of the isodar on the right is significantly less than that on the left, in agreement with theoretical predictions that it corresponds to the foraging scale. The isodar on the left corresponds to the dispersal scale. Regressions based on more distal segments of equal length were non-significant. This lack of correlation between distant population densities demonstrated the effective limit of density-dependent habitat selection in regulating population size. The analysis revealed a foraging scale in the order of 60 m and a dispersal scale in the order of only 140 m. Habitat selection's influence on the population regulation of deer mice occupying heterogeneous prairie

landscapes was thus limited to within 70 m of the prairie–badland boundary.

Habitat selection is likely to be a potent contributor to regional deer-mouse population dynamics only if prairie and badland habitats have extensive borders resulting from complex edges or highly interspersed patches of habitat. Prairie and badland habitats are juxtaposed along sinuous, dendritic river valleys and their tributaries, suggesting that habitat selection may indeed play a major role in population regulation between the two habitats. This example demonstrates how isodar analysis can:

1. identify the spatial scales of habitat selection and population regulation, and
2. guide the choice of critical landscape features for further interpretation.

5.3.2 INFERENCES OF TEMPORAL SCALE

Landscape analyses have recently benefited from a variety of techniques that assist spatial pattern analysis (Turner *et al.*, 1991; Rossi *et al.*, 1992). But ecologists also need models and techniques that relate spatial pattern to underlying ecological processes (Fox and Morris, 1990; Kareiva, 1990; Morris, 1990; Merriam, Henein and Stuart-Smith, 1991; Fahrig, 1992). Numerous processes are doubtlessly involved in the creation of spatial pattern, and the challenge for the theorist and empiricist alike is to select those processes appropriate to the spatial and temporal scales being analyzed. Theories of density-dependent habitat selection offer substantial promise at fulfilling this need, particularly at scales corresponding to habitat disturbance and fragmentation.

Imagine a habitat that is modified by either natural or human disturbance. The objective is to predict the effect of the disturbance on local populations and communities as well as the time course of 'recovery' to ambient conditions. One way of achieving this is to consider the effect that the disturbance will have on fitness–density curves, and their resulting isodars (Figure 5.6).

Shortly after disturbance the expected fitness at any given consumer density is likely to diverge dramatically from that of an undisturbed control habitat (Figure 5.6(a)). The differences are likely to dissipate with time as the disturbance is ameliorated via ecological succession. A comparison of isodars calculated from disturbances of different ages documents the time-course of possible convergence in population dynamics (Figure 5.6(b)).

The value of this technique can be illustrated by isodar analyses on white-footed mice (*Peromyscus leucopus*) inhabiting successional and mature forest habitats in southern Ontario. Regressions of the density of

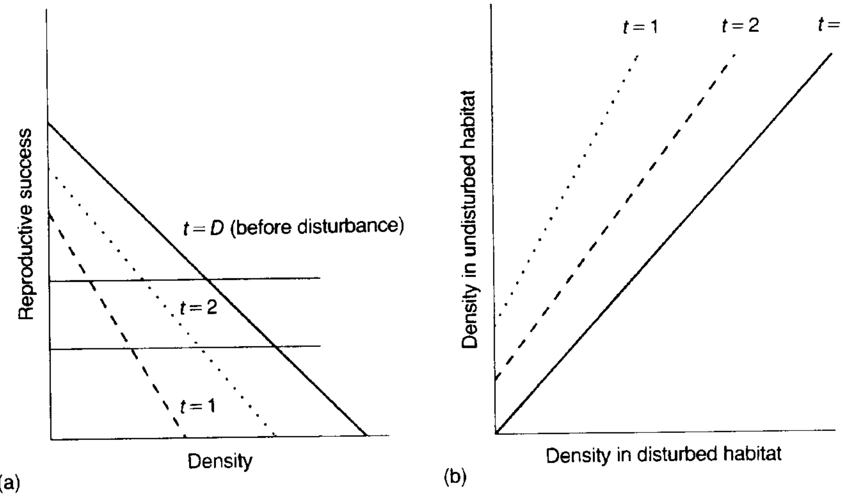


Figure 5.6 One example of how disturbance modifies habitat. (a) The disturbed habitat can be distinguished from its undisturbed neighbors by differences in the decline of fitness with population density (e.g. the line corresponding to $t=1$, the time interval since disturbance). These differences will be reduced through time ($t=2$) if the disturbed habitat becomes more similar to its neighbors. (b) The convergence of the disturbed habitat on the ambient control is reflected in a similar convergence of isodars. In both cases, the undisturbed controls are considered constant, but this assumption is not crucial to the use of isodars in the assessment of habitat convergence. (Source: Morris, 1990.)

white-footed mice occupying forest versus early succession old-field habitat revealed a consistent preference of white-footed mice for forest (isodar slope > 1.0, intercept > 0; Morris, 1988). Regressions of white-footed mouse density in 20-m tall forest versus that in mid-successional 3-m tall sumac generated an isodar with a slope very close to 1.0, and with an intercept not significantly different from zero (the densities were indistinguishable; Morris, 1988). As far as patterns in white-footed mouse population density are concerned, the sumac had converged on the forest even though the two were dramatically different in habitat structure and floristic composition (Morris, 1984). The example illustrates how isodars can be used to define habitats. Two habitats are recognized as different by a habitat-selecting species only when the isodar has an intercept different from zero, or a slope different from unity.

5.3.3 INFERENCES TO MULTISPECIES COMMUNITIES

Single-species models have obvious limitations when applied to multispecies assemblies. Isodar analysis can be easily modified to incorporate

species interactions (Morris, 1989b). Figure 5.7 demonstrates the solution. Instead of simply plotting the density of one species in one habitat against its density in a second habitat, the 'multispecies isodar' incorporates the effects of potentially interacting species. These effects are scaled by multiple regression analysis by representing species interactions as additional individuals of the 'target' species. The important result is that both the single-species and multispecies isodars are predicted to be the same, as long as all relevant interactions among species are included in the multiple regression equation (Morris, 1989b).

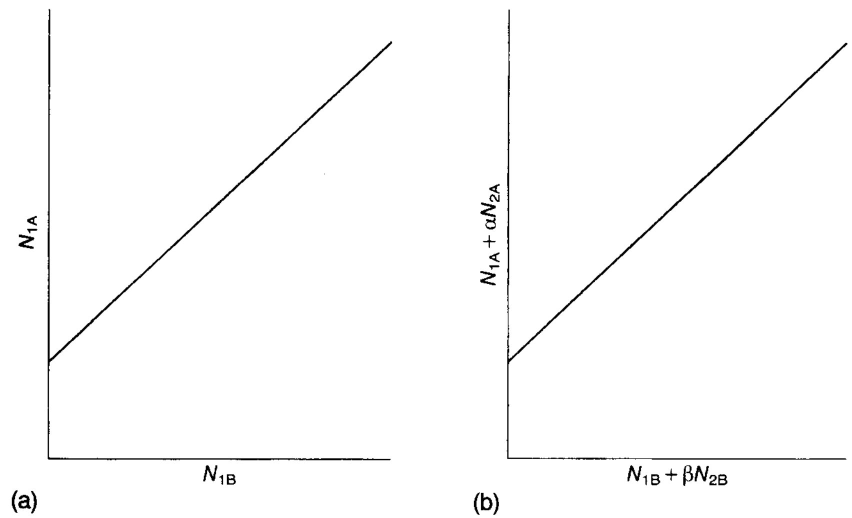


Figure 5.7 An illustration of the effect of interacting species on isodars. (a) An isodar constructed where the target species exists alone in allopatry. (b) An isodar constructed where the same species co-occupies the two habitats with a competitor in sympatry. The isodar remains unchanged as long as the appropriate species interaction is included for each habitat. (Source: Morris, 1989b.)

The prediction of equivalent isodars, whether generated from data on the target species in isolation, or from an intact set of interacting species, suggests a powerful test for species interactions. The isodar of each habitat-selecting species should be unchanged following removal of its competitors. If the isodar following species removal is different from that estimated prior to removal, we can be reasonably certain that some key or higher-order interaction was omitted in the first analysis. Perhaps the best example of a nonlinear effect is produced by distinct habitat preferences (Rosenzweig, 1979, 1981, 1989) where density-dependent habitat selection warps competitive isoclines to eliminate all evidence of competition when each species occupies only its preferred habitat. Such curved isoclines in response to habitat selection have recently been documented between pairs of competing gerbils in Israel (Abramsky, Rosenzweig and Pinshow, 1991; Abramsky, Rosenzweig and Zubach, 1992). If the theory is correct in its predictions, the single-species isodar should be reproduced with new data including the omitted interactions.

Experimental tests of the multispecies theory have not yet been published. Preliminary observational tests are encouraging but imperfect. Regressions of white-footed mouse density in either sumac or forest habitat versus that in an old field co-occupied by meadow voles (*Microtus pennsylvanicus*) detected no competitve interactions between the two species (Morris, 1989b). The mouse isodars suggested habitat partitioning related to both qualitative and quantitative differences between the two wooded habitats in comparison with the old field. Qualitative differences should lead to distinct habitat preferences (Pimm and Rosenzweig, 1981; Rosenzweig, 1985, 1987, 1989), a result in agreement with the markedly different habitats usually exploited by these two species. A reanalysis of habitat partitioning between two Arizona rodents similarly revealed density-dependent habitat selection (Morris, 1989b), but failed to confirm field manipulations demonstrating modest competitive interactions (Holbrook, 1979). Applications of isodar analysis to multispecies assemblages should therefore be interpreted with caution.

5.4 ALTERNATIVES

5.4.1 INFERENCES BASED ON HABITAT 'QUALITY'

Ecological folklore, and a good deal of theory, promulgates the view that population density is related to habitat quality. Current theories of density-dependent habitat selection argue that the density in any one habitat is also a function of the density in neighboring habitats. Modern versions of an idea dating at least to Joseph Grinnell (MacArthur, 1972) demonstrate that 'surplus' individuals produced in so-called source habitats may often spill over into unproductive sink habitat (Holt, 1985; Pulliam, 1988; Oksanen, 1990; Oksanen, Oksanen and Gyllenberg, 1992) with profound consequences on not only population size, but also on the interactions among species (Pulliam and Danielson, 1991; Danielson, 1991, 1992). This suspicion is confirmed by studies on rodents in northern latitudes where dramatic differences in population densities and population dynamics show strong correlations with habitat heterogeneity (Hansson and Henttonen, 1988). The challenge is to separate influences on population density caused by differences in habitat 'quality' (differences in the relationship between fitness and population density) from those caused by density-dependent habitat selection among different habitats.

The classic approach using multivariate statistics to infer habitat quality (for example, by regressions of population density against several independent microhabitat variables (Capen, 1981); excellent discussions of the strengths and weaknesses of this approach can be found in Verner, Morrison and Ralph (1986) and Wiens (1989)) fails to account for landscape effects that can modify population density. A simple example of such an effect can be demonstrated by biases of spatial scale. If the microhabitat variables are collected across sets of more or less homogeneous habitats and pooled for analysis, the ecologist may be misled into believing that population density is causally related to microhabitat, when in reality, animals are recognizing a much larger scale of habitat heterogeneity (Morris, 1987c, 1989c). The animals may be sampling the environment at a higher level of heterogeneity than that subsumed within the microhabitat variables (Kolasa and Rollo, 1991). Van Horne (1983) as well as Hobbs and Hanley (1990) offer several additional critiques. Isodar analysis provides little in the way of improvement because it includes no information on intrinsic habitat quality.

There are several reasons why density may not mirror habitat quality (Van Horne 1983, 1986; Maurer, 1986; Wiens, 1989; Kareiva, 1990) and thereby lead to a biased isodar analysis. One common reason may simply be that 'disconnected' populations are not at the same density relative to patch carrying capacity. Similar patches of habitat within a landscape may support quite different densities dependent upon the recent history of population growth within the patch (or nearby patches). This 'nonequilibrium' effect can be illustrated by representing the fitness–density curves for a pair of habitats by bands of parallel curves each representing a different patch (Figure 5.8(a)). The graph is drawn such that if the population could achieve equilibrium in all patches (intercepts along the abscissa), there would be a direct correspondence between population density and patch quality. Assume an ideal distribution of individuals between pairs of habitat patches. A regression of 'nonequilibrium' population density against patch quality will likely have substantial residual variation and low predictive power (Figure 5.8(b)).

An isodar plot of the same data illustrates the converse role that variation in quality can play in residual scatter about the isodar (Figure 5.8(c)). Note, however, that all error variation is eliminated if we use a hybrid technique that constructs the isodar with the residuals from the 'habitat quality' regression (Figure 5.8(d)). The slope of the original isodar, and thus our interpretation about population regulation, is different from that in the corrected residual isodar (0.72 in Figure 5.8(c); 1.0 in Figure 5.8(d)). The model presented here assumes that maximum reproductive success and equilibrium population density are perfect correlates of habitat quality (all patches have parallel fitness curves). The validity of these assumptions in any field study will depend upon

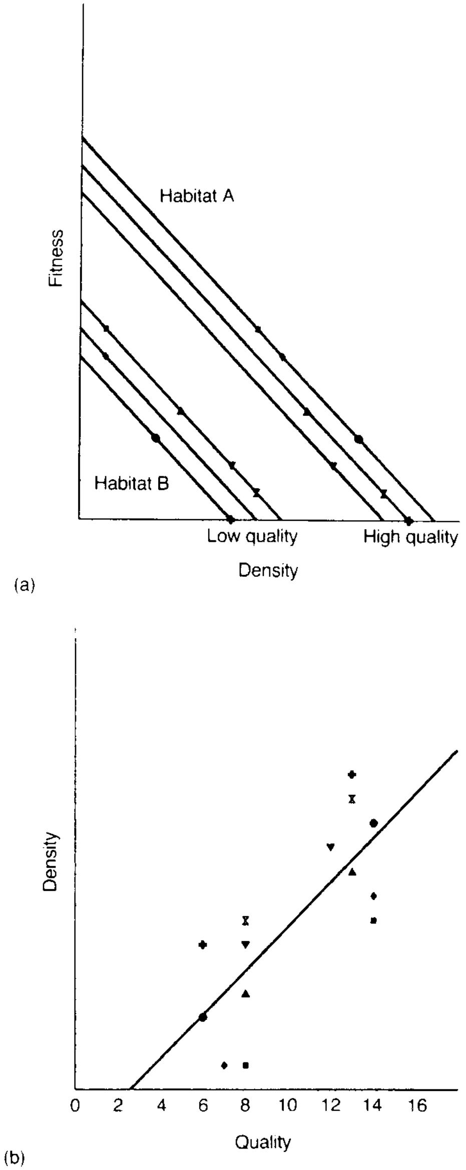
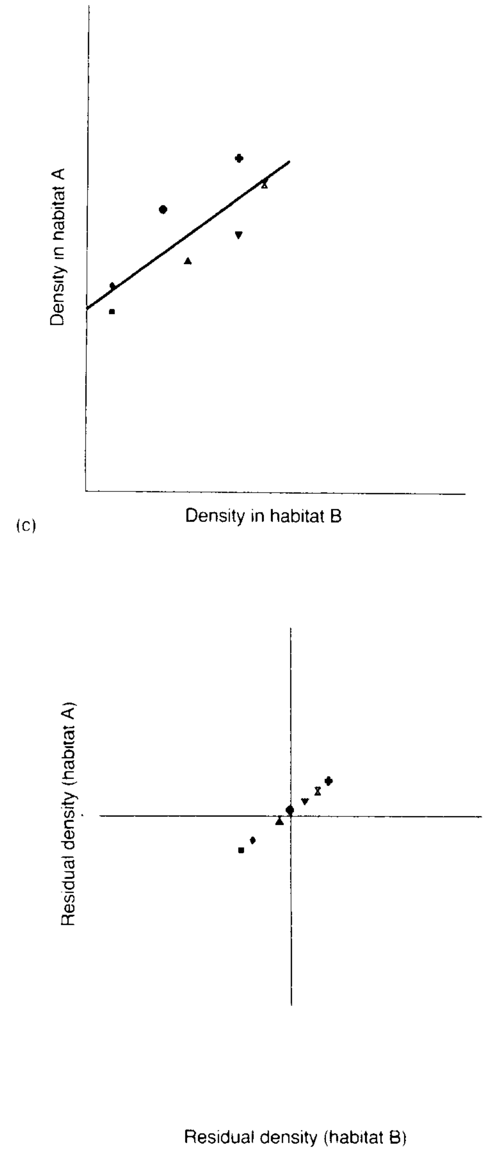


Figure 5.8 (a) Bands of fitness–density curves representing different patches of two habitats, A and B. The quality of each patch is given by its intercept with the abscissa. Paired symbols correspond to nonequilibrium ($N_i<K_i$) ideal distributions between nearby patches of the two habitats. Similar processes could act among patches within a single habitat. Interpretations about the relationship between habitat quality and population density would be complicated if the individual curves vary in slope or shape, but such differences could be detected by 'within-habitat' analyses. (b) The densities in (a) plotted against the quality of each patch.



(c) An isodar of the hypothetical data presented in (a) (isodar slope = 0.72). The residual scatter is the result of differences in population density among different pairs of habitat patches isolated throughout the landscape. (d) A residual isodar created by plotting the residuals from the regression in (b) (isodar slope = 1.0; with real data we expect a significant reduction in unexplained variation about the regression rather than complete elimination of error).

consistency in the shapes and slopes of the fitness–density functions, and on the correlation between habitat features and their quality.

The two isodars give different solutions because the relative qualities of alternative habitat choices selected by individuals change among replicate estimates of population density. The mix of patches of different qualities has warped the fitness–density curves so that they appear to converge (slope < 1) rather than remain parallel. The potential for habitat quality to obscure the real relationship between the density in the two habitats (different 'slopes' in the original and residual isodars) thus depends upon the mosaic of the habitats in the landscape. It is possible that the relative differences between such pairs could remain constant. The relative abundance of species in the two habitats would be unbiased among samples and there would be no improvement in the isodar solution if one used the density/quality residuals in place of the original densities.

An effective protocol for the assessment of density-dependent habitat selection may thus first regress densities against likely correlates of habitat quality, such as those used in earlier regression and correlation studies, before subjecting the residuals to a formal isodar analysis. The potential for nonequilibrium dynamics would be implicated whenever the residuals isodar gives a better fit to the data than the isodar based on the original densities.

Differences in the slopes, intercepts and shapes of the fitness–density curves will reduce the effectiveness of the residuals analysis in assessing habitat selection. Such differences imply that the analysis is confounded by more than the two habitats of interest because a habitat can be defined by similarity in the functional relationship between fitness and density. This definition depends on the choice of scale used in the analysis, an issue of crucial interest in landscape ecology. Regional comparisons of habitat use among many landscapes may inadvertently lump habitats that individuals of a habitat-selecting species would recognize as different.

An example of the landscape effect can be found in an isodar analysis used by Knight and Morris (unpublished) to study habitat selection by red-backed voles occupying wet and dry habitats in the Hudson Bay lowland. The pattern of residuals about the regression suggested that these voles may be selecting more than just two habitats (Knight, 1993). Instead of wet and dry habitats, the voles appeared to recognize three habitats; dry ridges, wetlands without trees, and wetlands with interspersed larch and spruce. Subsequent isodar analyses confirmed the three-habitat classification.

5.4.2 HABITAT MATCHING RULES

Habitat selection theories may allow us to predict how changes in landscape composition affect population size. Pulliam and Caraco (1984) demonstrated for a special case of the ideal free distribution where each individual's fitness is proportional to its fraction of total resource, that

$$K_i/p_i = K_j/p_j, \tag{5.1a}$$

where K is carrying capacity, and p is the number of individuals occupying patches i and j. (5.1) is the habitat matching rule that specifies how individuals should distribute themselves relative to the availability of resources. Rearrangement of (5.1a) shows that the ratio of individuals occupying different patches should be constant (Fagen, 1988)

$$p_i/p_j = K_i/K_j = \text{constant}, \tag{5.1b}$$

or put another way, the fraction of predators in a patch should be proportional to the fraction of prey in that patch (Sutherland, 1983; Fagen, 1987; see also Kacelnik, Krebs and Bernstein, 1992; Oksanen, Oksanen and Fretwell, 1992; Kennedy and Gray, 1993). Morris (1990) used similar logic to argue for constant niche breadth for ideal habitat selectors occupying qualitatively different habitats. (The matching rule assumes that all habitats are occupied at all densities (Sutherland, 1983; Pulliam and Caraco, 1984), an assumption most likely to be met if habitats differ qualitatively.) It should be possible, therefore, to test the ideal free theory by demonstrating that changes in predator population size have no effect on the ratio of individuals occupying each habitat (Messier, Virgl and Marinelli, 1990).

In the context of landscape ecology, (5.1b) can be used to predict changes in population size with changes in habitat supply (Fagen, 1988; but see Hobbs and Hanley, 1990). As noted above, the equation applies only to an ideal free distribution when each habitat is occupied across the full range of population sizes. This assumption may often be inappropriate to landscape applications of the theory. Isodar solutions (Morris, 1994) are preferable because they can be applied to a variety of forms of habitat selection, and because they implicitly specify lower and upper limits on population size (the range of densities along the isodar).

5.5 CAVEATS AND FUTURE DIRECTIONS

Habitat selection theories that I have reviewed here specify the expected relationships between population density and reproductive success in ideal landscapes. As such, they represent appropriate null models for landscape ecology. An ecologist searching for landscape-mediated effects on population density may wish to begin the search with an isodar analysis (Morris, 1994).

My enthusiasm for application of habitat selection theory to the landscape scale is tempered by the complexity of the patterns we wish to explain. Even the most ardent advocate of isodar analysis will surely recognize its limitations at differentiating certain kinds of processes and their interactions simply by examining patterns of population density. Application of the theory also requires that reliable estimates of population density be obtained at the spatial and temporal scales appropriate to habitat selection. It could frequently be misleading, for example, to use annual or single-season estimates of density when habitat preferences vary seasonally (Van Horne, 1983). Similar biases would occur whenever density estimates are influenced by landscape processes that are not directly related to density-dependent habitat selection (e.g. passive dispersal, local extinction and recolonization).

5.5.1 SOURCE–SINK DYNAMICS

Source–sink dynamics, where average reproductive success is greater in one habitat than in another, occurs only when habitat choice follows something other than an ideal free distribution (Oksanen, Oksanen and Fretwell, 1992). Pre-emptive (Pulliam, 1988; Pulliam and Danielson, 1991) and despotic models (Fretwell and Lucas, 1970) assume a habitat selection process whereby per capita population growth rates between pairs of habitats are unlikely to be equal, and where high-quality patches may function as sources to lower-quality sinks. The stable source–sink dynamics created by these forms of habitat selection have led to some of our most dramatic insights into the role of landscape heterogeneity on species interactions and ecosystem structure (Oksanen, 1990; Pulliam and Danielson, 1991; Danielson, 1991, 1992; Dunning, Danielson and Pulliam, 1992; Oksanen, Oksanen and Gyllenberg, 1992).

The population result of source–sink dynamics, compared to an ideal free distribution, is reduced density in high-quality habitats, and inflated densities elsewhere. One way of modeling this effect for an ideal despotic distribution is to rotate the fitness–density curves of the best habitat clockwise to represent the individual's perception of reduced fitness with interference (Fretwell and Lucas, 1970; Fretwell, 1972; Morris, 1987a). This has, depending upon one's viewpoint, the desirable or undesirable effect of reducing the isodar intercept (Figure 5.9). The two habitats would appear less different quantitatively, a result of inflation in population density in the sink habitat. At any given density, aggression increases the expected reproductive success of individuals relative to the expectations from ideal free habitat use. Aggression is not without cost. The increased fitness accrued by individuals occurs at the expense of an overall reduction in population density in each habitat, and thereby in overall population size (Figure 5.9).

The desirable aspect of a reduced isodar intercept with despotic behavior is that one can, in theory, differentiate between ideal free and despotic source–sink regulation, and measure their relative magnitudes by analyzing only graphs of population density. The design of the study is crucial because other effects can also modify the intercept of the isodar (Morris, 1987a, 1988, 1990, 1992). The undesirable effect is that it may often be impossible to detect the isodar shift unless we know, or can experimentally manipulate, the fitness–density functions. This latter point would be especially crucial in those instances where a large proportion of the population is forced into sink habitat producing population densities larger than those in the source (Wiens, 1989).

Fitness curves for ideal pre-emptive distributions are easily modeled by cumulative frequency distributions of breeding-site quality (Morris, 1994). The resulting isodars have a characteristic curvilinear or nonlinear signature. We do not know how applicable these and other curvilinear models may be because data analyzed so far give a reasonable fit to the linear model.

5.5.2 QUESTIONS FOR FUTURE STUDY

Few of the assumptions and predictions of isodar analysis have been tested experimentally. Can isodars detect the qualitative and quantitative differences in habitat that the theory suggests? Are competition coefficients estimated by isodar analysis valid indicators of competitive interaction? Are the cues that individuals use to assess habitats reasonable estimates of expected fitness?

The application of habitat models to landscape predictions raises new questions. What is the correspondence, if any, between the effective spatial and temporal limits of habitat selection and the patterning of habitat patches in the landscape? What is the interaction of dispersal between habitat patches and the dynamics of metapopulations (Chapter 4)? How important is density-dependent habitat selection to population persistence in heterogeneous landscapes? How does this role vary with landscape composition and pattern?

Many other unexplored effects offer fertile ground for habitat ecologists. Among these are interactions between landscape patterns such as the interspersion and orientation of patches, the relative proportions of patches of varying quality, and the nature of patch shapes and boundaries with habitat characteristics such as the variance in habitat quality within and between patches, with variation in the form of density-dependent feedback on fitness, and with the resistance of habitats to animal movement. The question is not whether such interactions occur, but whether

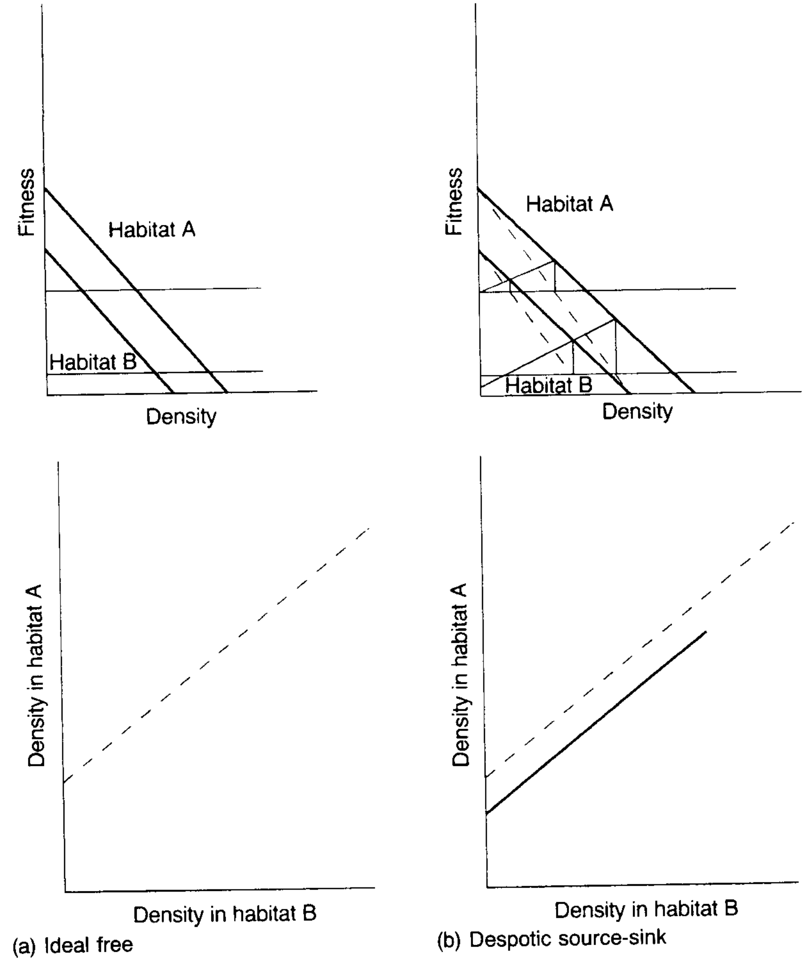


Figure 5.9 Comparison of (a) ideal free and (b) despotic source–sink regulation and their resultant isodars. Habitat B is of lower quality than habitat A. With source–sink regulation, the perceived fitness in habitat A is equal to that in habitat B (represented by dashed lines with negative slope). Unequal opportunities at reproduction inflate population densities in sink habitats (B) relative to the ideal free solution (intercepts of the two sets of solid lines). This is equivalent to reduced fitness–density functions that produce isodars with reduced intercepts (greater density in habitat B; compare the solid source–sink isodar with the dashed ideal free isodar). As shown here, the per capita decline in perceived fitness with despotic behavior is equivalent in the two habitats. If the assumption is violated the despotic isodar will have a different slope to the ideal free one.

their occurrence corroborates or invalidates the inferences we try to make from models of habitat selection.

5.6 SUMMARY

Density-dependent habitat selection is one of the key mechanisms capable of modifying the distribution and abundance of species at the landscape scale. Recent extensions of the theory based on isodars (plots of the density of individuals in pairs of habitats such that an individual's expected reproductive success is equal in both) demonstrate how we can measure habitat selection's role in spatial population regulation, and how differences between habitats can modify overall population size. One intriguing application of the theory uses patterns of density across habitat boundaries to estimate foraging and dispersal scales of habitat selection, and thereby the effective bounds of the landscape to different species. Other extensions allow us to follow the time course of community recovery following habitat disturbance, and to infer interactions between species in ecological communities. Under somewhat restricted conditions of an ideal free distribution it is possible to test for a perfect match between habitat quality and population density with only data on population density.

Observational studies generally support the theory, but definitive experiments testing assumptions at the landscape scale are lacking. The utility of habitat selection models to infer landscape processes and patterns may be compromised by nonequilibrium dynamics, by spatial differences in the quality of habitat patches, by source–sink dynamics, and by complicated relationships between fitness and population density. Many of these apparent limitations can be addressed by modified analyses that suggest productive avenues of future research at the interface between habitat selection and landscape ecology.

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