

# How can we apply theories of habitat selection to wildlife conservation and management?

*Douglas W. Morris*

Department of Biology and Faculty of Forestry and the Forest Environment, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada. Email: douglas.morris@lakeheadu.ca

**Abstract.** Habitat-selection theory can be applied to solve numerous problems in the conservation and management of wildlife. Many of the solutions involve the use of habitat isodars, graphs of densities in pairs of habitats such that expected fitness is the same in both. For single species, isodars reflect differences in habitat quality, and specify the conditions when population density will, or will not, match the abundance of resources. When two or more species co-occur, isodars can be used to assess not only whether the species compete with one another, but also differences in habitat, in habitat selection, and in the functional form of density-dependent competition. Isodars have been applied to measure scales of habitat selection, the presence or absence of edge effects, as well as the number of habitats that species recognise in heterogeneous landscapes. Merged with foraging behaviour, isodars reveal the relative roles of habitat selection, spatial structure, and environmental stochasticity on local populations. Habitat-selection models can be linked similarly with theories of patch use to assess the underlying cause of source–sink dynamics. Isodars can detect and measure Allee effects, describe human habitat selection, and use human occupation of habitat as a leading indicator of threatened biodiversity. Even so, we have only begun to reveal the potential of habitat selection, and other optimal behaviours, to solve pressing problems in conservation and management.

## Introduction

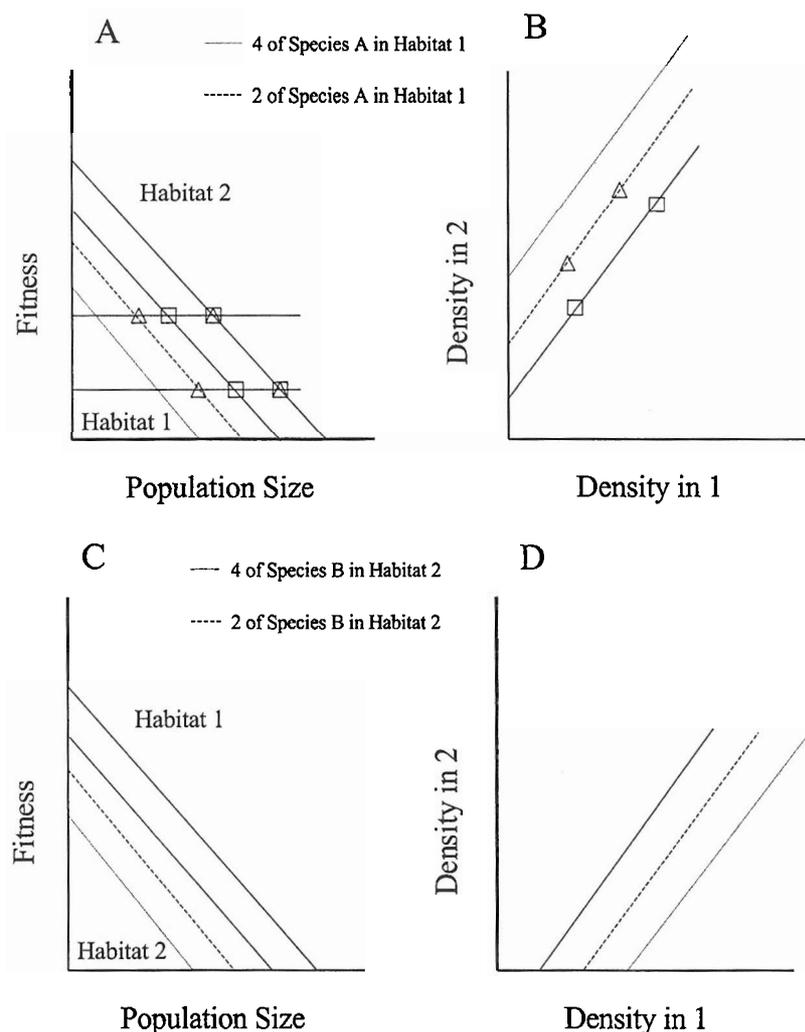
One fact is indisputable. The negative impacts of humans on the rest of biodiversity exceed those of any other species, and probably any other taxon, in the four-billion-year history of life on Earth. We reduce the densities of some species, and increase those of others. We alter, manipulate, destroy, and even move, habitat. We change the spatial context of habitat, habitat neighbours, the nature of edges, the relative abundance of habitats within the landscape, and the landscape itself. We change the structure of ecological communities, the geographical distributions of species, and the rules of regulation, succession, and assembly. And, we have a myriad of effects that we barely recognise, and about which we know even less, across all relevant scales in space and time.

Against this backdrop of unprecedented change, conservation ecologists and managers have three jobs. (1) We must develop and modify theories that predict the consequences of human actions on biodiversity, and contrast those predictions against the predicted consequences of alternative actions. (2) We must validate the theories that we use. (3) We must demonstrate, by example, that our theories can be applied to issues of conservation and management. I

believe that we can do each job with theories of habitat selection.

Let's be clear about what the human actions are, and about what it is that we wish to know. We alter habitats, so we must be able to differentiate one habitat from another and assess their quality. We alter the sizes of habitat patches and the relative abundances of habitat. We must be able to measure the scale of habitat selection and predict how the size and abundance of habitats in a landscape influences the species that live there, their population sizes, and their evolution. We change habitat neighbours, and the characteristics of landscapes. So we must be able to detect the influence of habitat selection on abundance, and the effects of landscape on habitat selection. Finally, we must remember that humans are animals too, and that our behaviour may also be explained by ideal habitat selection.

I begin by reviewing single-species isodar models of habitat selection. I assess how we can use isodars to assess quantitative and qualitative differences in habitat, and how isodars are altered by competitive interactions among species. I explore the scales of habitat selection to build a null model for landscape ecology, to assess edge effects, and to demonstrate how we can determine the number of habitats



**Fig. 1.** An illustration of the effect of interspecific competition on habitat selection. (A) The fitness of individuals of Species B declines with increasing density (negatively sloped solid lines) in both its preferred Habitat 2 and its less preferred Habitat 1. Intercepts with horizontal lines (squares) specify the ideal free distribution of individuals at different population sizes (fitness identical in both habitats). The single-species isodar (solid line) is plotted in (B). Dashed and dotted lines correspond to the effects of increasing arbitrarily assigned numbers of Species A on the fitness of Species B in Habitat 1. Intercepts with horizontal lines (triangles) represent the ideal free distribution in the presence of two individuals of Species A. The effect on the isodar is plotted in (B). Parts (C) and (D) show the same effect, but from the perspective of Species A, which has a distinct preference for Habitat 1 (horizontal lines and symbols are eliminated for clarity).

contained within any given landscape. The scales of habitat selection are also crucial to our understanding of source–sink dynamics and how effectively species match their densities to resource abundance. I illustrate how isodars allow us to identify Allee effects, and how they can be merged with foraging theory to measure environmental stochasticity. I conclude by evaluating whether isodars can be applied to humans, whether they can act as leading indicators of threats to the World’s biodiversity, and what the prospects are for their future.

### Isodar theory

Imagine a single species living in a landscape composed of two different and, for convenience, equal-sized habitats. Imagine further that within each habitat the species’ population growth can be modelled by the Verhulst–Pearl logistic equation

$$dN_i/dt = r_i N_i [(K_i - N_i) / K_i], \quad (1)$$

where  $N_i$  is population size in habitat  $i$ ,  $r$  is the maximum intrinsic rate of increase at low density, and  $K$  is the density at which the realised rate of increase,  $r$ , = 0 (carrying capacity). If individuals select habitat in a way that maximises their own fitness, they will attain an evolutionarily stable strategy (Maynard Smith and Price 1973; Morris *et al.* 2001) where their density in each habitat is adjusted such that the expected fitness in each habitat is identical (Fretwell and Lucas 1970; Fretwell 1972). Letting fitness equal *per capita* population growth rate, then

$$(1/N_2)(dN_2/dt) = (1/N_1)(dN_1/dt)$$

and substituting terms from equation (1),

$$N_2 = K_2[1 - r_1/r_2] + (r_1/r_2)(K_2/K_1)N_1 \quad (2)$$

represents the straight-line isodar (Morris 1987a, 1988), the set of densities corresponding to ideal habitat selection.

## Isodars and habitat quality

Each habitat can be categorised in terms of quantitative (i.e. resource density) and qualitative (e.g. habitat structure) differences (Rosenzweig 1987; Morris 1988) that have far-reaching implications on the organisation of ecological communities (Pimm and Rosenzweig 1981). Yet equation (1) reveals that habitats are distinguished only by differences in  $r$  and  $K$ , and it is instructive to ask how qualitative and quantitative differences affect population growth and carrying capacity.

Consider a pair of habitats that differ from one another only in the density and renewal rates of identical resources. Assuming that fitness is proportional to the amount of unused resource, the linear decline in fitness incorporated in logistic population growth can be modelled by the fitness function

$$r'_i = \gamma[R_i - (E_B/E_i)QN_i], \quad (3)$$

where  $r'$  is the realised fitness in habitat  $i$  ( $\gamma$  is a scaling constant,  $R_i$  is resource availability (includes the resource renewal rate),  $E_B/E_i$  is the efficiency of resource extraction, consumption and conversion into descendants in habitat  $i$  relative to the best habitat (*per capita* fitness declines more when  $E_i$  is small than when it is large), and  $Q$  is the *per capita* consumption of resource (Morris 1988)). The *per capita* decline in fitness in habitat  $i$  is proportional to the *per capita* resource consumption rate in that habitat. Setting  $N$  and then  $r$  equal to zero in equation (3), one can calculate  $r$  and  $K$  as

$$r_i = \gamma R_i \quad (4)$$

and

$$K_i = R_i / [(E_B/E_i)Q] \quad (5)$$

respectively. Substituting the values of  $r_i$  and  $K_i$  into equation (3), and noting that 'efficiency' in the best habitat (2) is defined as unity, ( $K_2 = R_2/Q$ ), then

$$N_2 = (R_2 - R_1) / Q + (E_1/E_2)N_1. \quad (6)$$

Equation (6) demonstrates that quantitative differences in habitat (variation in  $R_i$ ) alter the isodar intercept, whereas qualitative differences (alter efficiency) modify only the slope (Morris 1988).

Isodars need not be linear (e.g. Morris 1994), but when they are, they appear to reflect equation (6). Thus, isodars calculated for deer mice and red-backed voles occupying xeric and mesic forest habitats revealed both types of habitat differences (Morris 1996a). Voles perceived the mesic forest as quantitatively superior (isodar intercept significantly greater than zero), whereas the clear preference of mice for the xeric forest also depended on population density (quantitative and qualitative differences, intercept greater than zero, slope greater than 1.0). In prairie-badland

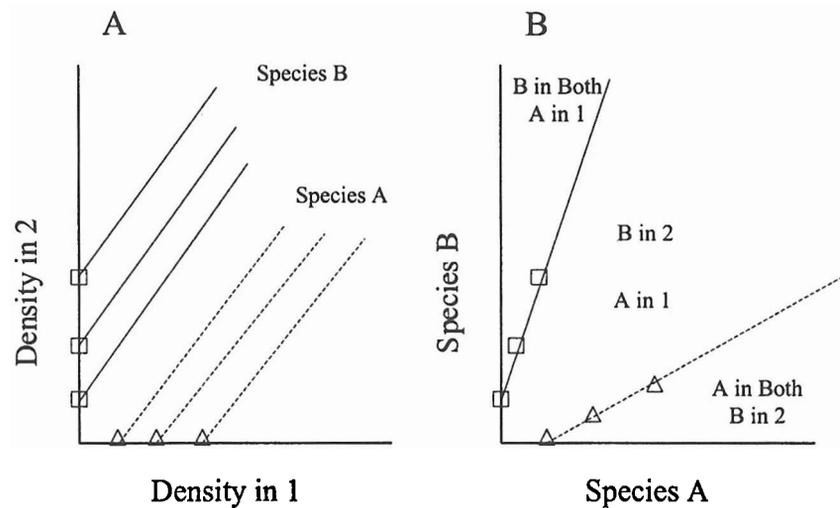
landscapes, deer mice also appear to view the two habitats as quantitatively and qualitatively different. Densities tend to be higher in badlands (Morris 1997), and to increase more rapidly there than they do in adjacent prairie (Morris 1992a). In sub-Arctic coastal habitats where isostatic rebound continues to create raised beach ridges with intervening wetlands, red-backed voles prefer the relatively dry tree-covered beach ridges. The degree of preference depends on the age (and associated tree cover) of the wetland habitat (Knight and Morris 1996). Isodars for voles occupying ridges adjacent to old 'tree-covered' wetlands possess intercepts greater than zero, but slopes less than unity (the covered wetland is increasingly favoured at high densities). Isodars contrasting densities on ridges with those in adjacent young 'open wetlands' reveal only qualitative differences (intercept not different from zero, slope greater than 1.0). Both quantitative and qualitative differences have emerged in isodars calculated for such diverse taxa as birds exploiting urban parks and tree-lined streets in Madrid (Fernández-Juricic 2001) and gerbils occupying dune and stabilised sand habitats in Israel (Ovadia and Abramsky 1995).

Definitive experiments manipulating quantitative and qualitative components of habitat have not yet been published. We can imagine, nevertheless, an indirect test where we manipulate population size and record the pattern of density between adjacent areas located in a single habitat. Since both areas are identical, there should be neither quantitative nor qualitative differences (isodar intercept = 0, slope = 1). Zvika Abramsky, Mike Rosenzweig and their team (Abramsky *et al.* 1991, 1992, 1994, 1997, 2001) have performed the test repeatedly on two different gerbil species preparatory to creative experiments on interspecific interactions. Population sizes of single species were varied in single enclosures, and rodents were allowed time to adjust their densities by moving through gates to bordering enclosures in identical habitat. Isodars, in each case, passed through the origin with a slope of 1.0.

It thus appears, for many species, that we can gain fundamental insights into the relative qualities of the habitats they occupy simply by analysing their patterns of abundance in adjacent habitats. Several additional factors influence the distribution and abundance of species and have the potential to mislead our estimates of habitat quality (e.g. Van Horne 1983, 1986). We now turn our attention to some of the apparent complications including interactions with other species, the influences of spatial scale, boundaries between habitats, the mismatch of densities with resources, and source-sink dynamics.

## Isodars and competing species

Abramsky and Rosenzweig's ingenious experiments rely on habitat selection to reveal inter-specific competition (and more recently, the influences of predators: Rosenzweig *et al.*



**Fig. 2.** An illustration of how the competitive effect displayed in Fig. 1 can be mapped as an isoleg. (A) A graph of the sets of isodars corresponding to different population sizes of the competitor. Species B prefers Habitat 2 (isodar intercepts on the ordinate); Species A prefers Habitat 1 (isodar intercepts on the abscissa). (B) The intercepts from (A) plotted as isolegs.

1997; Abramsky *et al.* 1998). Different densities of a target species are placed in an empty field enclosure, but individuals are free to move through gates to an adjacent enclosure located in the same habitat. After achieving an ideal distribution, the target individuals are tested against variable densities of a second potentially interacting species restricted, by the size of the gates, to using a single enclosure. Any change in habitat distribution by the target must be caused by the influence of the second species, and can be used to measure that species' density-dependent influence (Abramsky *et al.* 1991, 1992, 1994).

The Abramsky–Rosenzweig technique requires that habitat use is both density-dependent and capable of reflecting interspecific interactions. Not only have the assumptions been confirmed in the experiments, the Abramsky–Rosenzweig team has also been able to test key predictions that emanate only from theories of habitat selection.

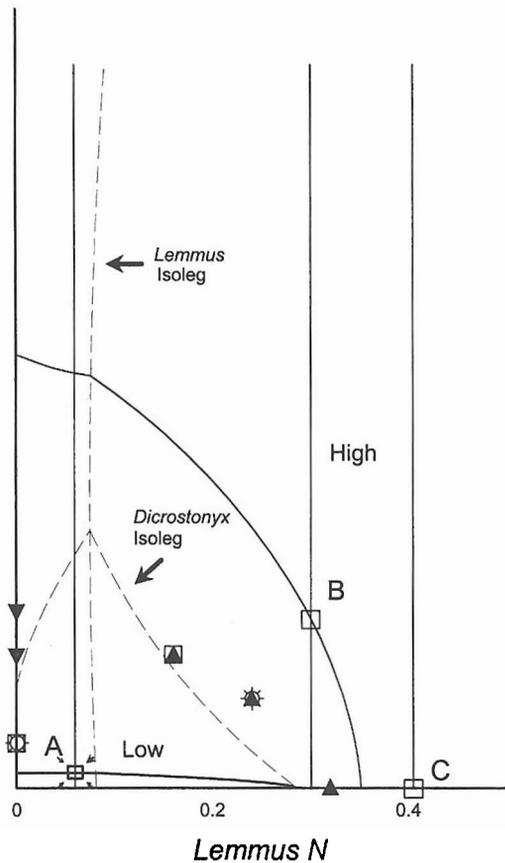
We can understand the Abramsky–Rosenzweig test as follows: Imagine that we are interested in testing competitive interactions between a pair of habitat-selecting species that have distinct habitat preferences for two different habitats. Imagine, first, that each species exists alone in a landscape composed of the two habitats. At low density each species will occupy only its preferred habitat because fitness is greater there than it is in the adjoining one (Fig. 1). At some threshold density, individuals abandon exclusive use of their preferred habitat and begin to use both. They have changed their behaviour from being selective to being opportunistic (Rosenzweig 1981). The population density at which behaviour changes from selective to opportunistic corresponds to the intercept of each species' isodar (Fig. 1).

Now, imagine that the two competing species co-occupy the same landscape. The choice of habitat must incorporate the reduced quality of the secondary habitat caused by its preferential occupation by the competitor. Each increase in the density of the competitor also increases the difference in

habitat quality. The net result is that individuals will switch from being selective in their preferred habitat and become opportunistic by using both habitats at a higher density than they would otherwise (the isodar intercept has increased) (Fig. 1). The density-dependent switch in behaviour, called an isoleg (Rosenzweig 1974), can be graphed as a function of the joint densities of the two species (Rosenzweig 1974, 1979, 1981, 1991) (Fig. 2). When species possess distinct habitat preferences, isoleg graphs always include a 'ghost' region where each occupies only its preferred habitat.

Similar patterns of 'habitat exclusion' are also common between dominant and subordinate species that share a preference for the same habitat. When the dominant species is abundant, the subordinate species is forced into using only its secondary preference (Rosenzweig 1991; Morris 1992a). Thus, the competitive dynamics responsible for habitat specialisation, and their associated competitive isoclines, are warped by habitat selection so that the competition, like a ghostly apparition, becomes invisible (each species occupies a separate habitat). Consistent with the theory, gerbil isoclines are dramatically non-linear (Abramsky *et al.* 1991, 1992, 1994).

The key to understanding the ghost of competition lies in the assumption that species' densities hover about the point of stable coexistence. Competition can be revealed only if species cross (or are forced to cross) their isolegs. When they do, individuals occupying the secondary habitat will be influenced negatively by the competitor that, in the area near the isoleg, is restricted to its preferred habitat. But the number of individuals of the target species occupying the secondary habitat will be small near the isoleg, and the competitive effect, averaged over all individuals, will also be small. The average competitive effect is represented by the slope of the isoclines that will bend gradually and smoothly away from the isoleg as more and more individuals occupy the competitor's preferred habitat (Morris 1999a). The competition is easily modelled with interspecific isodars.



**Fig. 3.** Isolegs (dashed lines) and isoclines (solid lines) for two lemming species living in hummock and wet-meadow habitats in Canada's arctic. Isoclines for *Dicrostonyx groenlandicus* are near horizontal or negatively sloped, those for *Lemmus trimacronatus* are vertical. Labelled points of potential short-term 'stability' are indicated by squares and arrows. Point A exists in the 'ghost' region (low densities of both species); whether the dynamics settle on point B or C at high density depends on whether the carrying capacity of *Lemmus* is greater (C) or less (B) than that for *Dicrostonyx*. Symbols: wedge – *Dicrostonyx* in both habitats; small square – *Dicrostonyx* in dry hummocks; sunburst – *Dicrostonyx* in wet meadows; triangle – *Lemmus* in both habitats (redrawn from Morris 1999b and Morris et al. 2000a).

Imagine that the respective dynamics for Species A competing with Species B in Habitats 1 and 2 are given by the classical Volterra–Gause competition equations

$$dN_{A2}/dt = r_{A2}N_{A2}[(K_{A2} - N_{A2} - \alpha_{AB2}N_{B2}) / K_{A2}] \quad (7)$$

and

$$dN_{A1}/dt = r_{A1}N_{A1}[(K_{A1} - N_{A1} - \alpha_{AB1}N_{B1}) / K_{A1}], \quad (8)$$

where  $\alpha_{ABi}$  is the competitive effect of Species B on Species A in Habitat *i*. Setting *per capita* growth rates equal in the two habitats

$$(1/N_{A1})(dN_{A1}/dt) = (1/N_{A2})(dN_{A2}/dt),$$

we obtain, following substitution from equations (7) and (8) (and letting  $C = [(r_{A2} - r_{A1}) / r_{A2}]K_{A2}$ ;  $b = (r_{A1}/r_{A2})(K_{A2}/K_{A1})$ ),

$$N_{A2} = C + bN_{A1} + b\alpha_{AB1}N_{B1} - \alpha_{AB2}N_{B2}. \quad (9)$$

Equation (9) represents the isodar for Species A in competition with Species B in Habitats 1 and 2. A comparable isodar describes competitive habitat selection by Species B.

Please note that the 'constant' competition coefficients in equation (9) represent habitat-dependent competitive effects. The competition coefficients represented by isoclines correspond to the average competition over all habitats occupied by the population. Thus, if two species occupy completely separate habitats, average competition is zero. If a small number of individuals occupy the preferred habitat of their competitor the average competitive effect will be less than when a large number of individuals co-occupy the same habitat. In each case, however, the potential competition from co-occurring individuals of the competitor [equation (9)] remains constant and independent of population size and habitat distribution.

One should be able, therefore, to use isodars from appropriate surveys of abundance in adjacent habitats to measure competition between species. The technique should work for any species whose habitat preferences are similar (the ghost region around the stable equilibrium is relatively small) and whose populations fluctuate away from equilibrium (where they may frequently cross the isolegs). Data confirm the prediction. Isodars have been used successfully to measure competitive interactions between coexisting salmonids in Quebec rivers (Rodríguez 1995), between coexisting lemmings in Arctic tundra (Morris 1999b; Morris et al. 2000a), and between Australian heathland rodents (Morris et al. 2000b). Moreover, the isolegs and isoclines revealed by the isodar tests hint at a wonderful unexplored richness in the ways that species interact and partition habitat (Fig. 3). Indeed, the mechanisms that species use to partition habitat should enable us to achieve Robert MacArthur's call for a functional classification of ecological communities (MacArthur 1972; Morris 1988). We must be careful when applying isodars (and other models of habitat selection), however, to ensure that the scale of our experiments, and our interpretations of habitat preference, correspond to the relevant scales of habitat selection.

### The scales of habitat selection

Habitat occupation occurs by the basic processes of habitat recognition, foraging and dispersal that operate at fundamentally different spatial scales. At some small scale, individuals cannot recognise the boundary between habitats and there can be no habitat selection. Foraging and dispersal scales are associated with substantially different benefits and costs of habitat selection (Morris 1987b, 1992a). Consider,

first, the scale at which organisms forage for resources. The strategic use of alternative fine-grained (MacArthur and Levins 1964) patches of resource will be based on the cost/benefit analysis of the respective density- and frequency-dependent qualities of those patches (e.g. Rosenzweig 1974, 1979, 1981, 1991). The value that the individual achieves through the selective use of high-quality patches comes at the expense of moving through or around patches of lower quality.

Contrast the foraging scale that we have just discussed with the exploitation of different coarse-grained habitats. Again, the optimal decision will be based on a cost/benefit analysis. The benefit is the potential for a dispersing individual to increase its fitness by moving to a different habitat. The cost is lost time and energy, and increased risks of mortality, that the individual faces as it disperses and establishes itself in the new habitat. The ability to measure each scale is crucial to understanding processes of habitat selection, to measuring how individuals and populations respond to landscape heterogeneity, and to ensuring that we have identified the appropriate scale for the use of techniques such as isodars.

The differences in costs simplify the analysis. Imagine a landscape composed of fine-grained 'patches' of two quantitatively different habitats. Contrast the pattern in density between the habitats if foraging occurs without costs, with that expected from costly habitat selection. In the cost-free alternative, individuals can select one habitat exclusive of the other, and the isodar will have a relatively high intercept. But if habitat selection is costly, individuals are forced to move through patches of the less profitable habitat. Even at low density, the more profitable habitat is devalued because individuals must use both habitats, and the isodar intercept will be reduced.

Now, imagine a coarse-grained landscape composed of the same two habitats. Individuals can select one habitat over the other only if they disperse. But an optimum dispersal decision must compensate for the reduced fitness associated with the time and risks of dispersal. Optimum dispersers should therefore move only if their expected fitness following dispersal to a new habitat exceeds their expectation of fitness in the current one. Fitness is higher at low, than at high, density, individuals should disperse down a density gradient, and the isodar intercept at the dispersal scale will be greater than in the cost-free alternative (Morris 1987b, 1992a).

But how can we know which scale we are measuring with isodars? The solution comes from the secret of all habitat analyses. Collect data on densities across sharp boundaries between dramatically different habitats. Very close to the boundary, individuals may not recognise differences between adjacent habitats, and no habitat selection is possible. Densities, if one could measure them at such small scales, would be the same on both sides of the boundary; the isodar

would have a zero intercept and slope of 1.0. Close to the boundary, individuals forage in both habitats, and an isodar will have a lower intercept than it will if calculated at greater distance. Farther from the boundary, individuals can select the distant alternative habitat only if they disperse, and the isodar intercept will increase. At still greater distances, the costs of dispersal become too great for habitat selection, and populations are regulated independent of the process of habitat selection (the isodar will not be statistically significant: Morris 1992a, 1995).

One of my favourite landscapes for testing theories of habitat selection consists of prairie-badland mosaics along river valleys in western North America. Productive grass- and forb-covered prairie changes precipitously to barren rock-strewn badlands at the erosion break of deep river valleys. Consistent with theory, deer-mouse isodars contrasting prairie and badland habitats at the foraging scale near the boundary had smaller intercepts than more distant isodars corresponding to dispersal. Isodars at still greater distances were non-significant, demonstrating that the population in each habitat was regulated independent of habitat choice. The distances of the foraging and dispersal scales that I calculated with isodars corresponded favourably with estimates from independent researchers using different techniques (Morris 1992a).

The ability to identify foraging scales with isodars may appear to be limited by the minimum area required to measure population density. How can we measure the scale at which individuals forage if we need to include several home ranges to estimate animal density? The problem may be overcome by 'point-estimates' of density that reflect the relative use of different patches. As local density varies, individuals should vary their relative use of alternative patches to maximise fitness. Point sampling should be valid as long as sampling does not bias habitat choice. Such 'activity-density' measures (e.g. as obtained from sand tracking: Kotler 1985; Abramsky *et al.* 1991), offer special promise because they integrate both the density-dependent and behavioural responses of individuals to habitat variation.

Theories of ideal habitat selection may also be key to improved understanding of the role of scale in ecological systems. Ideal-free theory can be applied at scales ranging from the behaviours of individual foragers to the assembly of ecological communities (Doncaster 2000). The processes differ, of course, but models at each scale share the common assumption that some measure of 'fitness' is equalised through the 'adaptive' movements of consumers.

Our success at measuring scales of habitat selection suggests that we may be able to use similar approaches to gain insights into other elusive patterns of abundance. Perhaps the most provocative pattern, and the most controversial and enduring in its application, is the belief that habitat edges increase the abundance and diversity of wildlife (e.g. Bolen and Robinson 1995).

## Detecting the 'edge effect'

There are at least three reasons why edges may support increased abundance. (1) The 'edge' may simply represent a third, and superior, habitat along the border of two others. (2) The edge may correspond to a fortuitous mix of different requirements (typically cover and food: Leopold 1933) for a single species. (3) Individuals may 'stack up' along the border between habitats if it represents a 'hard boundary' that individuals cannot cross (Stamps *et al.* 1987). But there are also several reasons why edges may harbour lower abundance, most notably the increased predation risk that is often associated with habitat boundaries (e.g. Paton 1984).

Some of the confusion regarding the role of edges may be caused by studies that implicitly exclude habitat selection. Edge effects have often been inferred from studies that examine patterns of density in only one of the adjoining habitats. Thus, for example, captures of meadow voles in fields near forest edges are reduced relative to more distant locations (a negative edge effect), while captures of white-footed mice are increased (a positive edge effect) (Manson *et al.* 1999).

The opposing edge effects for mice and voles become clear in the context of habitat selection. Remember that when the home ranges of individuals near the boundary between rich and poor habitats contain elements of both, preferential use of rich patches must come at the expense of moving through the poor ones (Rosenzweig 1981; Morris 1992a; Kingston and Morris 2000). The density of individuals in the poorer habitat will be higher than it would be otherwise because individuals subsidise their use of that habitat by using the rich one. Use of the rich habitat inflates the value of the poorer one near the boundary, and occupation of poor patches devalues the adjacent rich habitat. Thus, just as we have explored previously for issues of scale, the pattern of density in each habitat is altered by the presence of the ecotone. The ecotone's effect, which acts to reduce the isodar intercept, operates in a different direction for voles than it does for mice. Meadow-vole density declines in preferred field habitat as one approaches the boundary of the inferior forest while mouse density increases in the inferior field habitat toward the boundary with the highly preferred forest.

While both patterns by mice and voles are completely consistent with theories of habitat selection, we would like to also have evidence from habitat-selection studies that compare densities along transects crossing a habitat boundary. As we noted above, my prairie-badland studies used just such a design and, consistent with theory, the isodar intercept for deer mice was reduced near the habitat boundary (Morris 1992a). More detailed studies have revealed that the density effect is asymmetrical. Mouse densities in the highly preferred badland declined toward the prairie, but prairie densities were more-or-less constant at all

distances from the sharp 'edge' between the two habitats (Morris 1997).

By way of contrast, Kingston and Morris (2000) were unable to detect either a 'habitat-selection' or edge effect in comparisons of red-backed vole densities across gradual habitat boundaries in northern forests. The habitats may have been too similar to one another, and the vole densities too variable, to detect any consistent spatial signal from habitat selection (Kingston and Morris 2000). Regardless, it is obvious that any inferences about increased or reduced densities of individuals at habitat edges must be made in the context of density-dependent habitat selection. If early managers had access to our current knowledge of habitat selection, their legacy of managing habitats to increase edge may have been dramatically different.

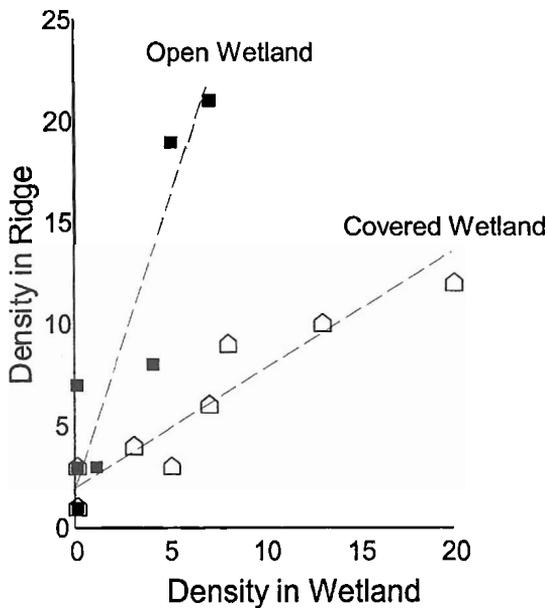
The ability to detect edges is crucial in identifying relevant processes of habitat selection, and their possible influences, on populations living in landscapes with different spatial patterns. But to do so, we need to know how many different habitats any particular landscape contains. Isodars provide a solution.

## How many habitats are there?

Imagine that we wish to assess the role of habitat selection in determining the distribution of a particular species. First, we identify adjacent pairs of two ostensible habitats for which we measure a variety of habitat variables that confirm our ability to distinguish between them. Next, we estimate the densities of individuals in replicates of each habitat, and plot the densities as an isodar.

Tom Knight and I (Knight and Morris 1996) followed this protocol while assessing the habitat choices of red-backed voles occupying dry beach ridges and intervening wetlands along the coasts of Hudson and James Bays in northern Canada. The resulting isodar, though significant, appeared heterogeneous, as might occur if the voles were recognising one or more additional habitats (Fig. 4). We reassessed our habitat classification with cluster analyses on measures of plant communities and habitat structure. The analysis revealed three distinct clusters: beach ridges plus tree-covered and open wetlands. Samples of all three habitats existed at each of our study locations that were separated by several hundred kilometres. Subsequent isodar analyses using the three habitats demonstrated that the voles treated the two-types of wetlands differently. The isodar contrasting ridges with adjacent open wetlands had a slope much greater than 1.0; voles preferred ridges at all densities. The isodar contrasting ridges with covered wetlands had a slope much less than 1.0; voles changed their preference from ridge to wetland at high density.

The Hudson Bay study also bears on issues of scale. Rodents appeared to respond similarly to the three different habitats at geographical scales representing tens of thousands of square kilometres. Interestingly, the rodents,



**Fig. 4.** Red-backed voles occupying dry ridge and wetland habitats appear to partition the wetland into two different types. The vole isodar for 'open' wetland (solid squares and solid line) has a high slope (a consistent preference for ridge habitat), whereas the isodar for 'covered' wetland (open symbols and dashed line) indicates a change in preference toward wetland habitat at high density (after Knight and Morris 1996).

whose selection of habitats operates on a scale of tens of metres, recognised far fewer habitats than remote sensing imagery (and presumably the 'communities' it identified) that subdivided the three vole habitats into seven classes (Knight and Morris 1996). The results are a poignant reminder that our classification of habitats must be matched with the assessment of their quality by the organisms that select some habitats over others.

### Habitat matching

The necessity of matching habitat quality with its assessment introduces the intriguing possibility that organisms may also match their densities against underlying habitat quality (Parker 1978; Sutherland 1983; Pulliam and Caraco 1984; Recer *et al.* 1987; Fagen 1987, 1988; Kacelnik *et al.* 1992). When individuals share resources equally, and when each individual's fitness is proportional to its fraction of total resources, an ideal-free distribution between habitats implies that

$$K_i/N_i = K_j/N_j.$$

The ratio of densities equals the ratio of carrying capacities

$$N_i/N_j = K_i/K_j. \quad (10)$$

There are several assumptions that limit the potential of habitat matching (Morris 1994). In its most restrictive form, habitat matching implies equal sharing of resources,

continuous input and instantaneous consumption. While the assumptions may be valid at small spatial scales in controlled experiments, many are unlikely to apply to the scales where habitat selection acts to regulate natural populations (Morris 1994). Even at small scales, numerous processes are known to cause a mismatch between densities and resource abundance (e.g. Kennedy and Gray 1993; Tregenza 1995; Ranta *et al.* 1999, 2000; Morris *et al.* 2001). 'Isodar matching' provides a hopeful alternative.

Consider a single species with logistic population growth that occupies two habitats according to an ideal-free distribution. If fitness is identical at low density ( $r_i = r_j$ ), the isodar passes through the origin (equation 2) and, if linear, its slope is the habitat-matching rule. There is a constant ratio of densities in the two habitats at all population sizes. But now consider what happens when the isodar intercept has a non-zero value. The ratio of population sizes (and carrying capacities) is not constant with population size, and can be determined only by knowing the density relationship in the two habitats (the isodar). An isodar analysis may thereby represent the most efficient test for habitat matching. More importantly, the pattern of densities always reflects the relative qualities of habitats irrespective of the intercept or shape of the isodar (Morris 1994).

There are, nevertheless, situations where density may be a misleading indicator of habitat quality (Van Horne 1983, 1986; Hobbs and Hanley 1990). Ecologists have been particularly concerned about systems where some individuals, incapable of securing breeding sites in high-quality habitat, make the best of their bad situation by occupying nearby sinks (Holt 1985; Pulliam 1988; Pulliam and Danielson 1991; Rodenhouse *et al.* 1997; Diffendorfer 1998; McPeck *et al.* 2001). If source habitats are large enough, or of high enough quality, the density in sinks can exceed that of the source and mislead our assessment of relative habitat qualities.

### Sources and sinks

Most treatments of source and sink dynamics assume that dominance or site pre-emption causes fitness differences among habitats. Dominance (and pre-emption) represents one mechanism of source-sink dynamics (1) where habitat-selecting subordinate (or late-arriving) individuals making the best of their misfortune flow directionally from high-fitness source into low-fitness sink habitat. Directional migration from source to sink habitats (or source to pseudosink: Watkinson and Sutherland 1995) can also emerge from at least five other mechanisms, including (2) both passive and balanced dispersal (McPeck and Holt 1992), (3) population structure and the asymmetrical advantage of residents (Anderson 1970, 1989), (4) temporal barriers to habitat selection (Boughton 1999), and (5) even ideal-free habitat selection in fluctuating environments (Morris *et al.*, unpublished). Source and sink dynamics may

often arise (6) when organisms are deceived by their evolutionary histories into making maladaptive habitat choices in altered landscapes (Dwernychuk and Boag 1972; Gates and Gysel 1978; Morris 1989, 1991, 1992*b*; Remeš 2000; Kokko and Sutherland 2001). Habitat and landscape change (e.g. fragmentation, mesopredator release, spill-over predation: Holt 1984, 1985; Oksanen 1990; Oksanen *et al.* 1992) can modify the value of a habitat without altering past reliable cues to habitat quality (Remeš 2000). Whether populations evolve to exploit (or recognise) newly emerging sink habitats will depend on the spatial and temporal pattern of habitats of varying quality (Holt and Gaines 1992; Holt and Gomulkiewicz 1997).

Whatever the process causing source–sink dynamics, the two crucial questions for conservation and management are: (1) Can we use habitat-selection theory (and most especially patterns in density) to differentiate sources from sinks? (2) Does the pattern in density reflect habitat choice?

The answers depend, in part, on the mechanisms of habitat selection. The effect of dominance, for example, can often be differentiated by isodars from ideal-free habitat selection because it yields a better fit to logarithmically transformed densities than to linear models (Morris 1994). Interference, often incorporated into foraging models as an exponent, is linearised by a logarithmic transformation (Morris 1994). Site pre-emption, another form of dominance, will frequently create curved or non-linear isodars (Morris 1994; Knight 2000). While it is unlikely that isodars alone can detect source–sink dynamics caused by factors unrelated to habitat selection, it should be possible, nevertheless, to merge isodars with creative experiments that test underlying assumptions of ideal habitat selection.

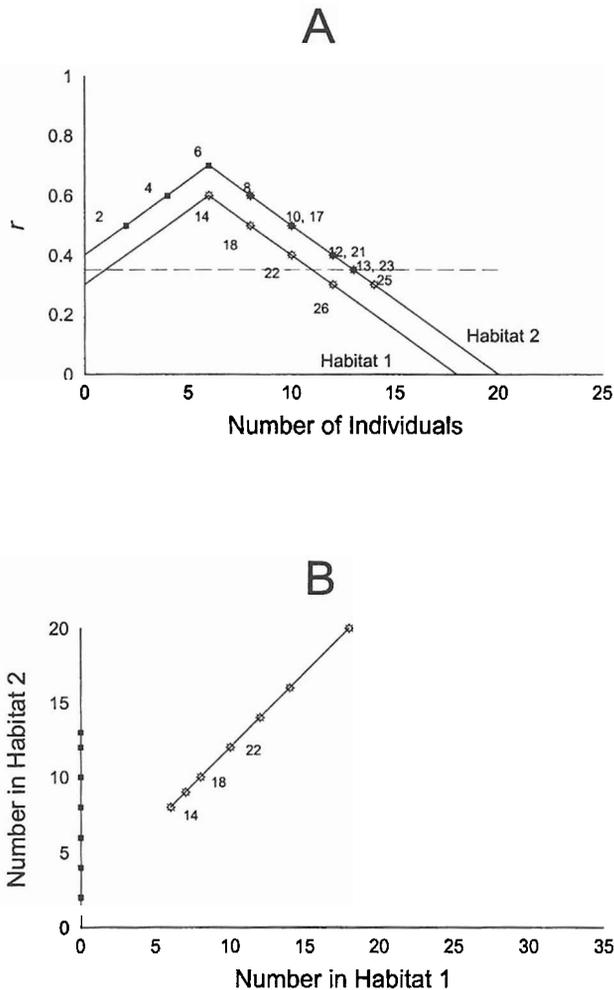
For the past 20 years, my associates and I have been working on such tests by collecting data on the dynamics, life history, and habitat choices of white-footed mice (*Peromyscus leucopus*) occupying an agricultural landscape in southern Canada. Isodars contrasting densities between adjacent forest, edge, and fencerow habitats appear to be linear (Morris 1996*b*), and mice achieve their highest density in forest. Estimates of fitness based on adult survival and recruitment of young born in wooden nest boxes are consistently greater in forest habitat than in either edge or fencerow (Morris 1989, 1991, 1992*b*, 1996*b*; Morris and Davidson 2000). Site pre-emption does not appear to be responsible for the movement of mice among habitats because there is no trend for any particular nest-box location to yield higher recruitment than any other (Morris 1991). Habitat selection appears, instead, to follow an ideal-despotic distribution where territorial breeding females exclude subordinate animals from the highest-quality (forest) habitat. Mice might also be deceived by their past cues of habitat quality (Morris 1989, 1991). Litter sizes are larger in fencerows than in the forest, but recruitment is low because native and feral predators appear to have larger

effects along fencerow and edge habitats than they do in the forest. Such evolutionary ‘self-deception’ means that it may be more important to evaluate the match between habitat preference and quality (Kokko and Sutherland 2001), than to assess classic forms of habitat matching between density and resources.

Douglas Davidson and I (Morris and Davidson 2000) attempted to differentiate among the competing hypotheses by assessing the foraging strategies of mice given the choice to feed in identical and depletable patches in adjacent forest and edge habitats. We predicted that mice should forage longer, and with greater profit, in the relatively safe forest habitat than in the riskier edge. We also predicted that mice given a choice between safe and risky foraging patches would have less preference for safe sites in the forest than in the edge. We confirmed the assumption that mice forage in our patches with diminishing returns, then tested our predictions in the field. Our results, using the giving-up-densities of seeds left in otherwise identical sand-filled foraging patches (Brown 1988, 1992), confirmed both predictions.

The results of our foraging experiments are important for at least three reasons. (1) They confirmed our *a priori* predictions that habitat selection in this system fits an ideal-dominance distribution (fitness different between habitats), and that the main source of differences in fitness is related to predation risk. (2) They demonstrate that proxies of fitness based on optimum behaviours can mirror more direct correlates associated with demography and life history. (3) They suggest that similar experiments can be used to assess the match between preference, density, and habitat quality of many other species.

Our white-footed mouse research confirms that isodars, when merged with appropriate field experiments, can overcome many of the reservations associated with using density as an indicator of habitat quality. But at low population sizes fitness may often be enhanced, rather than reduced, by increased density (the Allee effect: Stephens and Sutherland 1999; Stephens *et al.* 1999; Courchamp *et al.* 1999; Kokko and Sutherland 2001; Møller *et al.* 2001; Morris 2002 – the term ‘Allee effect’ has been used in other contexts, here I follow Stephens *et al.* in restricting its use to positive density-dependent fitness). If fitness increases with density at low population sizes, individuals may often alter their pattern of habitat preference. At low population size, individuals will occupy only the most preferred habitat where each increase in density acts to also increase the mean fitness of all individuals already present. But when fitness in that habitat declines at a higher population size, individuals may move out to capitalise on positive gains in fitness that now accrue while the secondary habitat has low density. Allee effects thus represent a seventh mechanism that can create directional migration between source and apparent sink habitats.



**Fig. 5.** An illustration of how an Allee effect creates a hiatus in an isodar. Numbers represent the rank order of settling by individuals in the two habitats (only a subset of individuals is illustrated). (A) All successive individuals occupy Habitat 2 until fitness is equal to that in Habitat 1 at low density (horizontal line). The 14th individual moves to Habitat 1 and is followed by successive individuals from Habitat 2. (B) A plot of the isodar reveals the preferential occupation of Habitat 2 (points on the ordinate) and a hiatus as individuals move quickly from Habitat 2 to Habitat 1. Points of stable density in Habitat 2 alone are denoted by solid symbols, points representing stable occupation of both habitats are denoted by sunbursts (redrawn from Morris 2002).

### Detecting Allee effects

Allee effects are important not only because they alter patterns of habitat selection, but also because they have profound effects on probabilities of extinction and recovery (e.g. Myers *et al.* 1995; Dobson and Poole 1998; Reed 1999; Hutchings 2000; Berec *et al.* 2001, Kokko and Sutherland 2001), and species distribution (Keitt *et al.* 2001). Ecologists are likely to debate whether such extreme effects are common or rare, but there can be little doubt, and especially so in sexually reproducing species, that positive feedback on

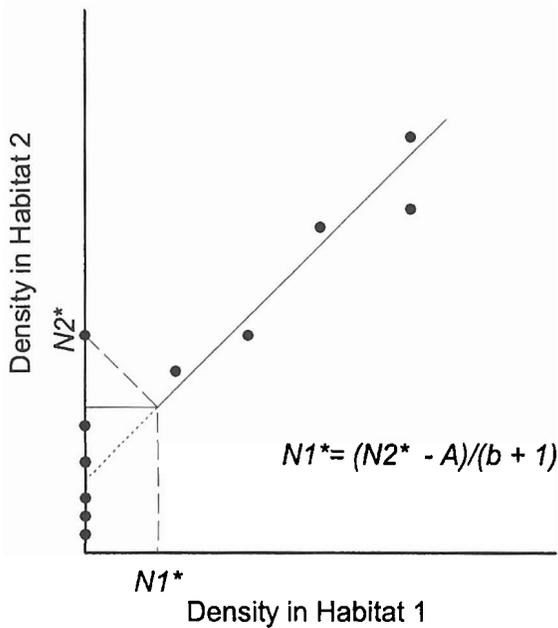
fitness occurs at low population sizes. At one level, it would be valuable to know the expected habitat-selection response under the influence of Allee effects. At another level, it would be even more valuable if we could use the pattern of habitat use to detect Allee effects in real populations.

Both issues can be resolved with isodars that reveal a characteristic instability arising from the Allee effect (Morris 2002). Imagine two habitats with identical Allee effects (Fig. 5), but within which the maximum fitness and carrying capacity in Habitat 2 are greater than in Habitat 1. At low population size, all individuals maximising their own fitness should pack into their preferred habitat (2) until they can achieve equal fitness in their secondary choice. As soon as individuals begin to occupy that habitat each additional organism will, until some threshold density, improve the mean fitness of those already present. Some individuals already occupying Habitat 2 should move to Habitat 1. Thus, in a plot of the isodar, individuals first stack-up along the ordinate as they preferentially occupy only Habitat 2. At the threshold, a subset of individuals move to Habitat 1 where each one increases the fitness of those already present. The end result is that the isodar will have a hiatus (or a 'J-shape' if the area of the secondary habitat is greater than that of the better one, or if the slope of positive density-dependence is less in the secondary habitat: Morris 2002) near the origin that corresponds to the 'instability' of habitat selection at low population sizes (Fig. 5). To find the hiatus, we collect data on abundance in pairs of adjoining habitats over a broad range of population sizes. We then calculate the isodar from those sites where both habitats are occupied. Next, we compute the lower critical density on the isodar that corresponds to the boundary where individuals show erratic habitat use. For a linear isodar, the lower critical density,  $N_1^*$ , is given by

$$N_1^* = (N_2^* - A) / (b + 1), \quad (11)$$

where  $N_2^*$  is the maximum density observed when Habitat 2 only is occupied, and  $A$  and  $b$  represent the isodar's intercept and slope respectively (Fig. 6, Morris 2002). Finally, to test for an Allee effect, we use an exact-probabilities test to contrast the number of data points falling within the hiatus region with those expected by chance alone (Morris 2002).

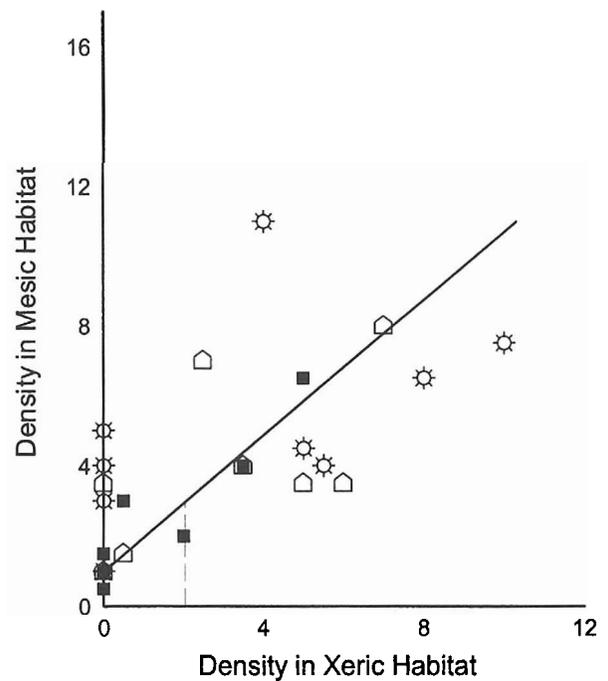
I tested the protocol on red-backed voles occupying xeric and mesic forest habitats in Canada's Rocky Mountains (Morris 2002). Population sizes varied among the nine sampling locations. Voles packed into their preferred mesic habitat at densities higher than some of those observed when both habitats were occupied (Fig. 7) (this pattern, by itself, is suggestive of Allee effects: Fig. 5). The number of data points falling in the hiatus region was significantly less than expected by chance. The analysis is exciting not only because it documents our ability to find elusive Allee effects, but also because we can actually calculate the density ( $N_1^*$ )



**Fig. 6.** An illustration of how to use the lower critical density ( $N_1^*$ ) of an isodar to find an Allee effect. The kinked dashed line connects the maximum density observed in Habitat 2 alone with the corresponding density 'on' the isodar. Allee effects produce either a hiatus or a J-shape to the left of the critical density. If the hiatus is caused only by sampling error, the number of data points that exist between the ordinate and the lower critical density should be similar to the number that lie on the ordinate above the isodar intercept (redrawn from Morris 2002).

where fitness switches from being positively to negatively density dependent. The ability to calculate that critical density may be crucial for the management and conservation of species exhibiting Allee effects. The approach will be more difficult, but certainly not impossible, with more complicated isodar shapes (Morris 2002).

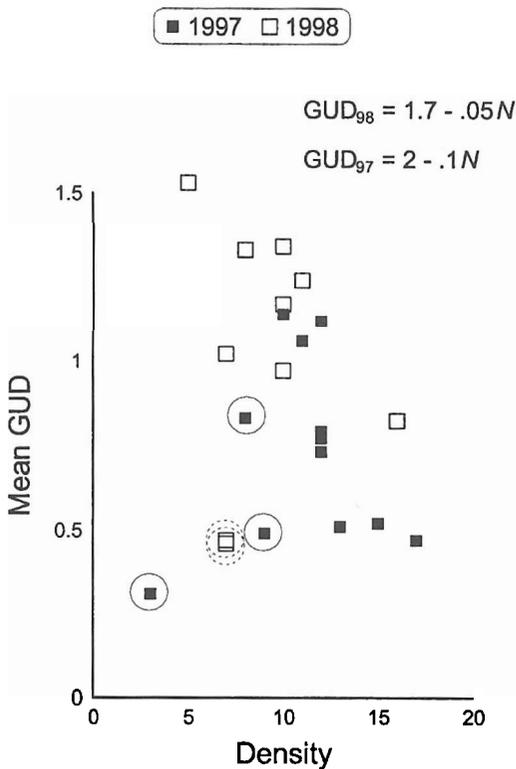
Our ability to calculate isodars with field data relies on spatial heterogeneity in population size. Some of the variation corresponds, no doubt, to local differences in carrying capacity (environmental stochasticity), but a large component is likely to also reflect other forms of historically stochastic variation in population size (Morris 2001). Stochastic effects, which are problematic in many other analyses of population regulation and species coexistence, are more easily accommodated with techniques that emphasise optimal behaviours (such as isodars, e.g. Morris 1996b). Whatever the cause of local variation in density, isodars capture the optimum solution to habitat selection at all densities, not just the perplexing and evasive equilibrium that exists only when population growth is precisely balanced against resources. Yet it would be very useful if we could measure the degree (and spatial scale) of stochasticity that exists in natural populations. Once again, a solution lies in the optimum selection of habitats.



**Fig. 7.** The isodar for red-backed voles occupying mesic and xeric forest habitats in Canada's Rocky Mountains. The lower critical density expected to emerge from an Allee effect is indicated by the vertical dashed line. Symbols correspond to densities accumulated from different sampling periods in nine different locations. Analysis of the hiatus in the isodar revealed a significant Allee effect (significantly more data points lie on the ordinate above the intercept than in the area between the ordinate and the critical density) (after Morris 2002).

### Measuring environmental stochasticity

Imagine a landscape where individuals select from two patchy habitats. Imagine that we have sampled the species' densities across pairs of habitats scattered throughout the landscape, and that we have summarised its habitat choice by drawing the isodar. Differences in the value of the isodar could reflect: (1) local differences in carrying capacity where habitat selection has equalised fitness across the landscape (habitat selection with stochastic variation in carrying capacity), (2) variation in density caused by the inability of habitat selection at limited spatial scales to equalise fitness at larger scales of habitat distribution (a spatially structured population without environmentally stochastic variability; differences in density are caused by a variety of ecological and historical processes including, but not restricted to, demographic stochasticity), or (3) environmentally stochastic effects in spatially structured populations where fitness is disconnected from local density. Any test for environmental stochasticity in habitat preference must include an assessment of the scales of habitat selection, the pattern of habitat use (e.g. the isodar), and estimates of fitness.



**Fig. 8.** Mean giving-up-densities (GUDs) of deer mice foraging in identical, but separated, food patches in two different years declined similarly with population density in two different years. In each year, different plots (circled: solid = 1997; dotted = 1998) had low GUDs for their population density (redrawn from Morris 2001).

If differences in density correspond only to local differences in carrying capacity of habitat selectors, the isodar should be significant with no residual density-dependent pattern associated with fitness (fitness equalised by habitat selection). If differences in density reflect the limited spatial ability of habitat selection to equalise fitness (a spatially structured population), estimates of fitness should, above any critical Allee density, decline with increased local density. A combination of spatial structure and stochasticity would yield a negative relationship between density and fitness, but with outliers that represent either higher or lower fitness than expected on the basis of population size (Morris 2001).

I illustrated the tests for stochastic effects with deer mice living in prairie–badland landscapes (Morris 2001). Deer mice, the only abundant rodent in this system, are known to be density-dependent habitat selectors (Morris 1997). Deer-mouse foraging reflects density-dependent competition (Davidson and Morris 2001). Deer mice are known to adjust densities to equalise the return from foraging (Morris 1997), and their scale of dispersal (~80 m) has been measured by isodars (Morris 1992a).

My assistants and I established small trapping grids within only the preferred badland habitat at a spatial scale

(~250 m) larger than that of dispersal, but not so large as to be associated with geographical differences in habitat quality. We estimated population density by live trapping, then used short-term foraging experiments to assess density dependence in fitness. In 1997, we manipulated population density by detaining different proportions of these nocturnal rodents in live traps overnight. In 1998, we assessed density-dependent resource harvest by varying the amount of resource available in large foraging patches.

The results of both experiments confirmed the influence of spatial structure and environmental stochasticity. Fitness, estimated by mean giving-up-density (GUD) in artificial food patches, declined with increasing population size in both years (Fig. 8). Yet a group of plots, whose identity varied between years, had lower GUDs than expected from their population density. Detention of one-quarter or one-half of the foraging mice in live traps led to a linear increase in GUD, but not in the ‘outlier’ grids. The same pattern occurred when we manipulated patch quality. Overall, GUD increased with resource addition, but remained constant in grids with low GUDs for their density. Thus, the effectiveness of habitat selection at equalising fitness in this system is attenuated by spatially limited dispersal. The results imply that when carrying capacity is reduced by environmental stochasticity, some mice are unable to disperse to sites where their fitness would be improved. In any given year, roughly 20% of the landscape appears to be influenced by this local depression in resource abundance. We are continuing our resource-manipulation experiments in this model system in an attempt to more fully document the temporal–spatial dynamics of stochastic variation in habitat quality.

Our results should not be interpreted as depreciating the role of habitat selection. Deer mice select between prairie and badland habitats in a density-dependent manner, a result confirmed by isodars and the local patterns of density and fitness across boundaries between the two habitats (Morris 1997). At the same time, it is quite apparent that the temporal and spatial dynamics of deer-mouse density in this highly seasonal system exceed the ability of habitat selection to equalise fitness across the landscape, even though the pattern of habitat selection itself appears invariant to landscape composition (Morris 1997).

I have concentrated, thus far, on illustrating how theories of habitat selection and patch use can be applied to the conservation and management of wildlife. As crucial as management and conservation might be, they assume implicitly that problems should be resolved by attention to the dynamics and distribution of wildlife. Yet many, if not most, of those problems originate not because wildlife have changed their habitat preferences, but because humans have altered, manipulated, or destroyed wildlife habitat. Rather than continue to seek solutions in how we manage other

species, perhaps it is time to examine, critically, our own habitat use.

### Habitat selection by humans

Steven Kingston and I (Morris and Kingston 2002) applied theories of habitat selection to the World’s population of humans. Our purpose was twofold: (1) we wished to test our theories with the data on humans that exceed, in many respects, the quantity and quality of data available for other species, and (2) we wanted to evaluate human habitat use because it may be crucial in our attempts to confront crises in the conservation and management of the rest of biodiversity. We chose to contrast the occupation of urban versus rural habitats, again for two reasons: (1) data on urbanisation have been summarised for most nations (we used data from the World Resources Institute: WRI 1998), and (2) the isodar for human urbanisation is easily modelled.

We began with Gilpin and Ayala’s (1973) general ‘theta-logistic’ equation,

$$(1/N_R)(dN_R/dt) = r_R[1 - (N_R/K_R)^\theta] \quad (12)$$

and

$$(1/N_U)(dN_U/dt) = r_U[1 - (N_U/K_U)^\theta], \quad (13)$$

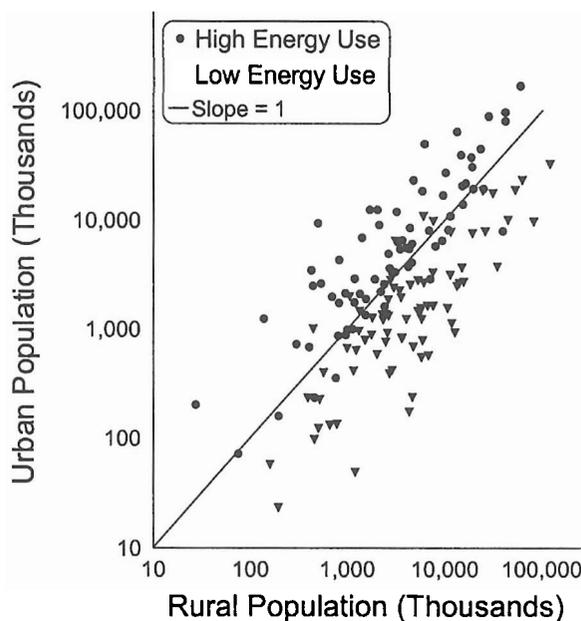
where  $\theta$  is the coefficient of curvature that represents the degree of interference among competitors, and where subscripts identify rural ( $R$ ) and urban ( $U$ ) habitats. A unique feature of urban versus rural habitats is that they converge at low density. The city becomes the country, and fitness is necessarily equal at low population size. Realising this, and setting equation (13) equal to equation (12), we can define the human isodar as

$$\log N_U = [\log K_U - (\theta_R/\theta_U)\log K_R] + (\theta_R/\theta_U)\log N_R,$$

which can be analysed by regression. The compound regression intercept is difficult to interpret, but the slope ( $\theta_R/\theta_U$ ) corresponds directly to the degree of density dependence in human population regulation in rural, compared with urban, habitats (Morris and Kingston 2002).

The human isodar, using data from 154 different nations, was highly significant but appeared to be heterogeneous. One large group of nations is urban, and another equally large group is rural. We searched the WRI data for variables that could reflect these apparent differences in the actual or perceived quality of rural versus urban habitats. An isodar including a nation’s binary status of high versus low *per capita* energy use (149 nations) accounted for a majority of residual variation in the isodar (Fig. 9).

The results of the human isodar analysis are encouraging on several different levels. (1) Humans appear to select habitat in a way that is consistent with our assessment of its density-dependent quality. (2) The pattern of urbanisation is astoundingly consistent among nations whose populations



**Fig. 9.** The global isodar for human occupation of urban and rural habitats. The line with slope of unity is included to help display the influence of each nation’s relative *per capita* energy use (based on 1980 data for 149 nations, and redrawn from Morris and Kingston 2002).

vary dramatically in social and economic systems, in religious beliefs, in ethnic origin, in culture, history, tradition, values, and in political ideology. (3) The isodar slope, when corrected for differences in energy use, was not significantly different from 1.0 (Morris and Kingston 2002). Unit slope suggests that human population regulation is similar in both rural and urban habitats.

We were most excited, however, at the prospect of using the global pattern of human habitat use, and by inference other patterns at different scales, to address the conservation and management of biodiversity. If human habitat selection is related to extinction risks, for example, we should be able to use projections of human population growth and migration to forecast future threats to the World’s wildlife. We might, even with a crude cut through the data, be able to identify nations most deserving of pre-emptive attempts to reduce negative human impacts on their biota. At the least, we should be able to provide a model for future tests of human habitat selection and its role in conservation and management. We now turn our attention to whether human habitat use can be used as a leading indicator of threats to the World’s biodiversity.

### Leading indicators for conservation and management

We used the isodar to calculate, for each nation, the predicted value of the number of humans living in the urban habitat. We then extracted, from the WRI tables, international data on the proportions of species threatened with extinction in four taxa, and used logistic regression to assess their association

with the isodar's predicted urban densities. The analysis demonstrated that the proportions of threatened mammals, birds, and higher plants are associated, positively, with the human isodar. We calculated, for each nation, the probability that, for any given taxon, it belonged to the set of nations where threats to biodiversity belong in the 'high threat' group.

Next, we linked our model with human population and demographic projections for 2020 to assess future human habitat selection, and its association with threatened biodiversity. We used the logistic regressions to calculate, again for each nation and each taxon, increases in the probability that the nation's biodiversity would belong to the 'high threat' group of nations. Nations with a large increase in their probability represent those where we can anticipate, over the next two decades, the greatest increase in threats to biodiversity. Nineteen of the 25 nations with the greatest increases in our analysis are in Africa (Morris and Kingston 2002). Thus, we can anticipate that the greatest return from the limited global resources available for conservation would come from investing, pre-emptively, in Africa.

Though I have concentrated on human habitat selection, we should be able to apply theories of habitat selection in many similarly creative ways to function as leading indicators of environmental and habitat change. Too often, conservation and management activities are allocated to solving problems of species already at risk of extinction, or for which declining populations signal impending concern. Changes in population size necessarily incorporate numerous, and generally poorly understood, time lags associated with underlying processes of population regulation and community structure. As such, they act as trailing, rather than leading, indicators of environmental change (e.g. Brown *et al.* 1999). By way of contrast, many adaptive behaviours, and especially those reflecting habitat and patch selection, act on comparably instantaneous time scales. An understanding of adaptive behaviours may allow us to develop novel solutions to a wide variety of management and conservation problems (Brown 2001). In future, we must become much more astute at interpreting and using behavioural cues to guide management. How might the application of habitat and patch-selection theories lead the way toward new, and more effective, conservation strategies and management protocols?

### **Future applications to management and conservation**

Despite the potential for applying theories of habitat selection and patch use to forecast future risks to biodiversity, we may be unable to make substantive headway unless we move away from current 'crisis management strategies' in conservation. Rather than concentrating on the rescue of species from the brink of extinction, and restoration of their habitats and communities, we must embark on brave new initiatives that reconcile human habitat

use with the rest of biodiversity (Rosenzweig 2001). I believe that theories and applications of habitat selection have a key role to play in reconciliation ecology. How else will we be able to predict how humans and other species react to new habitats? Moreover, I believe that we have already seen the development of key principles and designs that will be necessary to assess how individuals might respond to future habitats.

Recall Abramsky and Rosenzweig's design for the assessment of competitive coexistence. Individuals placed in one large enclosure are allowed to achieve an ideal distribution with another through portals in their shared boundary. Next, only one of the two enclosures is subjected to an environmental change (e.g. differing densities of competitors and changes in the intensity of predation risk). The experiment is completed by analysing the habitat response of the initial species to the manipulation. I predict that the Abramsky–Rosenzweig design will become the norm for future studies of habitat selection and reconciliation ecology. Rather than manipulate only the identities and densities of interacting species, I visualise series of enclosures where we assess the influences of numerous kinds of manipulations on key species. I believe that such an important instrument deserves its own special name. Let's call it a habitron. A habitron's critical design feature is the ability to assess density-dependent responses to experimentally controlled differences in habitat.

Habitron experiments overcome a limitation of isodar analysis: independent population growth in each habitat creates patterns in density whether individuals are ideal habitat selectors or not (Morris 1988). The predominant signature of habitat selection can easily be detected in a habitron, however, by experiments that begin with unequal densities in adjacent and identical habitats. Migration from the enclosure with high density must yield a linear isodar that passes through the origin (Abramsky *et al.* 1991).

What kinds of experimental protocols will be suitable for habitrons? Clearly, some will mimic the Abramsky–Rosenzweig protocol. I suspect that others will mimic some of my experiments across sharp natural boundaries. In both cases, they will eliminate the current necessity of searching Earth's surface for collections of species whose ranges span habitat discontinuities appropriate for tests of habitat selection. One might, given a fit of wishful thinking, imagine that nations would build large national habitrons, and associated human think tanks, for the assessment of principles and applications in reconciliation ecology.

The field work, requiring the capture, relocation and monitoring of population densities (or at least correlates of density) will be challenging, but much less so than under uncontrolled conditions. Moreover, habitrons can vary from large terrestrial enclosures to small laboratory microcosms similar to those that have been used to explore the dynamics of predator–prey interactions (e.g. Huffaker 1958; Holyoak

2000). Indeed, in addition to Abramsky and Rosenzweig's experiments, others have already adapted similar protocols to lotic systems by fencing streams in the field, and by using flow-through tanks in the lab (Knight 2000).

The habitron concept has merit because the application of habitat selection and patch-use theories lies not in species' preferences for natural habitats, but in the comparison of their choices between habitat alternatives. It would, nevertheless, be extremely useful to locate habitrons where human activities are most likely to modify habitat. My team has plans to build such a habitron. I hope that interested ecologists will join me in assessing and demonstrating its application to theory, conservation, and management of biodiversity.

Habitrons would also appear valuable as we expand and apply our understanding of habitat selection to the design of nature reserves and to problems of wildlife control. What, for example, is the optimum spatial structure for a reserve's internal mosaic of habitats? Should the boundaries between habitats be sharp or gradual? Should they be regular or sinuous? Should habitat edges mimic the boundaries around reserves, or should they be dramatically different? What kind of reserve boundary will be effective at containing 'problem' wildlife within the reserve? Does the same type of boundary minimise the intrusion of non-native, or otherwise destructive, species into the reserve or reserve network? If so, can we structure reserves to include different 'segregated' communities that maximise both local and regional diversity?

The theory and protocol for many of these questions is in place (e.g. Kingston and Morris 2000), but may require a change in research (and management) emphasis. As we build habitrons we should aim to do more than describe patterns of habitat suitability. We should, like Einstein (Rosenzweig 2001), concentrate our efforts on explicit attempts to connect patterns with their underlying dynamic processes (e.g. isoclines, isolegs, and isodars).

## Acknowledgments

I thank the two anonymous and helpful referees for candid suggestions on improvement, and Canada's Natural Sciences and Engineering Research Council that continues to sponsor my research on habitat selection and evolutionary ecology. My field research would have been impossible without the hard work of many trusted and valued assistants, and without the support of a caring and loving family. I thank them all.

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Manuscript received 7 May 2002; accepted 11 February 2003